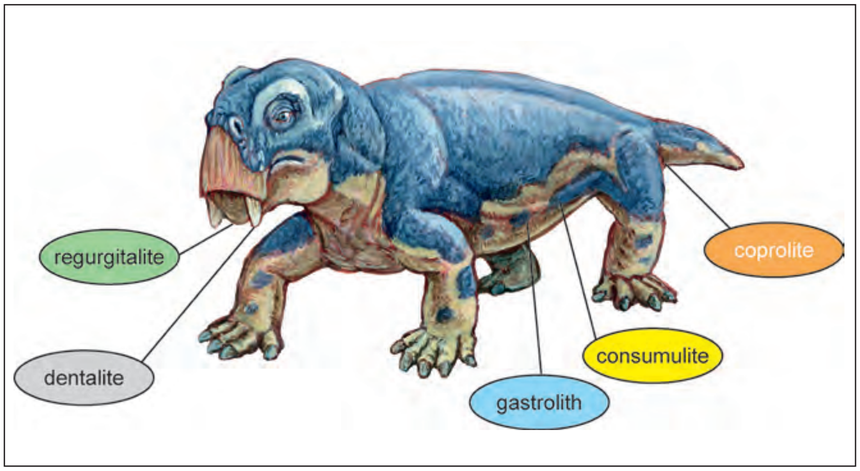
Bulletin 87

New Mexico Museum of Natural History & Science

A Division of the
DEPARTMENT OF CULTURAL AFFAIRS

THE ICHNOLOGY OF VERTEBRATE CONSUMPTION: DENTALITES, GASTROLITHS AND BROMALITES



by

ADRIAN P. HUNT and SPENCER G. LUCAS

Albuquerque, 2021

ADRIAN P. HUNT AND SPENCER G. LUCAS

THE ICHNOLOGY OF VERTEBRATE CONSUMPTION

NMMNH&S Bulletin 87

Bulletin 87

New Mexico Museum of Natural History & Science

A Division of the
DEPARTMENT OF CULTURAL AFFAIRS

THE ICHNOLOGY OF VERTEBRATE CONSUMPTION: DENTALITES, GASTROLITHS AND BROMALITES

by

ADRIAN P. HUNT and SPENCER G. LUCAS

New Mexico Museum of Natural History & Science

Albuquerque, 2021

STATE OF NEW MEXICO
Department of Cultural Affairs
Debra Garcia y Griego, *Secretary*

NEW MEXICO MUSEUM OF NATURAL HISTORY AND SCIENCE
Gary Romero, *Interim Executive Director*

Cover illustration: Principal trace fossils associated with feeding. Artwork of the Early Triassic synapsid *Lystrosaurus* by Matt Celeskey.

Associate editor for this bulletin: Jesper Milàn

Original Printing
ISSN: 1524-4156

Available from the New Mexico Museum of Natural History and Science,
1801 Mountain Road NW, Albuquerque, NM 87104; Telephone (505) 841-2800;
Fax (505) 841-2866; www.nmnaturalhistory.org

NMMNH Bulletins online at: http://nmnaturalhistory.org/bulletins and Google Books

BULLETIN OF THE NEW MEXICO MUSEUM OF NATURAL HISTORY AND SCIENCE

EDITORS

Spencer G. Lucas	New Mexico Museum of Natural History and Science, Albuquerque, NM, USA (NMMNHS)
Adrian P. Hunt	Flying Heritage and Combat Armor Museum, Everett, WA, USA
Jason L. Malaney	NMMNHS
Lawrence H. Tanner	Le Moyne College, Syracuse, NY, USA

MANAGING EDITOR

Asher J. Lichtig	NMMNHS

ASSOCIATE EDITORS

Guillermo Alvarado	Asociación Costarricense de Geotecnica, San José, Costa Rica
Marco Avanzini	Museo Tridentino di Scienze Naturali, Trento, Italy
David Berman	Carnegie Museum of Natural History, Pittsburgh, PA, USA
Brent Breithaupt	Laramie, WY, USA
William DiMichele	National Museum of Natural History, Washington, D.C., USA
John R. Foster	Utah Field House of Natural History State Park Museum, Vernal, UT, USA
Gerard Gierlinski	Polish Geological Institute, Warsaw, Poland
Jean Guex	University of Lausanne, Lausanne, Switzerland
Steven E. Jasinski	Harrisburg University, Harrisburg, PA, USA
Hendrik Klein	Saurierwelt Paläontologisches Museum, Neumarkt, Germany
Karl Krainer	University of Innsbruck, Innsbruck, Austria
Martin G. Lockley	University of Colorado at Denver, Denver, CO, USA
Jesper Milàn	Geomuseum Faxe, Østsjællands Museum, Østervej 2, DK-4640 Faxe, Denmark
Gary S. Morgan	NMMNHS
Donald R. Prothero	Occidental College, Los Angeles, CA, USA
Silvio Renesto	Università degli Studi dell'Insubria, Varese, Italy
Joerg W. Schneider	Technical University BergAkademie of Freiberg, Freiberg, Germany
Jingeng Sha	Nanjing Institute of Geology and Palaeontology, Nanjing, China
Dana Ulmer-Scholle	NM Bureau of Geology & Mineral Resources, Socorro, NM, USA
Sebastian Voigt	Urweltmuseum GEOSKOP/Burg Lichtenburg, Thallichtenberg, Germany
Bruce J. Welton	NMMNHS
Ralf Werneburg	Naturhistorisches Museum Schloss Bertholdsburg, Schleusingen, Germany
Richard S. White, Jr.	International Wildlife Museum, Tucson, AZ, USA

NEW MEXICO MUSEUM OF NATURAL HISTORY AND SCIENCE BULLETINS

47. Ichnology of the Upper Triassic (Apachean) Redonda Formation, east-central New Mexico, 2010. by Spencer G. Lucas, Justin A. Spielmann, Hendrik Klein and Allan J Lerner, 75 pp.
48. New Smithian (Early Triassic) ammonoids from Crittenden Springs, Elko County, Nevada: Implications for taxonomy, biostratigraphy and biogeography, 2010. by James F. Jenks, Arnaud Brayard, Thomas Brühwiler and Hugo Bucher, 41 pp.
49. Carboniferous-Permian transition in Cañon del Cobre, northern New Mexico, 2010. edited by Spencer G. Lucas, Jörg W. Schneider and Justin A. Spielmann, 229 pp.
50. Review of the tetrapod ichnofauna of the Moenkopi Formation/Group (Early-Middle Triassic) of the American Southwest, 2010. by Hendrik Klein and Spencer G. Lucas, 67 pp.
51. Crocodyle tracks and traces, 2010. edited by Jesper Milàn, Spencer G. Lucas, Martin G. Lockley and Justin A. Spielmann, 244 pp.
52. Selachians from the Upper Cretaceous (Santonian) Hosta Tongue of the Point Lookout Sandstone, central New Mexico, 2011. by Jim Bourdon, Keith Wright, Spencer G. Lucas, Justin A. Spielmann and Randy Pence, 54 pp.
53. Fossil Record 3, 2011. edited by Robert M. Sullivan, Spencer G. Lucas and Justin A. Spielmann, 736 pp.
54. Ichnology of the Mississippian Mauch Chunk Formation, eastern Pennsylvania, 2012. by David L. Fillmore, Spencer G. Lucas and Edward L. Simpson, 136 pp.
55. Tetrapod fauna of the Upper Triassic Redonda Formation, east-central New Mexico: The characteristic assemblage of the Apachean land-vertebrate faunachron, 2012. by Justin A. Spielmann and Spencer G. Lucas, 119 pp.
56. Revision of the Lower Triassic tetrapod ichnofauna from Wióry, Holy Cross Mountains, Poland, 2012. by Hendrik Klein and Grzegorz Niedzwiedzki, 62 pp.
57. Vertebrate Coprolites, 2012. edited by Adrian P. Hunt, Jesper Milàn, Spencer G. Lucas and Justin A. Spielmann, 387 pp.
58. A new archaic basking shark (Lamniformes: Cetorhinidae) from the late Eocene of western Oregon, U.S.A., and description of the dentition, gill rakers and vertebrae of the recent basking shark Cetorhinus maximus (Gunnerus), 2013. by Bruce J. Welton, 48 pp.
59. The Carboniferous-Permian transition in central New Mexico, 2013. edited by Spencer G. Lucas, W. John Nelson, William A. DiMichele, Justin A. Spielmann, Karl Krainer, James E. Barrick, Scott Elrick and Sebastian Voigt, 389 pp.
60. The Carboniferous-Permian transition, 2013. edited by Spencer G. Lucas, William A. DiMichele, James E. Barrick, Joerg W. Schneider and Justin A. Spielmann, 465 pp.
61. The Triassic System: New Developments in Stratigraphy and Paleontology, 2013. edited by Lawrence H. Tanner, Justin A. Spielmann and Spencer G. Lucas, 612 pp.
62. Fossil Footprints of Western North America, 2014. edited by Martin G. Lockey and Spencer G. Lucas, 508 pp.
63. Variation in the Dentition of *Coelophysis bauri*, 2014. by Lisa G. Buckley and Philip J. Currie, 73 pp.
64. Conodonts from the Carnian-Norian Boundary (Upper Triassic) of Black Bear Ridge, Northeastern British Columbia, Canada, 2014, by Michael J. Orchard, 139 pp.
65. Carboniferous-Permian Transition in the Robledo Mountains Southern New Mexico, 2015, edited by Spencer G. Lucas and William A. DiMichele, 167 pp.
66. The Marine Fish Fauna of the Middle Pleistocene Port Orford Formation and Elk River Beds, Cape Blanco, Oregon, 2015, by Bruce J. Welton, 45 pp.
67. Fossil Record 4, 2015. edited by Robert M. Sullivan and Spencer G. Lucas, 332 pp.
68. Fossil Vertebrates in New Mexico, 2015, edited by Spencer G. Lucas and Robert M. Sullivan, 438 pp.
69. The Pennsylvanian System in the Mud Springs Mountains, Sierra County, New Mexico, USA, 2016, by Spencer G. Lucas, Karl Krainer, James E. Barrick and Daniel Vachard, 58 pp.
70. *Eocyclotosaurus appetolatus,* a Middle Triassic Amphibian, 2016, by Rinehart and Lucas, 118 pp.
71. Cretaceous Period: Biotic Diversity and Biogeography, 2016, edited by Khosla and Lucas, 330 pp.
72. Rotten Hill: a Late Triassic Bonebed in the Texas Panhandle, USA, 2016, by S.G. Lucas, L.F. Rinehart, A.B. Heckert, A.P. Hunt and J.A. Spielmann, 97 pp.
73. The Red Corral (Proctor Ranch) Local Fauna (Pliocene, Blancan) of Oldham County, Texas, 2016, by G.E. Schultz,
74. Fossil Record 5, 2016, edited by Robert M. Sullivan and Spencer G. Lucas, 352 pp.
75. New Well Peak, 2017, by Karl Krainer, Daniel Vachard and Spencer G. Lucas, 163 pp.
76. The Lockatong Formation, 2017, by David L. Fillmore, Michael J. Szajna, Spencer G. Lucas, Brian W. Hartline and Edward L. Simpson, 107 pp.
77. Carboniferous-Permian transition in Socorro County, New Mexico, 2017, edited by Spencer G. Lucas, William A. DiMichele and Karl Krainer, 352 pp.
78. Smithian (Early Triassic) Ammonoids from Crittenden Springs, 2018, James F. Jenks and Arnaud Brayard, 175 pp.
79. Fossil Record 6, 2018, edited by Spencer G. Lucas and Robert M. Sullivan, 768 pp.
80. Late Cretaceous Ammonites from the Southeastern San Juan Basin, 2019, Paul L. Sealey and Spencer G. Lucas, 245 pp.
81. Stratigraphic, Geographic and paleoecological distribution of the Late Cretaceous shark genus *Ptychodus* within the Western Interior Seaway, North America, 2020, Shawn A. Hamm, 94 pp.
82. Fossil Record 7, 2021, edited by Spencer G. Lucas, Adrian P. Hunt and Asher J. Lichtig, 578 pp.
83. The Triassic Tetrapod Footprint Record, 2021, Hendrik Klein and Spencer G. Lucas, 194 pp.
84. Kinney Brick Quarry Lagerstätte, 2021, edited by Spencer G. Lucas, William A. DiMichele and Bruce D. Allen, 468 pp.
85. The Systematics of North American Peccaries, 2021, Donald R. Prothero, 76 pp.
86. Late Griesbachian, Dinwoody Formation, Ammonoids and Nautiloids, 2021, James F. Jenks, Takumi Maekawa, David Ware, Yasunari Shigeta, Arnaud Brayard and Kevin G. Bylund, 23 pp.

Hunt and Lucas, 2021, The Ichnology Of Vertebrate Consumption, New Mexico Museum of Natural History and Science Bulletin 87.

THE ICHNOLOGY OF VERTEBRATE CONSUMPTION: DENTALITES, GASTROLITHS AND BROMALITES

ADRIAN P. HUNT and SPENCER G. LUCAS

Contents

Hunt and Lucas, 2021, The Ichnology Of Vertebrate Consumption, New Mexico Museum of Natural History and Science Bulletin 87.

THE ICHNOLOGY OF VERTEBRATE CONSUMPTION: DENTALITES, GASTROLITHS AND BROMALITES

ADRIAN P. HUNT[1] and SPENCER G. LUCAS[2]

[1]Flying Heritage and Combat Armor Museum, 3407 109thSt SW, Everett, WA 98204, e-mail: adrianhu@flyingheritage.com; [2]New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104, e-mail: spencer.lucas@state.nm.us

Abstract—There is a long tradition of indirectly inferring feeding in fossil and Recent vertebrates from the functional morphology of bones and teeth. However, some trace fossils provide direct evidence of feeding, and the study of the ichnology of feeding dates to the 1820s–1830s. Trace fossils that document vertebrate consumption in all of its phases are dentalites ("tooth marks"), gastroliths and bromalites (includes coprolites, consumulites and regurgitalites, among others), and these trace fossils are key to understanding the evolution of nutrient acquisition and food processing in the evolutionary history of vertebrates. We review the fossil record and significance of these ichnofossils as they relate to feeding, which is to say we review the ichnology of vertebrate consumption. Beyond a review, we also indicate areas for further research, which are many, on dentalites, gastroliths and bromalites. Finally, we analyze our knowledge of the history of these trace fossils to identify critical biotic events and turning points in the evolutionary history of vertebrate consumption.

There is an extensive fossil record of vertebrate **dentalites** ("tooth marks"), principally on bony substrates, but also on invertebrate hard parts, coprolites, plants, lithic substrates and others, reviewed here for the first time. Two centuries of studies of dentalites show strong biases towards archeology, and towards dinosaurs as a result of the Taxophile Effect. This record merits more synthetic study in an ichnotaxonomic framework and the development of criteria for establishing inferences about behavior. Indeed, dentalites are of diverse paleoethological significance, including: (1) predation, including hunting strategies; (2) bite method and force; (3) dietary selection; (4) feeding; (5) scavenging strategies; (6) methodologies of bone accumulation; (7) trophic patterns; (8) intraspecific (agonistic) interactions; (9) tooth sharpening; and (10) bone and rock utilization for other purposes, including mineral extraction. What is now needed is a dentalite ichnology beginning with diverse documentation of the dentalite ichnofossil record, compilation and synthesis of the entire record, rigorous ichnotaxonomy and determination of analytical criteria for establishing inferences about the behaviors archived by tooth-mark ichnofossils.

Bromalites include regurgitalites, consumulites, coprolites, pabulites and digestilites. **Regurgitalites** are the least studied bromalites, the most difficult to identify, and their fossil record is strongly controlled by taxonomic and taphonomic factors. Bromalite pellets can represent coprolites or regurgitalites, and two-dimensional examples could be taphonomic artifacts (decayed specimens or physical concentrations). Many identified vertebrate regurgitalites were produced by fish or birds and are preserved in a limited range of environmental settings (e. g., aquatic low energy). Regurgitalites have diverse utility, including: (1) providing evidence of the evolution of predation and digestion; (2) analysis of taphonomy and sedimentary environments; (3) proxies for the presence of biotaxa; (4) loci for exceptional preservation; (5) biogeographic studies; (6) evaluating digestive processes of producers; and (7) evidence of the evolution of durophagy.

There are numerous descriptions of **consumulites**, reviewed for the first time here, but they are usually concealed within publications with a different focus. Consumulites give the most unambiguous dietary attributions of any bromalites and provide direct evidence of the nature of digestion and the structure of the digestive tract. However, the study of consumulites is in an early stage of development, though they also have great potential to provide direct evidence of aspects of patterns of digestion, such as: (1) assessing the chemistry of digestive systems by examining the etching and erosion of consumulite materials; (2) studying the evolution of the components of the digestive system; (3) analyzing dietary changes through ontogeny; (4) evaluating the evolution of diets within clades; and (5) identifying environmental tolerances. Consumulites may preserve a wide range of organic elements with a poor fossil record and thus can be Lagerstätten. In addition, consumulites can also preserve tissues of the gastrointestinal tract. The systematic study of consumulites will undoubtedly yield significant records of contained fossils, as has the recent focus on the contents of coprolites.

The term **gastrolith** refers to sand and/or gravel swallowed by an animal and retained in the digestive tract. Wings recently grouped objects with different origins under the single term gastrolith, so he proposed to add prefixes to the word gastrolith to create terms that identified their different origins: "bio-gastrolith" for the calcareous concretions formed in the bodies of some crustaceans; "patho-gastrolith" for concretions formed in the stomach pathologically; and "geo-gastroliths" for swallowed rock particles. These terms are unnecessary if gastrolith is restricted to the meaning we advocate, which is the same as Wing's "geo-gastrolith." Wings also advocated using the term

"exolith" for "stones" that might be gastroliths but that lack a convincing skeletal association. This term, however, enshrines the widespread misconception that highly polished "stones" are gastroliths, regardless of any skeletal association. It also lacks specificity, as any polished "stone" anywhere could be called an exolith. Thus, we do not use the term exolith. The distribution of gastroliths is very irregular in extant vertebrates and is often related to the presence of a muscular gizzard. Nevertheless, swallowing or not swallowing sand/gravel can be specific to some individuals within a species. A variety of functions have been suggested for gastroliths, only two of which are of significance: use in digestion to grind, pulverize and/or disintegrate food or use as ballast for buoyancy control. It seems likely that some crocodiles and marine mammals use/used gastroliths for buoyancy control, but all other gastrolith-bearing vertebrates appear to have used them in digestion. Identification of fossil gastroliths is only certain when the sand/gravel is found as a concentrated mass in an anatomically plausible position within the abdominal region of a fossil skeleton. There are various ways to polish stones, notably by the wind to make them ventifacts. Polished clasts identified as gastroliths are siliceous, mostly quartz or chert. These clasts could have been polished by wind and/or water, both before ingestion by an animal and/or after excretion or other removal from an animal's digestive tract. Furthermore, how a stomach or gizzard would polish siliceous clasts (which are very hard) is also unclear, and such polishing does not occur in extant birds. Only a small minority of bona fide gastroliths, particularly those of plesiosaurs, are highly polished. There is thus an inability to establish when and where the clasts were polished, and inferring that they acquired their polish while gastroliths is not supported by actualistic studies of gastroliths. The idea that any highly polished clast is a gastrolith needs to be abandoned. Most records of gastroliths are from plesiosaurs, birds and some dinosaurs. Gastroliths are trace fossils in need of ichnotaxonomy that provide important insights into various behaviors. Gastroliths clearly are the work of an animal. Unlike eggs, for example, the sand/gravel that comprise gastroliths (our definition) is not made by animals–it is swallowed by, concentrated by, transported by and, in some cases, altered by animals. So, the trace-fossil status of gastroliths is unimpeachable. We advocate development of an ichnotaxonomy for gastroliths. Ichnotaxonomic names, however, should not be assigned to individual grains/clasts of sand/gravel of fossil gastroliths. We favor naming the entire gastrolith mass from a single abdominal cavity. Ichnotaxobases could be the number of gastroliths in the mass, their general petrographic composition, and their overall size, shape, surface texture and other shared morphological features. This likely would produce a workable ichnotaxonomy that recognizes ichnotaxa that are readily distinguished by morphological differences that are a direct reflection of varied behavior. Gastroliths provide important insights into various behaviors, notably diet, digestion, buoyancy control and habitat preferences.

After footprints, **coprolites** are the most studied vertebrate trace fossils, and they are the subject of an extensive and rapidly growing literature. Coprolites have an extensive fossil record that has proven potential to address a broad range of paleontological issues: (1) coprolites as proxy for biotaxa have utility in biochronology, biogeography and faunal turnover; (2) coprolites as trace fossils can delimit a hierarchy of ichnocoensoes and ichnofacies; (3) coprolites as end products of the gastrointestinal tract can provide evidence of digestive processes; and (4) internally, coprolites can be Lagerstätten that preserve a wide range of organisms with an otherwise poor fossil record.

Other bromalites are digestilites, pabulites and micturalites. **Digestilites** is a new term for materials derived from the digestive tract. They are subject to chemical and physical processes that result in characteristic damage that can be recognized in regurgitated or defecated material. Digestilites composed of invertebrate debris provide a particularly important insight into the evolution of durophagous fish and also constitute a significant sediment source, particularly in the Cenozoic. Many late Cenozoic (and some earlier) microvertebrate accumulations consist of digestilites, and this large topic deserves substantial study. **Pabulites** are fossilized food that never entered the digestive tract. Footprints, some nests and other traces also can record evidence of vertebrate predation and consumption. **Mololite** is a new term for tooth wear, which is a type of trace fossil.

There are **taphonomic megabiases** in the trace fossil record of vertebrate consumption. The bromalite and dentalite records are heavily skewed towards carnivores. There are also significant size-related biases, for example that small and large coprolites and regurgitalites are rare, as are small dentalites. Certain time periods demonstrate strong, geologically-based biases. For example, the continental flooding of the Late Cretaceous resulted in extensive trace (and body) fossils preserved in the Western Interior Basin of North America, not only in the sedimentary deposits of the seaways but also in the rocks that formed on the associated coastal plains. The first large sample of vertebrate ichnofossils related to feeding is from the Devonian, but the largest acme is in the Late Cretaceous, which resulted from taphonomy (continental flooding), the evolution of predators (e.g., sharks, mosasaurs, large theropods) and the Taxophile Effect.

The fossil record of trace fossils provides substantial information about the evolution of vertebrate feeding. In addition, relevant vertebrate and invertebrate ichnofossils provide significant insight into major evolutionary events. The earliest evidence of predation is from terminal Neoproterozoic trace fossils. The earliest definitive vertebrate feeding traces are spiral coprolites and regurgitalites from the Late Ordovician, but earlier bromalites could pertain to vertebrates. The oldest dentalite is from the Middle Silurian. Consumulites occur in Middle Silurian fish, but the first recognizable contents are from the Early Devonian. Bromalites and dentalites provide evidence for major evolutionary events including the Great Ordovician Biodiversification Event, Middle Paleozoic Marine Revolution, and Mesozoic Marine Revolution, as well as various proposed mass extinctions, real and imagined.

Consumulites are important in understanding the evolution of the avian digestive Bauplan. We also introduce the following terms: (1) **cropalite** for preserved contents of the crop, (2) **proventrilite** for contents of the proventriculus; (3) **aspirationalite** (from the medical term for food in the airway) for consumulites that preserve prey in the oral cavity with a significant portion extending exteriorly; (4) **dislocational evisceralite** for a portion of the gastrointestinal tract is physically removed from a carcass; and (5) **preservational evisceralite** for preferential fossilization of the gastrointestinal tract. There is an almost 200-year history of naming vertebrate tracks, but there is an unjustified reluctance to apply a binominal ichotaxonomy to traces related to feeding that impedes the development of their study.

INTRODUCTION

Diet and food acquisition are fundamental biological traits of any organism. In extant organisms, dietary composition and acquisition can be observed directly. However, among extinct organisms, the inference of these traits has relied primarily on analyses of the body fossils of animals. In the case of extinct vertebrates, an extensive literature infers food composition and acquisition primarily by biomechanical analysis of skulls, dentitions and selected postcrania in an actualistic context. However, such inferences are almost always general in nature. Thus, an extinct vertebrate may be inferred to have been eating insects (an insectivore) based on skull and tooth structure as well as based on body size, but precisely what insects were consumed cannot be directly determined.

In contrast, vertebrate trace fossils can record the direct products of actual food acquisition and processing and thereby lead to the identification of very specific diets and modes of dietary acquisition. In these ways, dentalites ("tooth marks"), gastroliths and bromalites (includes coprolites, consumulites and regurgitalites, among others) are key to understanding the evolution of nutrient acquisition and food processing in the evolutionary history of vertebrates (Fig. 1). Here, we review the fossil record and significance of these ichnofossils as they relate to feeding, which is to say we review the ichnology of vertebrate consumption. Beyond a review, we also indicate areas for further research on dentalites, gastroliths and bromalites, which are many. Finally, we summarize the status of our knowledge of the history of vertebrate consumption based on these trace fossils. This summary thus identifies critical biotic events and turning points in the evolutionary history of vertebrate consumption.

Seilacher (1953) defined a mark in relation to ichnology as an abiogenic sedimentary structure (e.g., sole mark, flute mark). The current definition of trace is of a biogenic structure produced by the behavior of an organism modifying a substrate (Bertling et al., 2006; Vallon et al., 2015). Thus, a bite mark is more correctly termed a bite trace in ichnology. However, there is pervasive use in biology, pathology, paleontology, archeology and the vernacular of the term bite mark. We thus utilize the term "mark" in an informal sense, knowing that it is ichnologically incorrect but that it is easily understood. The usage of the formal term dentalite, which we recently introduced (Hunt et al., 2018), will obviate the need for future discussions of this topic.

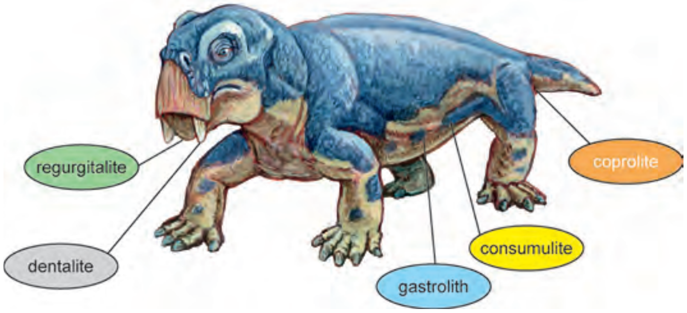


FIGURE 1. Principal trace fossils associated with feeding. Artwork of the Early Triassic synapsid *Lystrosaurus* by Matt Celeskey.

Herein we utilize the ichnological framework established by the consensus work of Bertling et al. (2006, p. 266) and the definition of a trace fossil as "a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate." Thus, for example we do not consider signs of human technology as ichnofossils (e. g., Noe-Nygaard, 1989; Bertling et al., 2006; Lucas, 2016, but see Hasiotis et al., 2007). All the trace fossils discussed here fall within the ethological class Digestichnia (Vallon, 2012).

ABBREVIATIONS

CMM, Calvert Marine Museum, Solomons, Maryland, USA; FHSM, Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas, USA; GLCA, Glen Canyon National Recreation Area fossil collection reposited at Museum of Northern Arizona, Flagstaff, Arizona, USA. NMMNH, New Mexico Museum of Natural History, Albuquerque, New Mexico, USA; OUM, Oxford University Museum of Natural History, Oxford, UK; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; USNM, United States National Museum, Smithsonian, Washington, DC, USA; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

SOME CONSIDERATIONS

Buckland (1822, 1835, 1836) first recognized and described coprolites, dentalites and consumulites. The concept of coprolites garnered immediate and widespread interest, and there is an extensive literature on these ichnofossils (e.g., Duffin, 2009, 2012a; Hunt et al. 2012f). The study of dentalites was intermittent until the past half century, but there never has been concerted research on consumulites. One of our goals is to review the voluminous and very dispersed literature on vertebrate dentalites, gastroliths and the most common bromalites (coprolites, consumulites and regurgitalites). The record of coprolites has already been reviewed by us, wholly or partially, several times during the past decade (e.g., Hunt et al., 2007, 2012d, 2013, 2018; Hunt and Lucas, 2013, 2014a, 2016c, 2018a, 2020a), so we limit our presentation on coprolites here to a synopsis. However, there has been no thorough synthesis of the literature on dentalites, consumulites, regurgitalites or gastroliths, although there have been some partial reviews (e.g., Wings, 2004, 2007; Lucas, 2016; Hunt et al., 2018), so we are more comprehensive in our treatment of the literature on these trace fossils (Appendix A). Similarly, there is a voluminous literature on Pleistocene trace fossils that document consumption that we summarize but do not list in detail, though for geologically older trace fossils we have attempted to evaluate the vast majority of examples.

In our reviews we have generally employed the taxonomy of the producers or victims utilized in the original descriptions. We have characterized traces as marine or nonmarine, again based largely on the original literature. We somewhat arbitrarily included lagoons in the nonmarine category, even though many such environments have marine influences. The sequence of the review follows the anterior-to-posterior progression through the gastrointestinal tract, commencing with dentalites and concluding with coprolites (Fig. 1).

There is a long history of the study of vertebrate functional morphology, dating back to Aristotle, but Cuvier laid the foundations of modern methodology with his concept of the correspondence of parts, namely that function could be inferred from structure (Cuvier, 1812, 1829; Appel, 1987; Russell, 1982; Ashley-Ross and Gillis, 2002). Cuvier applied this principle widely to vertebrate feeding, for example "there are several particular modifications, depending on the size, the manners, and the haunts for which each species of carnivorous animal is destined or fitted by nature; and, from each of these particular modifications there result certain minute conformations of particular parts" (Cuvier, 1818, p. 99-100). The inferred functional morphology of vertebrate hard parts has been the basis of almost all subsequent analysis of food acquisition and processing (e.g., Thompson, 1917; Gans, 1974; Schwenk, 2000). However, the extensive dataset of ichnofossils related to feeding also has important potential for analysis, and it should be further integrated with studies of the body fossil record (e.g., Miller and Pittman, 2021).

Vertebrate and invertebrate ichnology have different traditions (e.g., Hunt and Lucas, 2007b, 2016a; Melchor and Genise, 2004; Lucas, 2005; Lockley, 2007), which Hunt and Lucas (2003, 2004, 2005c, 2007b) termed the ethological and the biotaxonomic. The majority of invertebrate ichnologists, with the notable exception of those describing arthropod walking traces, have principally utilized an ethological approach to ichnology by describing and naming behavioral interactions between organisms and substrate. In contrast, vertebrate ichnologists have principally applied a biotaxonomic approach by attempting to relate traces to the taxonomy of the producer. Thus, vertebrate ichnologists treat vertebrate ichnotaxa as proxies of biotaxa (Hunt and Lucas, 2007b, 2016a; Lucas, 2007). The history of naming vertebrate tracks dates back to the 1830s (*Chirotherium* Kaup, 1835) and has been both widely accepted and utilized in analyses ranging from those of biochronology to ichnofacies (e.g., Lucas, 2007; Hunt and Lucas, 2007b). However, with some exceptions (e.g., Duffin, 2010; Laojumpon et al., 2012; Milàn, 2018; Rakshit et al., 2019; Duffin and Ward, 2020; Rummy et al., 2021), many workers have been explicitly reluctant to apply binomial nomenclature to bromalites and the other traces discussed here (e.g., Chin in Hunt et al., 1994; Bajdek et al., 2014; Francischini et al., 2018). Regardless of all opinions on variation in feces morphology, which in our opinion are not upheld by Recent studies, if morphotypes can be recognized then they should be named to facilitate communication and utility. Thus, we discuss ichnotaxobases for all of the groups of vertebrate trace fossils reviewed here and advocate the erection of binomial taxonomy, as has been universally advocated for all trace fossils (Bertling et al., 2006).

Significant factors influence the preserved pattern of the fossil record of dentalites, gastroliths and bromalites. Lagerstätten are particularly important in the preservation of these trace fossils, especially with regard to consumulites. Cambrian and Ordovician coprolites are almost exclusively recorded from Lagerstätten (e.g., Winneshiek, Soom Shale: Aldridge et al., 2006; Hawkins et al., 2018), and they are important sources of feeding traces through the later Phanerozoic. In particular, Lagerstätten preserve large samples of articulated skeletons, which are necessary for the unambiguous recognition of consumulites and gastroliths (e.g., Holzmaden, Solnhofen: Keller, 1976; Viohl, 1990). Articulated skeletons are not restricted to Lagerstätten, but they mainly are preserved in a limited number of depositional environments, principally those of aquatic low energy settings (lagoonal, lacustrine, shallow marine). These depositional environments also preserve most consumulites, regurgitalites and gastroliths.

The trace fossils discussed herein can provide significant information beyond feeding behavior. For example, dentalites provide prima facie evidence for intraspecific head-biting in serveral clades of large reptiles, including mosasaurs, phytosaurs, crocodylomorphs and tyrannosaurs (e.g., Currie and Eberth, 2010; Carr et al., 2020; Brown et al., 2021). And, latrinites indicate the behavior of producers such as cave utilization by ground sloths (Hunt and Lucas, 2018c).

All ichnofossils are facies fossils, but they have varied environmental restrictions. Coprolites are the only trace fossils that are routinely re-worked because of early lithification (e.g., Hollocher and Hollocher, 2012). They thus are present in intraformational, and even extraformational, lag deposits (Hunt and Lucas, 2010; Hunt et al., 2015).

There is a size bias, at least in the recognition of vertebrate feeding traces. The majority of dentalites, except for those of armored fish in the Devonian, and of consumulites, except for those from Lagerstätten, are reported from relatively large vertebrates. There is also ample evidence of the Taxophile Effect of Hunt et al. (2018)–preferential study of popular fossil groups, such as dinosaurs–for example, with publications on the dentalites of large Mesozoic reptiles greatly outnumbering those of small Paleogene mammals.

There have been few studies of the pattern of the overall fossil record of vertebrate trace fossils (e.g., Hunt et al., 2005a, 2018). There are clearly extensive taphonomic megabiases (Behrensmeyer et al., 2000) in this trace fossil record. The bromalite and dentalite records are, for example, heavily skewed towards carnivores. There are also significant size-related biases, such as that small and large coprolites and regurgitalites are rare, as are small dentalites. Certain time periods demonstrate strong, geologically-based biases. Thus, for example, the continental flooding of the Late Cretaceous resulted in extensive trace (and body) fossils preserved in the Western Interior Basin of North America, not only in the sedimentary deposits of the seaways but also in the rocks that formed on the associated coastal plains, and could reasonably be considered to be a mega-Lagerstätten or maybe a Lagerstätten province. Certain traces have abundant records not consonant with those of the relative abundance of their producers, such as the spiral coprolites of chondrichthyans. These megabiases should provide many lines of future inquiry into the nature of the record of vertebrate ichnofossils and are discussed further below.

VERTEBRATE FEEDING

The analysis of vertebrate feeding in the fossil record has almost totally been based on the functional morphological (biomechanical) analysis of body fossils (especially of skulls and dentitions). A vast literature exists on such analyses, and we do not review it or its conclusions here. Instead, we draw attention to those aspects of vertebrate feeding that are informed by trace fossils, some of which are not understood from the study of body fossils.

The Hard Parts

Dentitions and teeth

Vertebrate teeth are hard structures (usually enamel capped) in the vertebrate mouth that are used to process food. They are very variable in individual morphology and, in their groupings in a given mouth (Fig. 2), which are referred to as dentitions (e.g., Peyer, 1968). Typically, teeth in dentitions can be considered homodont (if all the teeth are of very similar structure) or heterodont (in which very different tooth structures are present). Thus, for example, the dentition of humans is

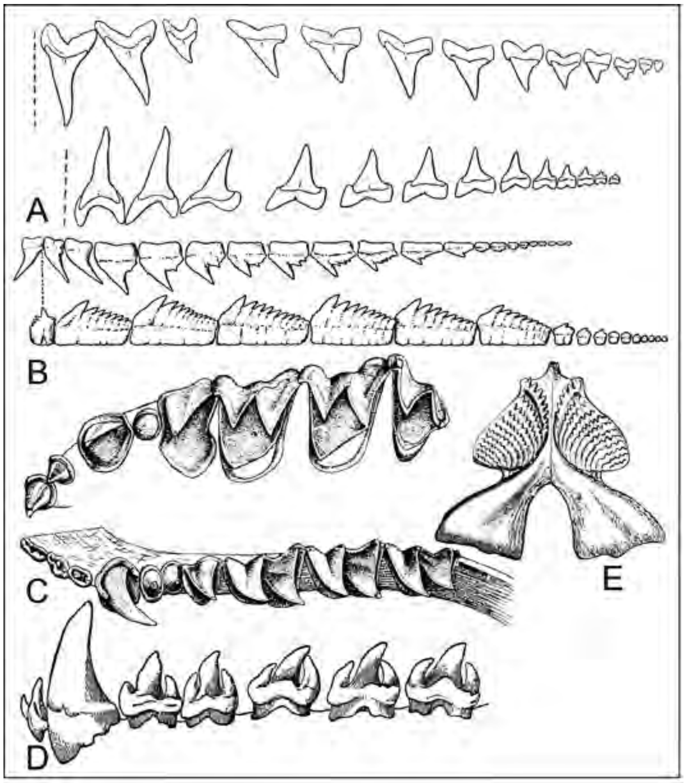


FIGURE 2. Selected vertebrate dentitions to document some of the wide range of morphology of individual teeth and of whole dentitions. **A,** Lateral view of the relatively homodont upper and lower tooth rows of the mackerel shark, *Isurus*. **B,** Much more heterodont upper and lower tooth rows of the sixgill shark, *Hexanchus*. **C,** Upper and lower tooth rows of the bat, *Corynorhinus*, showing the heterodonty characteristic of most mammals, by which teeth can be differentiated readily into incisors, canines, premolars and molars. **D,** Lateral view of the lower dentition of the seal, *Leptonychotes*. Posterior to the large canine, note the relative homodonty of the cheek teeth. **E,** Occlusal view of fossil toothplates of a Carboniferous lungfish, *Ctenodus*. Not to scale; modified from Peyer (1968).

very much heterodont, with the teeth readily distinguished as incisors, canines, premolars and molars based on their differing morphology. In contrast, the dentition of a dolphin consists of conical teeth that are essentially all of the same morphology, so the dolphin dentition is nearly homodont. Nevertheless, the terms heterodont and homodont are best viewed as ends of a spectrum of differentiation of tooth morphology in the dentitions of vertebrates.

Most vertebrates have teeth that are located "marginally," that is on the edges of the upper and/or lower jaws. However, many vertebrates, especially some fishes, amphibians and reptiles, do have teeth otherwise located, usually on the palate. Furthermore, all vertebrates have one or more tooth generations. Thus, in mammals there are typically two sets of teeth–deciduous and permanent–that succeed each other in ontogeny and are different from each other in morphology. Such dentitions are termed diphyodont. In contrast, most non-mammalian vertebrates have many generations of teeth, and such dental ontogeny is referred to as polyphyodont. Mammals are also distinguished from most other vertebrates by the ability to masticate food by virtue of large premolars and molars that fit together during occlusion. Some other groups, such as hadrosaurid dinosaurs, had dental batteries to reduce food to small particle sizes. Several groups of vertebrates are largely or completely edentulous, notably birds and turtles. There is little literature on their dentalites (e.g., Njau and Gilbert, 2016; Fernández-Jalvo and Andrews, 2016; Tables A.1-4 herein), although there are several studies related to the hypothesis that the preservation of the Taung child (*Australopithecus*) in South Africa and its associated fauna were the result of the predatory activity of eagles (Berger and Clarke, 1995; Sanders et al., 2003; McGraw et al., 2006; Gilbert et al., 2009).

Clearly, there is complexity to vertebrate teeth and dentitions, in morphology and in ontogeny. Thus, a similar complexity will be found in trace fossils made by teeth (dentalites). Furthermore, the processing of food by the teeth affects the structure and composition of vertebrate bromalites, a subject that has been little discussed. Finally, as detailed below, the use of gastroliths by some vertebrates (notably birds) can provide a food processing function not undertaken by the dentition.

Skeletal system

A major function of the vertebrate head is the acquisition and initial processing of food items, and the architecture of the skull relates in large part to diet. A good example is found in the semi-aquatic predator guild. Predators of this guild are often characterized by low, robust skulls with elongate jaws. This skull type is widely distributed among different taxonomic groups, including trematosaurs (temnospondyls), proterosuchids (archosauriforms), proterochampsids (archosauriforms), phytosaurs (archosauriforms), champsosaurs (sauropsids), crocodilians (eusuchians) and spinosaurs (saurischians). The low-profiled, elongate skull and lower jaws produce lower resistance when moved laterally through water. The long jaws allow for multiple pointed teeth that can hold slippery fish or other struggling prey, and the infliction of larger bites and higher tooth tip velocity; the robust structure offers protection from resisting prey (Taylor, 1987; Busbey, 1995; McHenry et al., 2006; Pierce et al., 2008; Walmesley et al., 2013). Detailed study of skull morphology can provide specific information about feeding behavior, such as with durophagous carnivorans (e.g., Tseng and Wang, 2010, 2011; Figueirido et al., 2013).

The bones of the skull preserve the attachment areas for the muscles associated with mechanics of the jaw. The reconstruction of muscle mass and insertion locations provides information about the feeding capabilities and behaviors of the organism, and this methodology has been widely utilized, principally in terrestrial tetrapods, for example in dicynodonts (e.g., Crompton and Hotton, 1967), theropods (e.g., Molnar, 2008), ornithischian dinosaurs (e.g., Weishampel, 1984) and herbivorous (e.g., Gambaryan and Kielan-Jaworowska, 1995) and carnivorous (e.g., Wroe et al., 2013) mammals.

The postcranial skeleton has indirect and direct significance for feeding. Food is often grasped with, sometimes even processed by, the fore limbs in many vertebrate taxa. For example, the strong fore limbs and thumbs of saber-toothed felines are inferred to have been used to achieve rapid immobilization of prey, thus decreasing the risk of injury and minimizing energy expenditure (Salesa et al., 2010), and claws in large herbivorous mammals are thought to have been utilized for browsing, digging and climbing to acquire food (Coombs, 1983). Other skeletal adaptations that have a direct correlation with locomotion are often directly reflective of the motions needed to acquire food.

The Soft Parts

Digestive System

The digestive tract of animals is an essential organ system. It allows animals to efficiently digest food and take up nutrients to maintain growth and sustain the body (Hejnol and Martín-Durán, 2015). The vertebrate digestive tract is a tubular soft-tissue structure that commonly can be divided into an esophagus, stomach and intestines. There is usually a constriction in the gut between the stomach and intestines, termed the pylorus, formed by the sphincter muscles. The foregut is anterior to the pylorus, and the posterior segment can be referred to as the hindgut or the midgut and hindgut (e.g., Romer, 1962; Stevens and Hume, 1995).

In the least derived fish, and even some teleosts, the foregut is a simple tube between the pharynx and intestines, but in most vertebrates it is separated into an anterior esophagus and a posterior stomach. The esophagus serves mainly to transport food, whereas the stomach is for storage and some food processing.

Most vertebrates are monogastric, with a simple, single-chambered stomach. However, digesting cellulose by microbial fermentation is most efficiently accomplished by a multi-chambered ruminant stomach consisting of the reticulum, omasum, abomasum and rumen. This is foregut fermentation (e.g., bovids), as opposed to hindgut fermentation (e.g., camelids), which occurs in the cecum at the beginning of the large intestine. Birds have digestive challenges, including a lack of teeth, high metabolism, weight constraints and rigidity of the abdominal cavity preventing distension of the alimentary canal. They have a two-chambered stomach consisting of a glandular proventriculus and a muscular ventriculus (gizzard), which may contain sand and/or gravel, as well as a crop that is an expanded portion of the posterior esophagus, serving principally for storage.

The digestive tract posterior to the stomach consists of the intestines. Many basal fish have a spiral valve, which comprises the majority of the intestinal length between the stomach and cloaca, and that may be helical or scroll-like in form (McAllister, 1987; Capasso, 2019a). More derived vertebrates have intestines that consist of elongate tubes, separated into a more anterior small intestine (midgut) and a posterior large intestine (hindgut), that terminate in a rectum. The liver, pancreas and gallbladder are associated with the midgut.

Most of the trace fossils discussed here have diverse relationships to the vertebrate digestive tract. Thus, bromalites, notably consumulites, are divided into different kinds specific to a particular part of the digestive tract, reflecting their site of origin (Fig. 3; Table 1). Gastroliths mostly reside in the stomach. These specific kinds of traces thus provide information about the structure and function of that part of the digestive system in which they reside.

DENTALITES

Introduction

Hunt et al. (2018, p. 500) introduced the term dentalite to encompass all traces produced on a substrate by the teeth or oral cavity of a vertebrate or invertebrate (Appendix B). These trace fossils were generally referred to previously as "bite marks" (e.g., Avilla et al., 2004; Drumheller et al., 2014) although technically they should be considered "bite traces" (see discussion above). Most examples of dentalites were made by vertebrates, but the term also applies to traces left by the jaw apparatus of invertebrates (e.g., *Bicrescomanducator rolli* – cephalopod dentalites on ammonites: Andrew et. al., 2010*:* echinoid dentalites on crinoids: Baumiller et al. 2010; Gorzelak et al. 2012). The substrate of dentalites is most often bone (Binford, 1981; Fernández-Jalvo and Andrews, 2016) but can be vegetation (Lucas, 2016), invertebrate hard parts (Kauffman and Sawdo, 2013), coprolites (Godfrey and Smith, 2010) or sediment (Gingras et al., 2007).

History of Study

The study of vertebrate dentalites has been reviewed recently by Drumheller-Horton (2012), Lucas (2016) and Hunt et al. (2018). It began with the work of Buckland (1822, 1824),

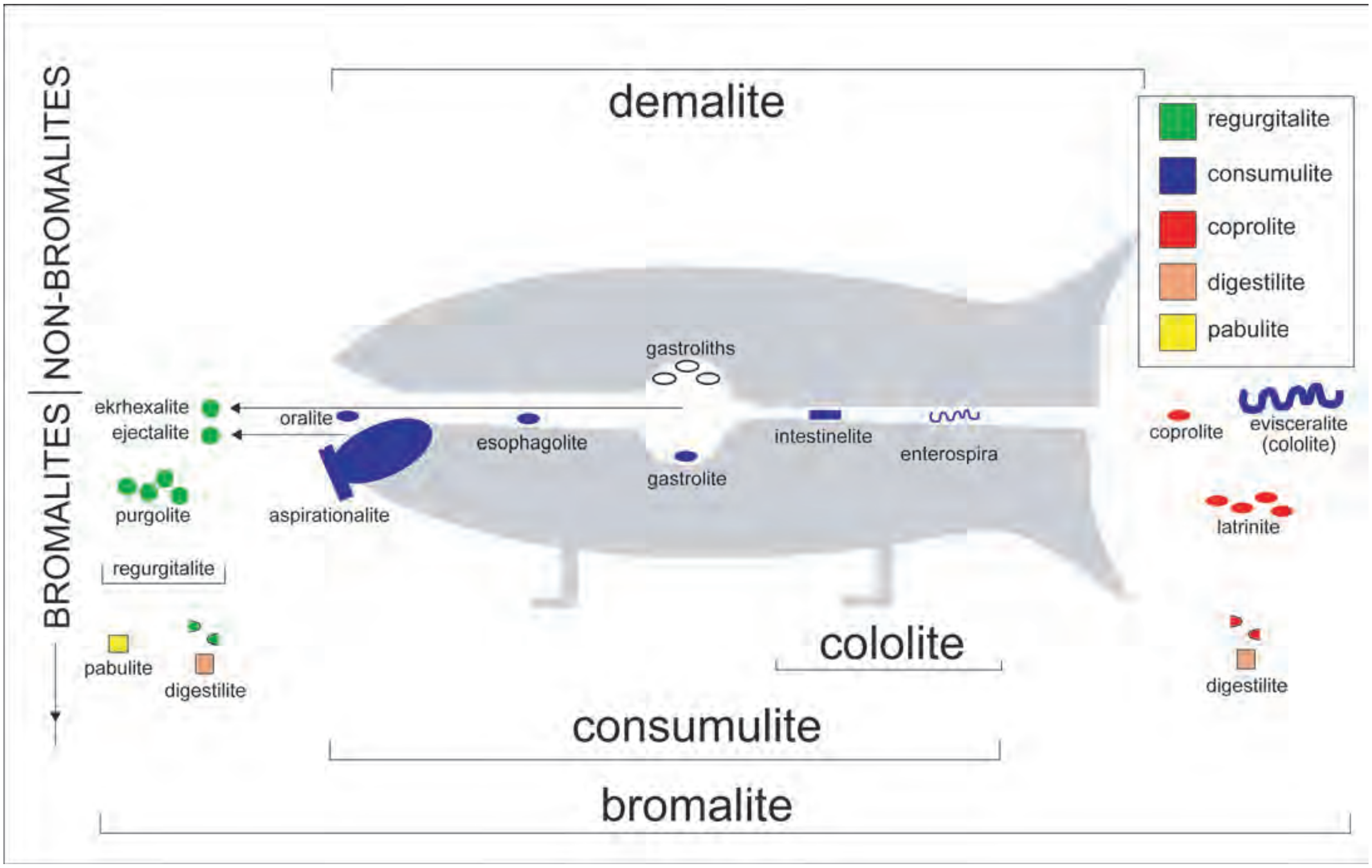


FIGURE 3. Selected classification terms for bromalites and associated trace fossils. Modified from Hunt and Lucas (2012a).

who analyzed a Pleistocene vertebrate fauna from Kirkdale Cave in northern England (Fig. 4). He utilized element representation, bone damage and dentalites to demonstrate that the bone deposit was not "Diluvial" (from the Flood) but actually represented an "Antidiluvian" hyena den (e.g., Boylan, 1977). This was the start of a remarkable period in which Buckland used theoretical and actualistic studies (e.g., feeding cow bones to a captive hyena, walking tortoises across dough) to make major contributions to the study of vertebrate ichnofossils – dentalites, coprolites and footprints (Buckland, 1822, 1824, 1835; Boylan, 1977; Pemberton et al., 2007; Duffin, 2009). Nevertheless, there was relatively little interest in dentalites for the remainder of the nineteenth century, with a few exceptions (e.g., Tournal, 1833; Dawkins, 1863). The exceptions included both Mudge (1877) and Williston (1898), who commented on the presence of mosasaur fossils with dentalites produced by sharks in the Upper Cretaceous strata of the western United States.

During the twentieth century, interest in dentalites grew in the context of a dichotomy between studies in archaeology and paleontology (Hunt et al., 1994b; Drumheller-Horton, 2012). Archeological studies of dentalites increased due to the advent of processual archaeology (e.g., Binford, 1981). A major motivation was to answer questions related to that posed by the title of Brain's (1981) well known book "The hunters or the hunted?" (also see Washburn, 1957), which was, in itself, a reaction to Dart's (e.g., 1957) hypothesis of the osteodontokeratic culture of *Australopithecus* (i.e., tool kits made from bones and teeth and utilized by hominoids). Paleontological studies of dentalites have been part of a broad resurgence of interest in vertebrate taphonomy (e.g., Behrensmeyer and Hill, 1980). The majority of this work, both actualistic and on fossils, relates to mammals, with a growing literature on crocodilians (e. g., Njau and Blumenschine, 2006). Fernández-Jalvo and Andrews (2016) provided an extensive photographic atlas of fossil and Recent dentalites.

FIGURE 4. Comparison of Pleistocene and Recent damage to bovid bones by hyena jaws (from Buckland, 1824, pl. 23). "1. Residuary part of the lower extremity of the tibia of an ox, which I saw given entire to a Cape hyaena in Mr. Wombell's travelling collection at Oxford, in December 1822: marks of the teeth are definitely distinctly visible at a, b, c, d, e, f….. 2. Fragment of a similar tibia from Kirkdale Cave, broken nearly in the same manner as No. 1, and bearing similar marks of teeth at a, b, c, d, e: in the recent, as in the antediluvian specimen, the lower condyle has, from its hardness, been left unbroken. 3. Splinter from another bome broken by the hyaena at Oxford: the cavity at A. was produced by the hyaena's tooth. 4. Similar splinter, bearing a similar cavity A., from the cave at Kirkdale, and partially incrusted with stalagmite. 5. Inside of the lower extremity of the recent specimen, No. 1, in which the hole A. was produced by the hyaena's bite……6. Lower extremity of another tibia from Kirkdale, in which the form of the cavity A. resembles that in No. 5. 7. Scaphoid bone of the left carpus of an ox, which, with the other component bones of the carpus, lay all night untouched in the hyaena's cage at Oxford. 8. Similar bone from Kirkdale, equally untouched" (Buckland, 1824, p. 276-277).

Cruickshank (1986) applied the first ichnogeneric name to dentalites. Subsequently, 18 additional ichnotaxa have been named (Table 2). The ichnotaxonomic process leads to a clear separation of description and interpretation, which are sometimes conflated in archeological studies. Jacobsen and Bromley (2009), Pirrone et al. (2014) and Lucas (2016) discussed ichnotaxobases of dentalites. Lucas (2016) recently named two substrate-based nonmarine ichnofacies: the *Cubiculum* ichnofacies for modifications to bone, including dentalites, and the *Palaeoscolytus* ichnofacies for modifications to vegetation, including dentalites.

Actualistic Studies

Buckland (1822, 1824) conducted the first actualistic study of dentalites by feeding cow bones to a hyena from a travelling show and comparing the bite marks with those present on Pleistocene bison bones from Kirkdale Cave (Fig. 4). Lyell (1863) provided porcupines at the London Zoo with bone and antler samples to gnaw upon, and he compared the results with marks on probable Pleistocene bones from Saint Prest in France. Modern actualistic studies were largely inspired by controversies generated by the interpretation of early archeological sites in East Africa and South Africa, including Olduvai Gorge (Tanzania), Koobi Fora (Kenya), and Sterkfontein, Klasies River Mouth and Swartkrans (South Africa) (Arriaza et al., 2021). This research started in the 1970s but reached a crescendo in the 1980s (e.g. Sutcliffe, 1970; Binford, 1981; Brain, 1981; Bunn, 1982, 1983; Haynes, 1980, 1982, 1983; Blumenschine, 1986, 1988). New methodologies are being developed (e.g., Domínguez-Rodrigo and Piqueras, 2003; Domínguez-Rodrigo et al., 2012). Arriaza et al. (2021) recently studied leopard dentalites, utilizing microphotogrammetry and geometric morphometrics. They demonstrated that tooth marks inflicted by leopards, spotted hyenas and lions can be statistically differentiated based on their morphology, and that the ratio of pits to scores inflicted by the leopard is closer to hyenas.

Actualistic studies on crocodile dentalites were notably spurred by dissertations and subsequent research by Njau (2006; Njau and Blumenschine, 2006, 2012; Njau and Gilbert, 2016) and Drumheller (Drumheller-Horton, 2012; Drumheller and Brochu, 2014, 2016). D'Amore (2009) studied tooth marks of *Varanus komodoensis* as analogues for dentalites of theropods.

Bony Substrates

Introduction

We organize our review of the dentalite record by the substrate on which the dentalite is registered, because identifying the producers of dentalites is often problematic. Lucas (2016) and Hunt et al. (2018, fig. 12.6) briefly reviewed this record. There are several clear patterns to the documented record of dentalites (Fig. 5):

1. There is a bias towards dentalites of large animals preserved on large pieces of substrate (e.g., cetaceans, dinosaurs, marine reptiles). This is presumably related to ease of recognition and to the fact that smaller animals may be wholly ingested or

TABLE 1. Consumulite ichnotaxonomy.

Placement of consumulite		Agassiz (1833)	Hoernes (1904)	Fritsch (1907)	Northwood (2005)	Hunt and Lucas (2012a); this paper		
Mouth	Protruding from oral cavity					Consumulite		Aspirationalite
	Within oral cavity							Oralite
Esophagus								Esophagalite
	Avian crop							Cropalite
Stomach/ ventriculus	Avian proventriculus				Gastrolite			Proventrilite
								Gastrolite
Intestines		Cololite					Cololite	Intestinilite
	Spiral valve		Enterolite	Enterospira				Enterospira
Preserved outside body cavity		Cololite						Evisceralite

totally destroyed by mastication.

2. Hunt et al. (2018) coined the term Taxophile Effect to refer to the disproportionate study of more "popular" taxonomic groups. This is well seen in the marked disparity between the numbers of reports of dentalites on dinosaur bones relative to those on the bones of Cenozoic mammals. The Taxophile Effect may also be at play with invertebrates, as there are more reports of dentalites on elegant ammonoids than on any other invertebrate taxonomic group.
3. Dentalites are non-randomly distributed in time, with notable acmes in the Late Triassic, Late Cretaceous and late Cenozoic (Fig. 5).
4. Prior to the Quaternary, with the exception of the nonmarine Mesozoic, most dentalites are reported from marine facies. In the Quaternary, a large percentage of dentalites are from cave deposits.
5. There is a clear seeker bias (seek and ye shall find), as careful investigation of large existing collections, at least of vertebrate specimens, has always led to the identification of multiple examples of dentalites (e.g., Jacobsen, 1995, 1998; Konuki, 2008; Drumheller et al., 2020; Dalman and Lucas, 2021).
6. Dentalites on a bony substrate pertain to the *Cubiculum* ichnofacies of Lucas (2016), those on vegetation to the *Palaeoscolytus* ichnofacies of Lucas (2016) and those on coprolites to the *Gaspeichnus* ichnofacies of Hunt et al. (2018).

Paleozoic

Marine

Putative jawed vertebrates date to the Ordovician (Karatajute-Talimaa and Predtechenskyj, 1995; Sansom et al., 1996; Smith and Sansom, 1997; Sansom et al., 2012), but the first definitive body fossil remains are of Early Silurian age (Zhao and Zhu, 2010; Brazeau and Friedman, 2015). The earliest record of a dentalite is on an unidentified jawless cyathaspid from the Middle Silurian (Wenlock) Man on the Hill (MOTH) site in the Mackenzie Mountains, Northwest Territories of Canada (Randle and Sansom, 2019a,b). There are no other recorded Silurian examples, but dentalites become relatively common in the Devonian, and the study of ostracoderms indicates increasing frequency of these traces on aquatic vertebrates through the period (Lebedev et al., 2009; Randle and Sansom, 2019a).

Early Devonian dentalites are present on heterostracans in Canada, the USA, England, Wales, Scotland, Ukraine, Sweden, and Russia (Tarrant, 1991; Lebedev et al., 2009; Elliott and Petriello, 2011; Randle and Sansom, 2019a: Fig. 5). Dentalites of Middle Devonian age are known in heterostracans, arthrodires, and antiarchs in Latvia, Estonia, Russia, and the USA (Obruchev and Mark-Kurik, 1965; Lebedev et al., 2009; Johansen et al., 2013; Tuuling, 2015; Randle and Sansom, 2019a). Late Devonian dentalites are present on heterostracans, arthrodires, antiarchs and osteolepiforms in Scotland, Estonia, Russia, Canada, and Morocco (Capasso et al., 1996; Lebedev et al., 2009; Scott et al., 2012; Cloutier, 2013; Glinskiy and Mark-Kurik, 2016; Randle and Sansom, 2019a). Although eurypterids might be considered the perpetrators of some putative Devonian dentalites (e.g., Romer, 1933, but see Lamsdell and Braddy, 2009), there are only two probable recorded occurrences (Lebedev et al., 2009; Elliott and Petriello, 2011; Blieck, 2017).

There are very few reports of dentalites on Carboniferous or Permian fish fossils. The marked decline after the Devonian probably relates in large part to the extinction of many of the armored fish, as sheets of dermal armor provide a preferential substrate to preserve dentalites. Zangerl and Richardson (1963) published a classic study of fossiliferous Pennsylvanian black shales that contain fossils that appeared to preserve abundant examples of bite marks. They documented a range of incomplete skeletons of fish, which they interpreted as representing dismembered carcasses and "gastric residues" (regurgitalites). However, subsequent study has made it clear that the partial skeletons represent normal decay processes, most of the putative regurgitalites are not regurgitalites, and there are no preserved dentalites (Elder, 1985; Elder and Smith, 1988).

Nonmarine

There are only a small number of reports of Paleozoic nonmarine dentalites (Fig. 5). However, one of the oldest tetrapod fossils, a humerus from the Famennian (Late Devonian), has puncture marks on the dorsal and ventral surfaces that may be dentalites (Shubin et al., 2004). The earliest example in the nonmarine Paleozoic of multiple dentalites is on an articulated skeleton of the early Permian synapsid predator *Varanops,* which preserves traces interpreted to be the result of scavenging by a dissorophoid amphibian (Reisz and Tsuji, 2006). Reisz and Tsuji (2006, p. 1023) opined that "few Paleozoic tetrapods have been prepared with the kind of care required to readily identify bite marks, or studied with these taphonomic features in mind." The early Permian Craddock Bone Bed in Texas yields abundant dentalites produced by *Dimetrodon* that have not been described in detail (Houpt et al., 2020). Dentalites are present on a snout of the amphibian *Diplocaulus* but most commonly on skeletal elements of adult dimetrodonts and subadult diadectids. Damage is concentrated on distal limb elements and has been interpreted as the result of feeding on major muscle masses (Houpt et al.,

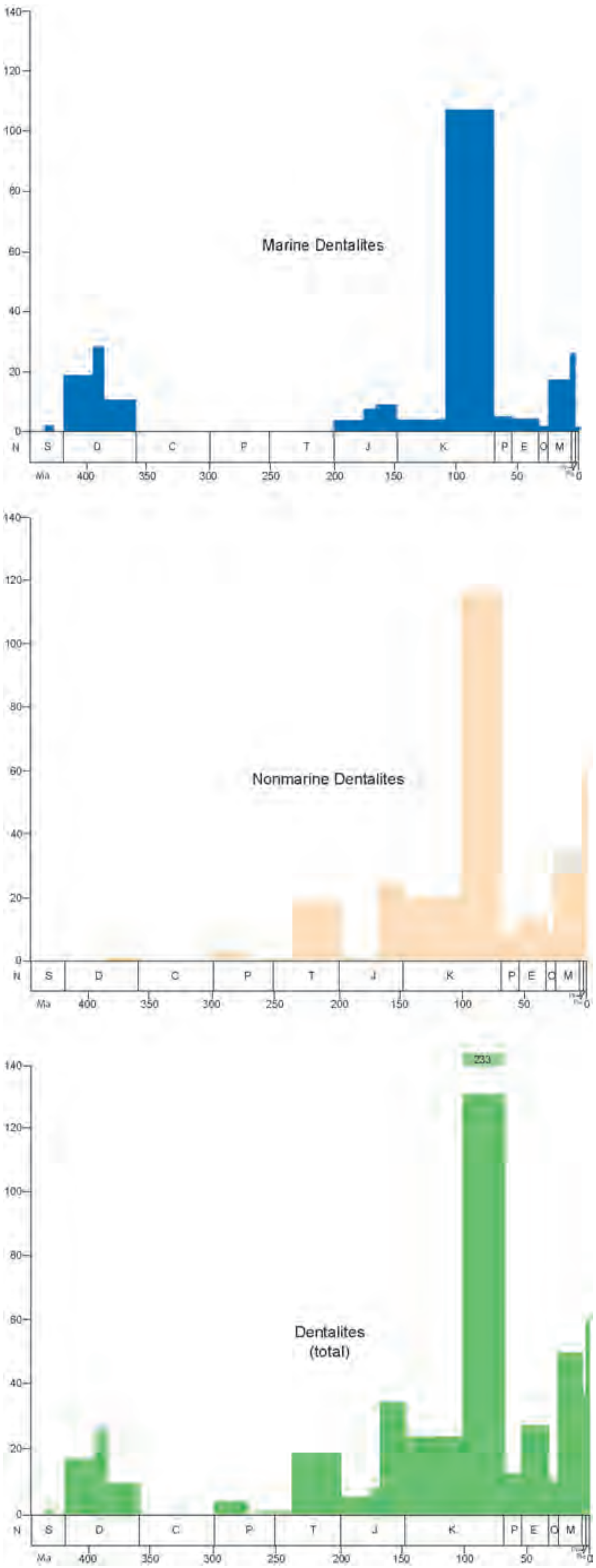


FIGURE 5. Temporal distribution of reports of dentalites. Sources are in the text and Tables A.1-4.

2020).

Another early Permian example is represented by a puncture dorsal to the caniniform tooth of the skull of *Dimetrodon* (*Bathygnathus*) *borealis* (Langston 1963; Brink et al., 2013, 2015). The classic late Permian Karoo faunas preserve few reported dentalites, but one example is of dentalites, likely made by the gorgonopsian *Aelurognathus,* on a therapsid skeleton (Fordyce et al., 2012).

Mesozoic

Marine

There are a large number of dentalites reported from the marine Mesozoic (Fig. 5; Table A.1). The majority are related to marine reptiles, and many dentalites in the Cretaceous were produced by sharks. Marine tetrapods provided an important substrate for the preservation of dentalites throughout the Mesozoic and Cenozoic. They generally have larger body sizes and more robust skeletal elements than chondrichthyans and bony fish, both factors that aid in the preservation and recognition of dentalites. The greatest number of occurrences is from the Late Cretaceous, with many from the sedimentary record of the Western Interior Seaway of western North America.

There are two dentalite records from the Early Jurassic, both from ichthyosaurs. Five specimens of the ichthyosaur *Temnodontosaurus* from Germany have dentalites attributed to *Temnodontosaurus* and the crocodylomorph *Steneosaurus* (Pardo-Pérez et al., 2018). A skull of the ichthyosaur *Leptonectes* cf. *L. tenuirostris* from England has a healed wound that appears to have been a dentalite (Maisch and Matzke, 2003).

There are a number of dentalites reported from the Middle Jurassic of England and one from Scotland. One example of the fish *Leedicthys* preserves a tooth of the marine crocodylomorph *Metriorhynchus* in a dentalite (Martill, 1985a). Four specimens of the plesiosaur *Cryptoclidus* or cf. *Cryptoclidus* from England include dentalites, three of which are attributed to a pliosaur maker and one to *Metriorhynchus* (Martill et al., 1994; Forrest, 2000, 2003; Rothschild et al., 2018). Two ichthyosaurs, one from England and one from Scotland, include dentalites, one identified as having been produced by a pliosaur (Martill, 1996; Brusatte et al., 2015).

Late Jurassic dentalites are not numerous but are more broadly distributed than those from earlier parts of the period. Two specimens of turtles from Switzerland assigned to *Plesiochelys* sp. and an indeterminate taxon have dentalites attributed to the crocodyliform *Machimosaurus* (Meyer, 1991). Bones of the marine crocodyliforms *Geosaurus vignaudi* and *G. saltillense* from Mexico include dentalites (Frey et al., 2002; Buchy et al., 2006). Late Jurassic plesiosaurs with dentalites occur in the USA, England and Mexico, and Late Jurassic ichthyosaurs with dentalites are present in Russia, Poland and Norway (Martill et al., 1994; Wahl, 2006; Buchy, 2007; Druckenmiller et al., 2012; Novis, 2012; Zverkov et al., 2015; Tyborowski, 2016). One of the plesiosaur and one of the ichthyosaur occurrences are attributed to bites from pliosaurs (Buchy, 2007; Zverkov et al., 2015).

The majority of Early Cretaceous dentalite records are from Australia (Table A.1). These specimens include dentalites on the ichthyodectiform fish *Cooyoo australis* (Wretman and Kear, 2014). The holotype of the "elasmosaur" *Eromangasaurus carinognathus* has dentalites made by the "pliosaur" *Kronosaurus* (Thulborn and Turner, 1993; Kear, 2005; McHenry, 2009). In turn, there are two examples of dentalites on *Kronosaurus*, one produced by intraspecific interaction (McHenry, 2009) and one by a cretoxyrhinid shark (Holland, 2018). Kellner et al. (2010) described shallow punctures on an ornithocheiroid pterosaur wing metacarpal. Early Cretaceous dentalites outside of Australia include specimens of the crocodyliform *Pachycheilosuchus trinquei* from the USA (Rogers, 2003) and a spinosaur tooth

TABLE 2. Named dentalite ichnotaxa.

Ichnotaxon	Morphology	Author	Producer	Substrate	Age	Stratigraphic unit	Location
Bruatlichnus brutalis	Straight to arcuate grooves	Mikuláš et al. (2006)	Carnivore	Carnivores+	Early Miocene	Ahníkov locality	Czech Republic
Daandavichnus batoideum	Sub-circular to trapezoid outline with the anterior area preserves a curved impression with a M-shaped boundary. Posterior area preserves two circular depressions with smooth borders, occasionally connected by striations forming an arch	Rodríguez-de la Rosa et al. (2021)	Batoid	Lithic	Early Cretaceous	San Juan Raya Formation	Puebla, Mexico
Heterodontichnites hunti	Imprint of straight or slightly arcuate partial dentition with rounded and antero-posteriorly elongated tooth impressions	Rinehart et al. (2006)	Phytosaur	Metoposaur, dycnodont	Late Triassic	Chinle Group	New Mexico, USA
Knethichnus parallelum	Parallel grooves of serrated tooth	Jacobsen and Bromley (2009)	Theropods (holotype) Sharks	Dinosaurs (type), dolphin, whale, mosasaur	Late Cretaceous (type) Pliocene	Dinosaur Park Formation (type), Niobrara Formation	Alberta, Canada (type) Italy - Cigala-Fulgosi (1990) California - Deméré and Cerutti, 1982) Kansas-Schwimmer et al. (1997), Corral et al., (2004)
Linichnus bromleyi	Single groove with a non-serrated edge	Muñiz et al. (2020)	Shark	Mysticeti and *Homiphoca* sp.	Early to early late Pliocene	Pliocene Unit I	Spain
Linichnus serratuse (type ichnospecies)	Elongate groove of serrated tooth	Jacobsen and Bromley (2009)	Theropods (tyrannosaurs, *Troodon*, *Saurornitholestes*)	Ornithischians, theropods	Late Cretaceous	Horseshoe Canyon Formation	Alberta, Canada
Machichnus bohemicus	Shallow, serial parallel or subparallel, oriented perpendicular to substrate edge, arcuate in cross section, representing gnawing (rasping) traces. *M. bohemicus* has shallow, thin, parallel to subparallel, smooth-bottomed scratches that occur in small groups	Mikuláš et al. (2006)	Rodent (beaver), crocodile	Not specified	Early Miocene	Ahníkov locality	Czech Republic
Machichnus fatimae	Regularly arcuate, large-sized grooves with smooth-bottomed surface, enlarged and U-shaped in cross section, branching may be present	de Araújo-Júnior et al. (2017)	Large-sized canid *Protocyon troglodytes*	*Glyptotherium* sp.	Late Pleistocene-Holocene	Lajedo da Escada locality	Brazil
Machichnus harlandi	Isolated, systematically recurring, scratches, some longitudinally striated with transverse cross section that resembles the letter W	Chumakov et al. (2013)	Probably fish	Phosphatic pebble	Late Cretaceous	"Cambridge Greensand"	England
Machichnus jeansi	Deep thin parallel scratches, narrowing to one end	Chumakov et al. (2013)	Probably fish	Phosphatic pebble	Late Cretaceous	"Cambridge Greensand"	England

Ichnotaxon	Morphology	Author	Producer	Substrate	Age	Stratigraphic unit	Location
Machichnus multilineatus	Shallow, serial parallel or subparallel, oriented perpendicular to substrate edge, arcuate in cross section, representing gnawing (rasping) traces. *M. multilineatus* has longitudinally striated grooves	Mikuláš et al. (2006)	Rodent (beaver), crocodile	Not specified	Early Miocene	Ahníkov locality	Czech Republic
Machichnus normani	Two parallel series of short scratches consisting of tens of subparallel striae with minor crosscutting and V cross section	Chumakov et al. (2013)	Probably fish	Phosphatic pebble	Late Cretaceous	"Cambridge Greensand"	England
Machichnus regularis (type ichnospecies)	Shallow, serial parallel or subparallel oriented, perpendicular to substrate edge, arcuate in cross section, representing gnawing (rasping) traces. *M. regularis* has grooves with smooth surface	Mikuláš et al. (2006)	Rodent (beaver), crocodile	Not specified	Early Miocene	Ahníkov locality	Czech Republic
Mandaodontites coxi	Imprint of partial arcuate dentition with round tooth impressions	Cruickshank (1986)	Archosaur	Dicynodont	Middle Triassic	Manda Formation	Ruhuhu Valley, Tanzania
Nihilichnus nihilicus	Isolated or grouped tooth impressions	Mikuláš et al. (2006)	Amphicyonidae (type)	Carnivores, herbivores	Early Miocene (type) Late Cretaceous	Ahníkov locality (type)	Czech Republic (type) Alberta, Canada
Osculichnus labialis (type ichnospecies)	Bilobate mounds, generally elliptical or crescentic in outline, having a smaller and a larger, lip-like lobe separated by undulate furrow	Demírcan and Uchman (2010)	Fish	Lithic	Eocene-Ologocene	Mezardere Formation	Thrace Basin, Turkey
Osculichnus tarnowskae	Bilobate pit, mostly elliptical or crescentic in outline, having a smaller and a larger lobe separated by an undulate furrow. Some specimens have a deeply accurate line or more often a trapezoidal depression is present instead the line. The surface inside the pit is undulating with additional wrinkles	Szrek et al. (2016)	Dipnorhynchid lungfish	Lithic	Early Devonian	Winna Formation	Holy Cross Mountains, Poland
Osculichnus tepitsin	Lenticular in outline, with two elongate lip-like lobes, separated by a M-shaped elongate furrow. Differ from other ichnospecies in having an elongate, nearly sub-rectangular, lower jaw lobe, with fusiform lateral ends and upper jaw lobe with a ventral convex projection in its medial portion. Two short, sub-triangular, maxillary barbel impressions	Rodríguez-de la Rosa et al. (2021)	Benthic feeding fish	Lithic	Early Cretaceous	San Juan Raya Formation	Puebla, Mexico
Piscichnus waitemata	Bowl-shaped depressions filled with sediment, sub-elliptical to circular in outline, with the longer axis of the ellipse or radius ranging from 5 to 45 cm in length. Outline is mostly regular, sharp and smooth. Depressions are usually up to 15 cm deep, exceptionally up to 35 cm deep	Gregory (1991)	Batoid	Lithic	Miocene	Waitemata Group	Northland, New Zealand

within a dentalite on the pterosaur *Anhanguera* sp. from Brazil (Buffetaut et al., 2004; Kellner, 2004).

Late Cretaceous marine dentalites are nearly global in their distribution, present in New Zealand, Australia, Japan, Italy, France, Germany, Belgium, Netherlands, Sweden, Jordan, Angola, Mali and Chile. However, the vast majority of occurrences are from the Western Interior of the USA and Canada. A wide range of taxonomic groups preserve dentalites, but the most characteristic group from the Late Cretaceous is the marine lizards, the mosasaurs. Dentalites produced by sharks, notably *Squalicorax* sp. and *Cretoxyrhina*, become abundant in the Late Cretaceous (e.g., Schwimmer et al., 1997; Everhart, 2005c), and this trend extends into the Cenozoic.

There are 20 records of dentalites on large chondrichthyans and teleosts from the Late Cretaceous, including on specimens of *Cretoxyrhina mantelli*, *Eumylodus laqueatus*, *Xiphactinus audax* and *Pachyrhizodus caninus* (Shimada, 1997; Schwimmer et al., 1997; Shimada and Everhart, 2004; Cicimurri et al., 2008; Amalfitano et al., 2019). One of these specimens is from Italy, and the remainder are from the USA. Of the identified tracemakers, 16 represent *Squalicorax* sp., and one is *Cretoxyrhina mantelli* (Table A.1).

Published Late Cretaceous dentalite records on marine turtles number about 23 (Table A.1). These include single occurrences from Italy, Angola, Jordan and The Netherlands, with the remainder from the USA (Mulder, 2003a; Kaddumi, 2006; Mateus et al., 2012; Amalfitano et al., 2017; Fig. 6). All dentalites on Jurassic turtles are attributed to crocodylomorphs. Late Cretaceous dentalites include two or three attributed to crocodylomorphs, four or five to mosasaurs and 17 to sharks, principally *Squalicorax* with a few attributed to *Cretoxyrhina* or other taxa (Table A.1). Marine crocodylomorphs are less common in the Late Cretaceous, and there are only three examples with dentalites from Mali, France and the USA, and the two identified tracemakers are selachians (Hua et al., 2007; Boles and Lacovara, 2013; Hill et al., 2015).

There are more than 50 documented examples of dentalites on Late Cretaceous mosasaurs (Fig. 6: Table A.1). The majority of the specimens are from the United States, but they also are present in The Netherlands, Belgium, Germany, Spain and Angola (Bardet et al., 1998; Dortangs et al., 2002; Corral et al., 2004; Lingham-Solar, 2004; Rothschild et al., 2005; Strganac et al., 2015; Fig. 5). There are 10 examples of dentalites on mosasaurs produced by mosasaurs, some due to presumed intraspecific head biting (e.g., Rothschild and Martin, 1993; Everhart, 2008; Carr et al., 2020). There are approximately 40 examples attributed to sharks, about a quarter of these produced by *Squalicorax* and several by *Cretoxyrhina,* but many are attributed to undetermined selachians (e.g., Schwimmer et al., 1997; Everhart, 1999; Konuki, 2008).

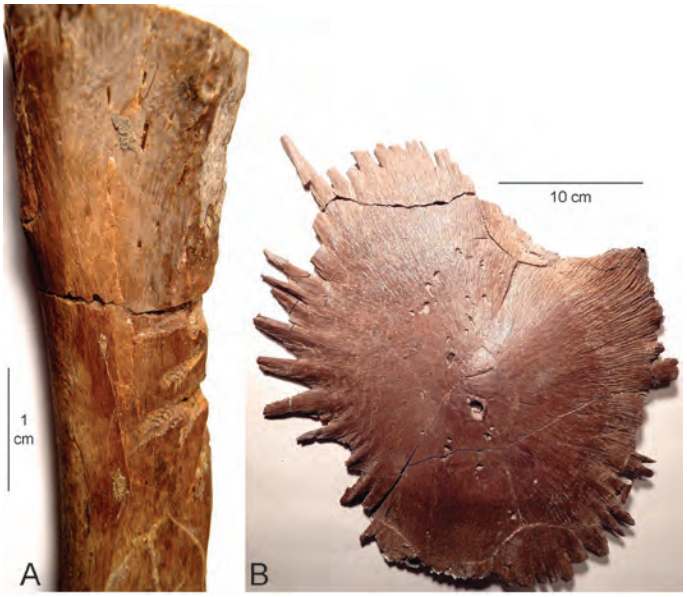


FIGURE 6. Some Late Cretaceous dentalites from marine strata of Kansas, USA. **A,** Proximal end of mosasaur rib with characteristic serrated dentalites (*Linichnus serratus*) produced by *Squalicorax* sp. (Everhart, 2017, fig. 6.13). **B,** Left hyoplastron of the marine turtle *Protostega gigas* (FHSM VP-17979), in ventral view, from Santonian chalk, preserving mosasaur dentalites (Everhart, 2017, fig. 6.13). Photographs courtesy of Michael Everhart.

There are 14 reports of dentalites on plesiosaur bones, half from the USA and the others from Sweden, Japan, Chile, Argentina and New Zealand (Sato et al., 2006; Barnes and Hiller, 2010; Einarsson et al., 2010; Shimada et al., 2010; Kubo et al., 2012; Otero et al., 2014; Araújo et al., 2015; Table A.1). The majority of specimens preserve dentalites produced by sharks, primarily *Squalicorax*, with two examples of *Cretoxyrhina* (e.g., Schwimmer et al., 1997; Everhart, 2005a; Araújo et al., 2015). There is one report of a mosasaur-produced dentalite on a plesiosaur (Einarsson et al., 2010), and two plesiosaur skeletons that record dentalites derived from both a mosasaur and one or more selachians (Konuki, 2008; Barnes and Hiller, 2010).

Six dinosaur specimens that preserve dentalites have been recovered from marine strata in the USA – four hadrosaurs, a nodosaur, an ornithomimosaur and another theropod (Schwimmer et al., 1997; Everhart and Hamm, 2005; Everhart and Ewell, 2006; Schein and Poole, 2014; Brownstein, 2018; Brownstein and Bissell, 2021). All but the theropod, whose dentalite is attributed to a crocodylomorph, were bitten by sharks. Two specimens of the pterosaur *Pteranodon* preserve dentalites produced by *Squalicorax* (and a small fish) and *Cretoxyrhina* (Konuki, 2008; Ehret and Harrell, 2018; Hone et al., 2018a, b). There is one record of dentalites on the bird *Hesperornis* produced by a polycotylid plesiosaur (Martin et al., 2016).

Nonmarine

Although there is only a small data set, it seems that dentalites are relatively less common in the Paleozoic than the Mesozoic (Fig. 5; Table A.2). We posit that this may be caused by several factors that distinguish most Mesozoic vertebrate predators from most Paleozoic vertebrate predators, including: (1) the evolution of laterally compressed teeth in terrestrial predators, which would penetrate through soft tissue to bone more effectively; (2) the development of a more upright gait among predators that would provide for more three dimensional predation – more opportunity for biting the dorsal as well as the lateral regions of prey; and (3) increased body size of prey that would invite more extensive scavenging of carcasses than is feasible with small-bodied prey.

There are few unambiguous reports of dentalites from the nonmarine Early and Middle Triassic. Modesto and Botha-Brink (2010) described a possible puncture on the scapula of a juvenile *Lystrosaurus* from the Early Triassic of South Africa. Fernandez et al. (2013) reported possible dentalites on the temnospondyl *Broomistega putterilli* from a burrow, also in the Early Triassic of South Africa. Cruickshank (1986) proposed the first ichnotaxonomic name for a vertebrate dentalite, *Mandaodontites coxi* for the imprint of a partial dental arcade with round tooth impressions (Table 2). This dentalite, from the Middle Triassic of Tanzania, is on a dicynodont bone and is attributed to an archosaur.

There are a large number of reports of Late Triassic dentalites from a wide range of taxa across a broad geographic area (North and South America and Europe), although they are never abundant in any given fossil assemblage (Fig. 5).

The extent of the dentalite record thus broadly parallels that of the osseous record, with many more specimens known from the Late Triassic than in the earlier part of the period. The prevalence of dentalites correlates to a marked increase in the diversity of taxa with dorsal armor in Late Triassic nonmarine environments (non-archosaurian archosauriforms [*Vancleavia*], pseudosuchians [*Revueltosaurus*], aetosaurs, phytosaurs, paracrocodylomorphs, crocodylomorphs and turtles). Hunt et al. (2018) recently reviewed the record of Late Triassic dentalites.

The only record of dentalites on a Late Triassic amphibian is a clavicle fragment of *Koskinonodon perfectum* from New Mexico that preserves two rows of tooth marks made by blade-like and rounded teeth (Rinehart et al., 2006). Rinehart et al. (2006) named these dentalites *Heterodontichnites hunti* and attributed them to a phytosaur. Dentalites on several phytosaur skulls of *Nicrosaurus* and *Pseudopalatus* in North America and Europe represent intraspecific head biting, as occurs in modern crocodylians (Abel, 1922a, b; Camp, 1930; Ruben, 1990). There are only two reports of dentalites on aetosaurs. Both specimens are on the aetosaurs *Typothorax* and *Desmatosuchus* from the southwestern United States (Zeigler et al., 2002; Drymala and Bader, 2012).

Dentalites on terrestrial carnivores include two incomplete femora of paracrocodylomorphs ("Rauisuchia") from northern New Mexico, USA (Drumheller et al., 2014), with the dentalites interpreted to be from phytosaurs. A humerus of the holotype of the paracrocodylomorph *Postosuchus kirkpatricki* preserves dentalites of unknown origin (Weinbaum, 2013). The holotype skeleton of the crocodylomorph *Dromicosuchus grallator* from North Carolina, USA, preserves damage to the cervical area and mandible attributed to the paracrocodylomorph whose skeleton was found immediately above it, and it is inferred that the two animals died and were buried together during the act of predation (Sues et al., 2003). Sereno and Novas (1994) described healed intraspecific bite marks on the saurischian *Herrerasaurus.*

The majority of dentalites described from the Late Triassic occur on dicynodont skeletons, which are always the largest bodied herbivorous taxa in their faunas (in contrast, they are not often registered on the bones of prosauropod dinosaurs, which dominate vertebrate faunas in certain environments/geographic locations). A femur of a dicynodont similar to *Ischigualastia* from New Mexico, USA, has multiple dentalites that are tooth marks of a phytosaur assigned to *Heterodontichnites hunti* (Lucas and Hunt 1993; Hunt and Lucas, 2014b). Budziszewska-Karwowska et al. (2010) described bite marks on a dicynodont tibia from Poland. The bone has longitudinal dentalites on the anterior side of its shaft, as well as a row of small oval pits that are interpreted to represent the scavenging of more than one carnivore.

Elsewhere in southern Poland, there are six small dicynodont bones with dentalites (Table A.2). These traces were assigned to the dentalite ichnotaxa *Linichnus serratus, Knethichnus parallelum* and *Nihilichnus nihilicus,* and attributed to theropod dinosaurs (Dzik et al., 2008; Niedźwiedzki et al., 2010). Dentalites also occur on ribs of the dicynodont "*Jachaleria" candelariensis* and other dicynodonts from Brazil (Braunn et al., 2001; Vega-Dias and Schultz, 2007). Niedźwiedzki et al. (2010) suggested that dentalites on dicynodont bones indicate that an increase in the size of dicynodonts through the Late Triassic may have been driven by selection pressure to reach a size refuge from early dinosaur predators.

Other dentalites on herbivore bones include the topotype of the pseudosuchian *Revuelosaurus callenderi* that preserves dentalites (gnaw marks: Hunt et al., 2005c; Hunt and Lucas, 2014b). Müller et al. (2015) described dentalites on bones of the traversodontid cynodont *Exaeretodon*, from Brazil, which were attributed to an ecteniniid cynodont. Romo-de-Vivar-Martínez et al. (2017) reported a pathology in the rhynchocephalian *Clevosaurus brasiliensis*, also from Brazil, that resulted from injuries (including bites) produced during intraspecific fights. Holgado et al. (2015) recognized dentalites that were produced by fish on a skeleton from Italy of a protorosaurian within a regurgitalite.

The Jurassic and Cretaceous have nonmarine faunas dominated by dinosaurs that yield most of the described dentalites (Table A.2). The Jurassic and Cretaceous share with the Triassic a pattern of an increasing volume of dentalites towards the end of each period, reflecting the increase of preservation of nonmarine vertebrate specimens. Throughout the Mesozoic, the majority of nonmarine dentalites are from North America. Hunt (1984, 1987) predicted that dentalites would be more rare on dinosaur bones than on mammal bones because non-avian theropods lacked the dentition or jaw mechanics to manipulate and modify bones in a similar manner. Fiorillo (1991a) validated this hypothesis by demonstrating that dinosaur faunas exhibited 4% or less of bones with dentalites, whereas in the mammal faunas he studied the percentages varied from 13.1 to 37.5% (but see Drumheller et al., 2020, for a notable exception).

Dentalites are rare in the Early Jurassic, but include occurrences of a crocodylomoprh bite on a prosauropod bone from China (Xing et al., 2018) and a theropod bitten by a theropod from Antarctica (Hammer and Hickerson, 1993). There are no reports of dentalites from the Middle Jurassic, which in large part probably reflects the paucity of nonmarine faunas of that age.

The Late Jurassic has a record of dentalites that is fairly diverse taxonomically and geographically, although it is dominated by specimens associated with sauropods from North America (Table A.2). Two turtles from Germany preserve dentalites, one produced by a theropod and one by a crocodylomorph or a theropod (Joyce, 2000; Karl, 2012). The remaining Late Jurassic dentalites are registered on dinosaur bones. There are four records of dentalites from large theropods. Specimens of *Sinraptor dongi* from China and *Allosaurus* from the United States preserve cranial or mandibular dentalites that probably resulted from intraspecific combat (Gilmore, 1920; Tanke and Currie, 1998). Another specimen of *Allosaurus* preserves a pubic foot bitten by *Ceratosaurus* or *Torvosaurus* (Chure et al., 1998). Augustin et al. (2020a, b) described dentalites of a metriacanthosaurid and of a mammal, respectively, on different mamenchisaurid sauropod dinosaur specimens from China.

Cetiosauriscus greppini from Switzerland and *Europasaurus holgeri* from Germany are sauropods with dentalites produced by the huge crocodile *Machimosaurus* and a small crocodylomorph or shark, respectively (Meyer and Thüring, 2003; Slodownik and Wings, 2011; Wings, 2015a). Osborn (1904) first reported dentalites on a sauropod from the Upper Jurassic Morrison Formation of the western USA. Subsequently, dentalites have been described from many taxa from the Morrison, including the sauropods *Camarasaurus*, *Apatosaurus*, *Diplodocus* and a brachiosaur (e.g., Osborn, 1904; Mathew, 1908; Jensen, 1988; Chure et al., 1998; Jacobsen, 1998; Hunt et al., 1994b; Myers, 2004; Kirkland et al., 2005; Jennings and Hasiotis, 2006; Myers and Storrs, 2007; Bader et al., 2009; Storrs et al., 2013; Hone and Chure, 2018). Virtually all of these dentalites are attributed to theropods, in general, and most to *Allosaurus,* in particular (e.g., Osborn, 1904; Mathew, 1908; Chure et al., 1988; Jennings and Hasiotis, 2006). Dentalites on the holotype skeleton of *Camarasaurus lewisi* may pertain to *Torvosaurus* (Jensen, 1988; Hunt et al., 1994b). There are only single occurrences of dentalites on other Morrison herbivorous dinosaurs – the ankylosaur *Mymoorapelta maysi* and the stegosaur *Stegosaurus* (Carpenter et al., 2005; Kirkland et al., 2005).

It is notable that, during the Jurassic, dentalites attributed to crocodylomorphs are restricted to small-bodied tetrapods such as turtles (e.g., Karl and Tichy, 2004), with only two possible associations with sauropods (Meyer and Thüring, 2003; Bader et al., 2009). One of these is attributed to *Machimosaurus,* the largest crocodyliform of the Jurassic, with a body length of up to approximately 6.9 m (Young et al., 2016). While some species of this genus were more marine, the Late Jurassic *M. mosae* was adapted to a semi-aquatic lifestyle (Young et al., 2014).

There is a time interval from the beginning of the Jurassic until the Early Cretaceous, possibly the Aptian, when there are no known large, semi-aquatic predators. In the Late Triassic, phytosaurs such as *Smilosuchus gregorii* (Camp, 1930; Long and Murry, 1985) had a body length longer than that of contemporaneous terrestrial tetrapods. Prosauropods were longer, but apparently were geographically and ecologically separated from phytosaurs. However, after the extinction of the phytosaurs (an earliest Jurassic event: Lucas and Tanner, 2018), no semi-aquatic predators were more than half the length of the largest associated terrestrial predators or herbivores until the Cretaceous. As Young et al. (2016, p. 11) noted, "it is unclear whether *Machimosaurus rex* (~7.15 m) was the largest crocodylomorph of the pre-Aptian Early Cretaceous, as the ages and body sizes of the giant pholidosaurids *Sarcosuchus hartti* (Marsh, 1869) and *Chalawan thailandicus* (Buffetaut and Ingavat, 1980) are uncertain." By the Aptian-Alban, large crocodylomorphs such as *Sarcosuchus* (Sereno et al., 2001) and large, semi-aquatic theropods such as *Suchiomimus* and *Baronyx* entered this niche. We term this interval without large semi-aquatic predators the "SAP (semi-aquatic predator) Gap." The prevalence of theropod footprints on lake margins (Hunt and Lucas, 2007b; Milner and Kirkland, 2007) and biomechanical data (Molnar, 1973; Bakker and Bir, 2004; but see Yun, 2019) suggest that terrestrial non-avian dinosaurs may have partially exploited this niche during the SAP Gap. However, the paucity of dinosaur dentalites on either turtles or crocodiles in the Mesozoic suggests otherwise (Table A.2)

Early Cretaceous dentalites are less numerous than those from the Late Jurassic and include traces on a turtle from France and on crocodyliforms from Spain and England, all produced by crocodyliforms, with most attributed to goniopholidids (Andrade et al., 2011; Buscalioni et al., 2013; Ristevski et al., 2018; Gônet et al., 2019; Table A.2). There are only two reports of Early Cretaceous theropods with dentalites, which are an ornithomimosaur from France and a tetanuran from Australia (Gônet et al., 2019; Poropat et al., 2019). Several ornithopod specimens preserve dentalites, including *Tenontosaurus tilletti* from the USA, *Lurdusaurus arenatus* from Niger and *Camptosaurus* and an iguanodont from Romania (Grigorescu, 1992; Taquet and Russell, 1999; Posmoşanu, 2003; Gignac et al., 2010). There are a smaller number of occurrences on sauropod specimens, including *Dongbeititan dongi* from China, a titanosauriform from Spain and an indeterminate taxon from Korea (Paik et al., 2011; Xing et al., 2012; Alonso et al., 2017). Buffetaut et al. (2004) described the oldest dentalite on a pterosaur bone, an Early Cretaceous record of a spinosaurid tooth within a dentalite.

The Late Cretaceous has the largest number of recorded dentalites from nonmarine depositional environments before the Pleistocene (Fig. 5: Table A.2). Taxa with dentalites include multiple examples of turtles and crocodylomorphs, scores of examples of non-avian dinosaurs (theropods, sauropods, thyreophorans, marginocephalians, ornithopods) as well as a pterosaur and a mammal (Table A.2). These traces have a broad geographic range in North America (Canada, USA, Mexico), South America (Argentina, Brazil), Europe (Hungary, Romania, Spain), Asia (Russia, China, Mongolia, Pakistan) and Africa (Madagascar). There are several reasons why this dataset is so large: (1) the Late Cretaceous yields the largest sample of excavated vertebrate fossils of large size before the Pleistocene; (2) the Western Interior Basin preserved large volumes of Late Cretaceous vertebrate fossils, and later tectonics, climate and human history led to large numbers of collections and studies; (3) the Taxophile Effect is a strong influence, as many bones or skeletons of dinosaurs with dentalites warrant individual papers, which skews the dataset, and the most popular dinosaurs (tyrannosaurs) have a disproportionately large literature; and (4) the large body size of many Late Cretaceous terrestrial vertebrates results in more recognition and preservation of dentalites. The large dataset demonstrates several patterns:

1. The majority of dentalites on turtles were produced by crocodylomorphs (Carpenter and Lindsay, 1980; Fiorelli, 2010; Noto et al., 2012; Botfalvai et al., 2014).
2. Most dentalites on crocodylomorphs represent instraspecific aggression or predation (Williamson, 1996; Avilla et al., 2004; De Vasconcellos and Carvalho, 2010; Codrea et al., 2010, 2012; de Araújo Júnior and da Silva Marinho, 2013; Botfalvai et al., 2014)
3. Crocodylomorph-produced dentalites are rare on bones of dinosaurs, except for examples that record biting by the giant *Deinosuchus* (Rivera-Sylva et al., 2009, 2011; Schwimmer, 2010).
4. Intraspecific head biting was common among large theropods, including tyrannosaurs (e.g., Bell and Currie, 2010; Currie and Eberth, 2010; Hone and Tanke, 2015) and abelisaurs (Rogers et al., 2004; Malkani, 2006, 2009, 2010; Brown et al., 2021a).
5. Cannibalism is demonstrable in tyrannosaurids (e.g., Dalman and Lucas, 2021; Fig. 7).
6. The most common dinosaurian substrates of dentalites are bones of hadrosaurs and ceratopsians. Jacobsen (1998) analyzed 1000 dinosaur bones from the Dinosaur Park Formation in Alberta, Canada, and recorded the highest percentage of dentalites on hadrosaurid bones (14%), whereas

FIGURE 7. Dentalites on a right femur of a tyrannosaurid (NMMNH P-25083) from the Upper Cretaceous (Campanian) De-na-zin Member, Kirtland Formation, New Mexico, USA. **A,** Femur, in anterior view. **B,** Close-up of the anterior surface of the femoral head showing dentalites (adapted from Dalman and Lucas, 2021, fig. 6).

only 5% of the ceratopsid bones showed tooth marks, and 2% of the tyrannosaurid bones. One of the most well-known examples of putative evidence of carnivore biting involves the mid-caudal neural spines of the Late Cretaceous hadrosaur *Edmontosaurus*, possibly bitten by *Tyrannosaurus* (Carpenter, 1998), but the damage is more likely due to trampling, with the putative tooth marks actually related to a pyogenic infection in which the openings allowed the discharge of pus (Tanke and Rothschild, 2014).

7. The earliest mammalian-produced dentalites occur in the Late Cretaceous and include traces on *Champsosaurus* from Canada (Longrich and Ryan, 2010), the theropods *Buitreraptor gonzalezorum* from Argentina (Gianechini and de Valais, 2016) and *Velociraptor* from Mongolia (Saneyoshi et al., 2011), the protoceratopsians *Protoceratops* and *Bagaceratops* from Mongolia (Saneyoshi et al., 2011), ornithischians from Canada (Longrich and Ryan, 2010), the mammal *Eodelphis* from Canada (Longrich and Ryan, 2010) and multiple taxa from Argentina (de Valais et al., 2012).

8. Large sample sizes of both dentalites and associated body fossils facilitate study of the producers and their behavior (e.g., Brown et al., 2021b).

Cenozoic

Marine

Marine dentalites are less common in the Cenozoic than in the Mesozoic (Fig. 5; Table A.3). The majority of examples were produced by selachians on a substrate of marine mammal bones in (decreasing order of abundance) cetaceans, pinnipeds and sirenians.

Two sawfish from the Pliocene of Italy and the USA preserve dentalites of unknown origin, and one specimen of a tuna (*Thunnus*) from the Pliocene of the USA has dentalites produced by istiophorid billfish (Purdy et al., 2001; Schneider and Fierstine, 2004; Collareta et al., 2017a). A *Carcharhinus* from the Miocene of the USA contains a conspecific tooth in a dentalite, and a *Carcharodon megalodon* from the Pliocene has a shark dentalite (Purdy et al., 2001; Godfrey, 2003).

There are only three recorded Paleogene turtles and one crocodylomorph with dentalites. An indeterminate chelonioid from the Paleocene of Denmark preserves three types of dentalites, *Nihilichnus nihilicus,* interpreted as crocodilian, *Machichnus bohemicus,* interpreted as selachian and small, circular traces from sharks or bony fish (Milàn et al., 2011). Myrvold et al. (2018) describe other Paleocene specimens from Denmark consisting of fragments of a carapace of a chelonid turtle and a hypoplastron of *Ctenochelys* cf. *C. stenoporus*, both with marks produced by a crocodilian and the former with shark dentalites. A dryosaurid from the Paleocene of Niger has dentalites of crocodylomorph origin (Martin, 2013).

There is a small but widespread record of dentalites on fossil penguin bones. These include the Eocene *Palaeeudyptes klekowskii* from Antarctica, cf. *Spheniscus* and an unidentified form from the Miocene of Argentina and Pliocene *Tereingaomis moisleyi* from New Zealand (McKee, 1987; Walsh and Hune, 2001; Cione et al., 2010; Hospitaleche, 2016). The producers of the dentalites were identified as teleost, *Galeocerdo aduncus,* cf. *Carcharhinus* and a dolphin, respectively (McKee, 1987; Walsh and Hune, 2001; Cione et al., 2010; Hospitaleche, 2016). Terrestrial carnivores also produced dentalites on penguin bones (Table A.3). A ?charadiiform bird from the Pliocene of Spain preserves dentalites attributed to a shark (Muñiz et al., 2008).

The largest number (> 40) of reports of marine dentalites from the Cenozoic relate to large, non-delphin cetaceans (Table A.3). The earliest example is the basilosaurid *Dorudon atrox* from the Eocene of Egypt that preserves dentalites attributed to *Basilosaurus isis* (Fahlke, 2012). There are currently no Oligocene records. The earliest records of odontocete (e.g., Lambert et al., 2018) and mysticete (e.g., Noriega et al., 2007; Collareta et al., 2017b) dentalites are from the Miocene, and these, and all younger examples, are attributed to sharks. About a third of all records of dentalites are merely attributed to unspecified cetaceans. The majority of Pliocene dentalites that are attributed to a specific genus are attributed to *Carcharodon* (e.g., Bianucci et al., 2002; Ehret et al., 2009; Govender and Chinsamy, 2013; Govender, 2015, 2019). There are very few reports of Pleistocene marine dentalites (e.g., Cicimurri and Knight, 2009).

Reports of dentalites on dolphins are restricted to the Oligocene, Miocene and Pliocene (Table A.3). Pervesler et al. (1995) describe a specimen from the Oligocene of Austria. The three examples from the Miocene are from the eastern United States. Specimens of *Eurhinodelphis,* a ?eurhinodelphinid, and *Hadrodelphis* preserve dentalites of sharks (Dawson and Gottfried, 2002; Godfrey, 2003; Godfrey et al., 2018). There are three Pliocene examples from northern Italy. Specimens of *Astadelphis gastaldii*, *Hemisyntrachelus cortessi* and an indeterminate taxon preserve dentalites attributed to *Cosmopolitodus hastalis* and *Carcharodon carcharias* (*Knethichnus parallelum*), respectively (Portis, 1883; Cigala-Fulgosi, 1990; Bianucci et al., 2000; Jacobsen and Bromley, 2009).

Eight pinnipeds preserve dentalites (Table A.3). A pinniped from the Miocene of the USA preserves dentalites attributed to a shark (Bigelow, 1994). Two specimens from the Miocene and Pliocene of the USA have dentalites produced by mammals, possibly a pilot whale or beluga-like cetacean, a terrestrial carnivore, a dusignathine or odobenine walrus, or a conspecific otariid (Boessenecker and Perry, 2011). Collareta et al. (2017b) described dentalites produced by *Carcharocles megalodon* on a pinniped from the Miocene of Peru. Two specimens of *Homiphoca* from the Pliocene of Spain preserve *Linichnus* produced by teleosts or small sharks (Rahmat et al., 2018; Muñiz et al., 2020). An example of *Eumetopias jubatus* from the Pleistocene of Canada yields dentalites attributed to a bull of that species (Harington et al., 2004).

There are only three records of dentalites on sirenian bones (Table A.3). The oldest are Oligocene specimens of *Halitherium schinzii* from Germany and Austria that preserve shark-produced dentalites (Pervesler et al., 1995; Diedrich, 2008). A Miocene specimen from Venezuela was also bitten by a shark (Aguilera and de Aguilera, 2004).

Nonmarine

As mammalian faunas typically yield an order of magnitude more dentalites than reptilian faunas (Fiorillo, 1991a), one would expect a very large literature on Cenozoic dentalites, particularly relative to the Mesozoic, but this is not the case (at least until the Pleistocene). It is clear that the Taxophile Effect is important in the large volume of literature on dinosaur dentalites. Many individual examples of dinosaur dentalites warrant individual papers, which is clearly not the case for Cenozoic mammals (Fig. 5; Table A.4). The volume of dentalite reports in the Pleistocene also reflects in part the Taxophile Effect relative to hominin evolution, as well as other factors, including: (1) the large volume of Pleistocene vertebrate fossils relative to earlier time periods; (2) the widespread preservation of cave faunas – large sample sizes, often accumulated by predators and carefully studied to document this, hominin fossils are sometimes present, and surface preservation of bones is very good; and (3) the ease of using modern analogues, which has promoted study. The dataset for the nonmarine Cenozoic (Table A.4) is thus the most incomplete in this study. Many pre-Pleistocene dentalites are not recorded, or the occurrences are buried within taxonomic or faunal discussions and are difficult to find.

Sinclair and Granger (1914, p. 310), who amassed important collections of early Paleocene mammals from New Mexico, USA, noted that "A quarter, at least, of the Puerco specimens, collected by the 1913 expedition, show traces of gnawing, probably by small plagiaulacids [multituberculate mammals]." In marked contrast, we have only found five other published mentions of dentalites on Paleocene mammal bones (Simpson and Elftman, 1928; Gingerich, 1987; Bloch and Boyer, 2001; Secord et al., 2002; Longrich and Ryan, 2010). In addition, the literature on Pleistocene dentalites, particularly with regard to hominins and cave faunas, is very extensive, and we have not captured all of it here. Instead, we have attempted to record the significant literature and a sampling of the remainder.

There is only one dentalite recorded from a lizard, which occurs on *Varanus* sp. from the Miocene of Greece and is interpreted to have been produced by the hyaenid *Protictitherium* (Georgalis et al., 2018). There are many reports (18) of dentalites on Cenozoic turtles and crocodylomorphs (6), and occurrences are mainly clustered in the Paleocene-Eocene and the Pleistocene (Table A.4). The majority of these dentalites are attributed to crocodylomorphs (e.g., Sawyer and Erickson, 1998; Fuentes, 2003; Njau, 2006; Mackness et al., 2010; Böhme et al, 2011; Hastings et al., 2015; Scheyer et al., 2018; Falk et al., 2019).

There are relatively few reports of dentalites on avian specimens. Occurrences include on *Cayaoa brunetti* and a penguin from the Miocene of Argentina (Cione et al., 2010; De Mendoza and Haidr, 2018) and on the ibis *Geronticus* cf. *G. calvus* from the Pliocene of South Africa (Pavia et al., 2017). The sources of the dentalites are identified as mammals or unknown. In the Holocene of New Zealand, moas were subject to predation by the eagle *Harpagornis,* producing dentalites (Farlow and Holtz, 2002).

Eocene mammals with dentalites are known in the USA and Germany, with one occurrence in France and one in England. Specimens from the United States include on the pantodont *Coryphodon,* resulting from intraspecific combat, and on the "condylarth" *Apheliscus chydaeus*, the carnivore *Viverravus* and the primate *Notharctus* (Gingerich, 1987; Lucas and Schoch, 1987; Alexander, 1992; Gingerich, 1994: Table A.4). Alexander and Burger (2001) described an unusual occurrence of a dentalite on a perissodactyl within a consumulite of the crocodilian *Pristichampsus vorax*. They also listed several primate specimens (*Notharctus*, *Omomys*) that appear to preserve raptor dentalites. The German Eocene includes the two important Lagerstätten of Messel and Geiseltal. Dentalites produced by crocodiles occur on several mammal fossils from these Lagerstätten, including equids, the ceratomorph *Lophiodon* and the primate *Europolemur* (Franzen and Frey, 1993; Franzen, 2001; Falk et al., 2019). Mammals from Quercy in France preserve dentalites produced by rodents such as *Archaeomys* (Laudet and Fosse, 2001). The rodents *Isoptychus* sp. and *Thalerimys fordi* from southern England preserve dentalites produced by the amphicyonid *Cynodictis* cf. *C. lacustris* (Vasileiadou et al., 2007, 2009).

There are multiple reports of Oligocene dentalites from the United States and one from Egypt (Table A.4). The dentalites from the USA occur on several taxa, including oreodonts, entelodonts, and *Titanotherium,* and include bite marks and evidence of gnawing (Sinclair, 1922; Scott and Jepsen, 1936; Tanke et al., 1992; Effinger, 1998; Tanke and Currie, 1998; Longrich and Ryan, 2010). Four species of primates (*Aegyptopithecus*, *Propliopithecus*) from the Fayum Formation of Egypt preserve dentalites produced by carnivore-like mammals (Gebo and Simons, 1984).

Miocene dentalites are much more widely distributed than those from the Paleogene, and they occur in Hungary, Greece, Austria, China, Uganda, South Africa, Kenya and the USA (Table A.4). The substrates for these dentalites includes rhinocerotids (Antunes et al., 2006a; Deng and Tseng, 2010), a cervid (Havlik et al., 2014), a proboscidean (Havlik et al., 2014), an equid (Diffendal, 2003), a climacoceratid (Pickford, 1996), a tragulid (Sánchez et al., 2015), camelids (Winkler, 1987; Morgan and Williamson, 2000), a primate (Zapfe, 1981) and a hominim (Gommery et al., 2007). All of the above have dentalites attributed to mammalian predators, except for the climatococeratid from South Africa that was bitten by a crocodilian. The most important study of Miocene dentalites was by Mikuláš et al. (2006; also see Ekrt et al., 2016), who studied multiple dentalites on ungulates, small mammals and carnivores and erected six ichnotaxa for these traces, which are starting to be widely used – *Nihilichnus nihilicus, N. mortalis, Machichnus regularis, M. multilineatus, M. bohemicus* and *Brutalichnus brutalis.* They attributed these ichnotaxa to squirrels, the carnivore *Amphicyon* sp. and crocodilians.

There is a smaller number of records of Pliocene dentalites. Ungulates from Italy have traces produced by the hyena *Pachycrocuta brevirostris,* and a glyptodont (cf. *Eosclerocalyptus lineatus*) from Argentina was bitten by the procyonid, *Chapalmalania* (Mazza et al., 2004; Mazza, 2006; de los Reyes et al., 2013). A Canadian mammoth was gnawed by a beaver, and a rodent from Chad was bitten by a mammalian carnivore (Harington, 1996; Denys et al., 2003). Diverse mammals from Tanzania have traces of indeterminate mammalian predators (Su and Harrison, 2008). Sahle et al. (2017) reported crocodile dentalites on diverse large mammals from Tanzania (bovids, equid, ungulate) and on *Australopithecus anamensis* and *A. afarensis* from Ethiopia.

There are large numbers of reports of dentalites from the Pleistocene from every continent, except Antarctica. Much of the impetus for the rise of interest in dentalites relates to studies focused on the taphonomy of Pleistocene hominins, in particular, which has expanded more broadly to other bone accumulating agents, notably in caves (e.g., Binford, 1981; Brain, 1981; Andrews, 1990; Hart and Sussman, 2005). Indeed, the most well-known examples of dentalites relate to Pleistocene hominins – leopard predation on *Paranthropus robustus* (Brain, 1981), eagle predation on the Taung child, *Australopithecus africanus* (Berger and Clarke, 1995), bites of *Crocodylus anthropophagus* on *Homo habilis* (Davidson and Soloman, 1990) and *Pachycrocuta brevirostris*-produced dentalites on *H. erectus* (Boaz et al., 2000).

Dentalites occur on a wide range of Pleistocene taxa. It is notable that many dentalites in the Old World are attributable to hyenas, principally *Crocuta crocuta spelaeus,* but also *Pachycrocuta brevirostris*. Cave hyena dentalites occur in England, Germany, the Czech Republic and Morocco (Buckland, 1824; Diedrich, 2011, 2012a, c, 2013), and those of the giant, short-faced hyena are present in Spain, China and Pakistan (Palmquist et al., 1996; Boaz et al., 2000; Dennell et al., 2008). There are several occurrences in Australia of dentalites of the marsupial "lion" *Thylacoleo carnifex* (Horten and Wright, 1981; Runnegar, 1983; Camens and Carey, 2013; Dortch et al., 2016). It is also notable that intraspecific dentalites occur in several Pleistocene taxa, including *Ursus spelaeus* in Spain (Capasso, 1998; Pinto Llona and Andrews, 2004; Rabal-Garcés et al., 2012), *Canis lupus* in the United States (Courville, 1953), *Smilodon fatalis* in the United States (Miller, 1980; Akersten, 1985; Rothschild and Martin, 1993), *Panthera leo spelaea* in Germany (Diedrich, 2011) and *Crocuta crocuta spelaea* in the Czech Republic (Diedrich, 2012a).

Sutcliffe (1973) first identified osteophagia in herbivorous mammals as a significant phenomenon, notably ungulates such as giraffes and some deer that chew antlers and bone, presumably for nutritional supplements. This behavior has been recognized in several Recent taxa (e. g., Haynes, 1991, figs. 4.30-31) but not yet in fossils.

Invertebrate Hard Tissue Substrate

The ichnological record of predation on invertebrates by vertebrate predators and scavengers is surprisingly small. There are, in fact, only two main taxa that have been documented in any detail: (1) predation on sessile echinoderms; and (2) predation on nektonic nautiloids and ammonoids (Table A.5).

There are three reports of dentalites, possibly produced by vertebrates, on Paleozoic crinoids from the Middle Devonian of Germany (Bohatý, 2008, 2009) and Poland (Gorzelak et al., 2011) and the early Carboniferous of the United States (Gahn, 2004). There are single examples, all from Poland, from the Middle Triassic (Salamon and Gorzelak, 2008), Late Jurassic (Lach et al., 2015) and Late Cretaceous (Salamon and Gorzelak, 2010). Crinoids have relatively massive skeletons and lack a large volume of easily digestible tissue, so they are not attractive to Recent fish (Gahn, 2004). However, since the Ordovician, crinoids have served as substrate hosts to a wide range of organisms, including brachiopods, bryozoans, corals, gastropods, ophiuroids, myzostomid annelids and clionid sponges. Thus, at least some of the dentalites on crinoids may be "collateral damage" resulting from predation on their epibionts (Gahn, 2004). Cione et al. (2010) suggested a similar origin for some dentalites on Miocene penguin bones.

Echinoids, in contrast to crinoids, appear more attractive as a food source because of their thin test and relatively more abundant soft tissue. The earliest example of a vertebrate dentalite on an echinoid is from the Middle Jurassic of Israel (Wilson et al., 2014). There are 11 reports of Late Cretaceous dentalites on echinoids from Germany and The Netherlands. The mosasaur *Prognathodon* is proposed as the producer of a dentalite from Germany (Neumann and Hampe, 2018), and the shark *Squalicorax* for another specimen from that country (Neumann, 2000). Other examples are generally attributed to indeterminate fish (e.g., Thies and Reif, 1985; Jagt et al., 2018). Current records suggest that there is great potential to find additional dentalites on echinoids.

There are three examples of dentalites on nonmarine bivalves from the Late Triassic of Poland (Gorzalak et al., 2010), and the Early Cretaceous of Spain (Bermúdez-Rochas et al., 2013) and Australia (Kear and Godthelp, 2008). Nonmarine invertebrates are much less studied than vertebrates from the same environments, so we expect more dentalites to be present but not yet documented.

A few other sessile invertebrates yield dentalites of vertebrate origin, including a Late Cretaceous rudist (Hattin, 1988), an Early Jurassic brachiopod (Tasnadi-Kubacska, 1962) and marine bivalves from the Middle Devonian (Nagel-Myers et al., 2009), Middle Jurassic (Phipps, 2008) and Late Cretaceous (Kauffman, 1972). There are only two dentalites reported from fossil coral. Galle and Mikuláš (2003) described predation of fish on rugose coral from the Middle Devonian of the Czech Republic, and Kauffman (1981) described gall-like growths on Late Pleistocene coral from Jamaica that resemble Recent examples of predation by threespot damselfish. Given the importance of predation on coral reefs by Recent vertebrates such as parrotfish (Peyrot-Clausade et al., 2000), we expect there to be many more examples of dentalites on scleractinian corals and, by analogy, in extinct coral groups (and other reef-forming invertebrates).

There are only three examples of dentalites on vagrant fossil invertebrates. Zatoń et al. (2007) and Neumann (2000) describe traces on sea stars from the Middle Jurassic of Poland and the Late Cretaceous of Germany, respectively. Bishop (1972) reported a dentalite on the crab *Raninella* from the Late Cretaceous of the United States.

Kauffman and Kesling (1960) wrote an influential paper describing putative predation on the Late Cretaceous ammonite *Placenticeras cf. P. whitfieldi* by a platecarpine mosasaur. Subsequently, there has been a large number of reports of dentalites on nautiloids and ammonoids, with the majority being of Late Cretaceous age. Older dentalites on cephalopod fossils are reported from the Late Devonian (Slotta et al., 2011), Late Mississippian (Bond and Saunders, 1989), Early Pennsylvanian (e.g., Mapes and Hansen, 1983), Early Triassic (Hoffman and Keup, 2015), Late Triassic (Tichy and Urbanek, 2004), Early Jurassic (e.g., Takeda and Tanabe, 2014), Middle Jurassic (e.g., Richter, 2009) and Early Cretaceous (Hoffman and Keupp, 2015). The inferred sources of these dentalites include teleosts (e.g., Martill, 1990), sharks (Vullo, 2011) and marine reptiles, including a nothosaur (Tichy and Urbanek, 2004). Late Cretaceous examples occur in Morocco (Gale et al., 2017), Madagascar (Hoffman and Keupp, 2015), Mexico (e.g., Ifrim, 2013) and Canada (e.g., Hewitt and Westermann, 1990). There are multiple reports from the USA, and Kauffman (1990b) mentions more than 100 specimens. One report from Mexico identifies the tracemaker as the shark *Ptychodus* (Ifrim, 2013), but the remainder are identified as being produced by mosasaurs (e.g., Saul, 1979; Tsujita and Westermann, 1998). Some sub-circular traces on Late Cretaceous ammonoids represent limpet (patellogastropod) home scars (e.g., Knsc et al., 1994), and it has been proposed that these caused all of the putative dentalites (Kase et al., 1994, 1998; Johnston et al., 1997; Seilacher, 1998). However, this seems an overstatement, and many putative dentalites are correctly identified as such (Tsujita and Westermann, 2001; King, 2009; Mapes and Chaffin, 2003). Other dentalites occurring on nektonic invertebrates include examples of a foraminiferan with parottfish traces from the Eocene of India (Syed and Sengupta, 2019) and a Late Cretaceous squid with marks of the mosasaur *Tylosaurus proriger* (Stewart and Carpenter, 1990).

Tischlinger (2001) described the only vertebrate dentalites on flying insects. Two specimens of insects, the odonatan *Cymatophlebia longialata* and the neuropteran *Archegetes neuropterum*, have damage to their wings, including absence of a wingtip that he attributed to pterosaur predation.

There is a distinct paucity of dentalites attributed to teleosts, even though many Recent teleost taxa feed on a variety of invertebrates (e.g., Backus, 1964; Brown-Sarracino et al., 2007). However, it is difficult to identify teleost dentalites because there is so little known about fish traces, notably in temperate areas (Cione et al., 2010)

Coprolite Substrate

Coprolites containing dentalites have only been recognized in the past decade, principally by Godfrey and co-workers. They are all from aquatic environments, mainly marine, and all but one is definitely Cenozoic in age. Hunt et al. (2018) erected the *Gaspeichnus* ichnofacies for traces on a coprolitic substrate, which also include footprints and borings.

Godfrey and Smith (2010; Fig. 8) first described dentalites on coprolites of unknown origin, which derive from the Miocene Calvert Cliffs of the United States. They describe two coprolites with dentalites produced by sharks that could have resulted from: (1) aborted coprophagy, (2) benthic or nektonic exploration, or (3) predation. Moore (2021) recently described another coprolite from this location. Godfrey et al. (2020) record a Paleocene crocodile coprolite from the United States with dentalites made by a chondrichthyan, actinopterygian, or small crocodilian.

Godfrey and Palmer (2015) described a coprolite bitten by the gar *Lepidosteus* from South Carolina, USA, from a mixed lag of Late Cretaceous, early Paleocene and Plio-Pleistocene taxa. Frandsen (2020, p. 25-26, 28, 31, 33, 36, 39) illustrated seven additional coprolites with putative dentalites. Godfrey and Frandsen (2016) described another dentalite of *Lepidosteus* from another locality in South Carolina in a coprolite that

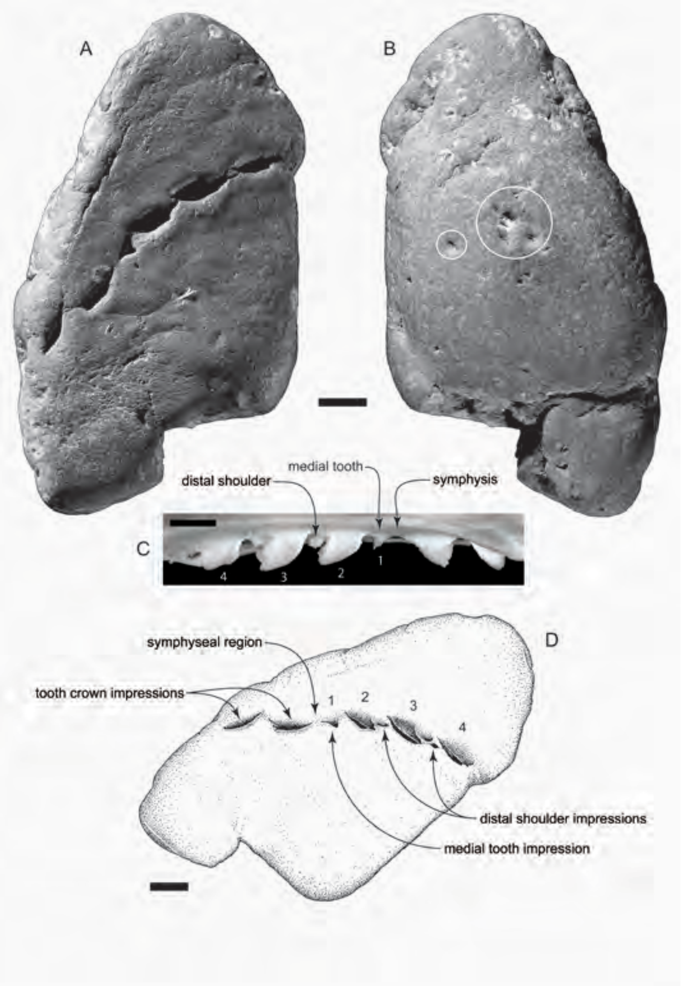


FIGURE 8. Coprolite (CMM-V-2244) from the Miocene of Maryland, USA with dentalites of six tooth marks, possibly produced by a tiger shark (cf. *Galeocerdo* sp.). **A,** Flattened lower surface with six deeper tooth impressions. **B,** Convex upper surface showing at least five shallower tooth impressions. **C,** Silicone rubber cast of the tooth impressions in labial view. Cast teeth 1–4 in C correspond to numbered impressions 1–4 in D. **D,** Drawing of the flattened lower surface of CMM-V-2244. Scale bars equal 10 mm (Godfrey and Smith, 2010, fig. 2). Figure courtesy of Stephen Godfrey.

might pertain to a crocodile. Subsequently, Frandsen and Godfrey (2019) illustrated two coprolites within the jaws of an articulated specimen of the gar *Atractosteus simplex* from the lacustrine Eocene Green River Formation of Wyoming, USA. A crocodilian coprolite from the Paleocene of Maryland, USA, exhibits dentalites of unknown origin (Godfrey et al., 2020).

Frandsen (2020) illustrated two Pre-Cenozoic coprolites with putative dentalites. However, a specimen from the Late Triassic of New Mexico, USA, has longitudinal striations that we identify not as dentalites but rather the characteristic surface texture of *Alococoprus* (Frandsen, 2020, p. 22). Thus, the oldest of his specimens that we concur is a dentalite is from the Early Jurassic of Lyme Regis, England, with conical depresssions (Frandsen, 2020, p. 76).

Dentzien-Dias et al. (2018) described teleost (Serrasalmidae?) dentalites on coprolites from the Miocene of Venezuela. A coprolite of a carnivorous fish, likely a shark, from the Miocene of Italy contains dentalites possibly attributed to both selachians and teleosts (Collareta et al., 2019b). Dentzien-Dias et al. (2021) described multiple dentalites on fish coprolites from the Eocene of Virginia, USA. Cueille et al. (2020) described 17 coprolites from the Rhaetian of the United Kingdom with probable dentalites. Rozada et al. (2021) recently noted a coprolite from the Early Cretaceous of France with a possible shark dentalite.

Lithic Substrate

A variety of vertebrate behaviors involve direct interaction between mouth parts and the lithic substrate, notably feeding by aquatic fish and tetrapods, feeding by aerial birds and pterosaurs and digging by rodents. Several Recent vertebrates substantially disturb the substrate during aquatic feeding, including chondricththyans (e.g., Common Skate *Raja erinacea*, Bat Ray *Myliobatis californicus*: Cook, 1971), actinopterygians (e.g., Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*: Armitage and Gingras, 2003; Pearson et al., 2007), osteichthyans (e.g., Goat fish – Mullidae: Geister, 1998; flatfish such as California Halibut *Paralicthys californicus*: Cook, 1971), pinnipeds (e.g., walrus *Odobenus rosmarus*: Kastelein et al., 1989), cetaceans (e.g., Grey Whale *Eschrichtius robustus*: Nelson et al., 1987, 1992) and otters (e.g., Sea Otter *Enhydra lutris*: Calkins, 1978).

The oldest marine traces attributed to vertebrate feeding were described by Fischer (1978) from the Ordovician Harding Sandstone of Colorado, USA. He erected the ichnogenus *Agnathichnus* for what he interpreted to be the feeding trace of a jawless fish. However, one of us (SGL) is revising this ichnofauna and considers *Agnathichnus* to be a synonym of *Treptichnus*, a zig-zag style of arthropod feeding trace.

Osculichnus tarnowskae is an ichnotaxon from the Early Devonian of Poland. It consists of a bilobate, generally elliptical, epichnial pit in the substrate that was produced by a fish probably feeding on bivalves, polychaetes and arthropods (Szrek et al., 2016). The producer was probably a lungfish similar to *Dipnorhynchus* (Szrek et al., 2016). *Osculichnus* also occurs in the Late Devonian of China (Fan et al., 2019), and the type ichnospecies, *O. labialis*, is from the late Eocene-early Oligocene of Turkey (Demírcan and Uchman, 2010; 2016; Table 2). *Osculichnus* and cf. *Osculichnus* occur in the Lower Jurassic of Poland and the Upper Jurassic of Spain (Pieńkowski, 1985; Rodríguez de la Rosa et al., 2021). Rodríguez de la Rosa et al. (2021) described *Osculichnus repitsini* from the Lower Cretaceous of Mexico as well as *Daandavichnus batoideum*, a complex ovoid trace they identified as a batoid feeding trace.

Geister (1998) described sigmoidal epichnial grooves from Early Devonian limestones of the Czech Republic that are 20 to 35 cm long, 3 to 5 cm wide, and less than 3 cm deep. He interpreted these as feeding traces made by jawless or jawed fishes feeding on the muddy sea floor.

Large furrows, up to 60 cm wide, up to 30 cm deep and up to 9 m long, are present on a Middle Jurassic bedding plane of limestone in northern Switzerland (Geister, 1998). There are three morphologies of trace. Geister (1998) suggested that the traces more than 40 cm wide were produced by the snout of the pliosaur *Liopleurodon*, and the smaller ones, less than 15 cm wide, could have been made by plesiosauroids or by the narrow pointed snouts of ichthyosaurs.

Calvo et al. (1987) named *Megaplanolites ibericus* for a large tubular trace fossil from the Late Jurassic of Spain. They interpreted it as a feeding or locomotion trace of a large worm, but Geister (1998) suggested that it represents a vertebrate feeding trace.

Thousands of ovate depressions on bedding planes of Late Cretaceous strata from Spain had been previously identified as dinosaur tracks but were re-interpreted by Martinell et al. (2001) as traces of the feeding activity of rays or other fish with similar behavior. Martinell et al. (2001) assigned them to *Piscichnus*.

Poropat et al. (2021) describe two morphologies of trace fossil from the Cenomanian–?lowermost Turonian Winton

Formation of Australia, which they attribute to feeding traces of fish. One morphotype consists of two indentations and superficially resembles feeding traces made by the Recent sturgeon *Acipenser oxyrinchus* (Pearson et al., 2007). There are multiple examples of a U-shaped trace that are interpreted as snout marks of a lungfish (Poropat et al., 2021).

Undichna is a common sinuous trace produced by a swimming fish (Minter and Braddy, 2006). Martin et al. (2010) described a specimen of *Undichna* cf. *simplicatas* from the lacustrine Green River Formation (early Eocene) of the western United States that preserves overlapping ellipsoids along the midline. These were interpreted as being produced by the ventral mouth of *Notogoneues osculus* during feeding (Martin et al., 2010).

Howard et al. (1977) described how rays excavate large pits in shallow estuarine conditions to search for infaunal food sources. They described how the excavation was accomplished by flapping the "wings" to hydraulically erode the sediment. Howard et al. (1977) noted Pleistocene and Cretaceous examples of this trace. However, Gregory et al. (1979) describe how the New Zealand eagle ray, *Myliobatis tenuicaudatus*, hydraulically excavates much of its vertical-sided feeding depression by the action of water jetted downwards through the mouth and/or gill clefts and noted that other rays probably use a similar methodology. In this case, the depression would arguably represent a dentalite. Gregory (1991) named this trace *Piscichnus waitemata*. However, *Piscichnus* is a trace often attributed to the shallow, disc-shaped nests that many fish excavate in sediment, so most of its records are not dentalites (e.g., Feibel, 1987). Uchman et al. (2018) described *Piscichnus waitemata* from the Pliocene of Santa Maria Island (Azores Archipelago), which they interpreted to have been produced by ray fishes hunting for polychaetes, crustaceans and bivalves. Belvedere et al. (2011) described more than two hundred crescentic traces from the Middle Eocene of Italy that they assigned to *Piscichnus* isp. and interpreted as the feeding traces of sturgeon-like fishes rather than rays or flat fishes.

Excavation by hydraulic jetting through the oral cavity is also used by walruses. Gingras et al. (2007) described Pleistocene pits from the northwestern United States that they attributed to walruses feeding on deep-burrowing bivalves. Walruses root for prey with their snouts and emit a jet of water that liquefies the bottom sediments where a bivalve has burrowed (Gingras et al., 2007).

Both birds and pterosaurs produced feeding traces on substrate. Erickson (1967) first described dabble (surface grazing) marks associated with a trackway of *Presbyornis* from the Eocene of the United States (also see Lockley and Hunt, 1995, p. 253; Hunt and Lucas, 2007a, fig. 3). Subsequently, Falk (2004; Falk et al., 2010, 2014) described a wide range of avian feeding interactions with the substrate from the Early Cretaceous of Korea, including pecking, probing and scything traces.

Analogous feeding traces have also been attributed to pterosaurs. There are several occurrences of shallow, paired, rounded impressions interpreted as beak traces associated with pterosaur tracks from the Middle Jurassic of Utah (Lockley and Wright, 2003), the Early Cretaceous of England (Wright et al., 1997) and the Late Cretaceous of Utah (Parker and Balsey, 1989; Wright et al. 1997; Mazin et al., 2003). Sinuous traces from the Late Cretaceous of Utah and Mexico, some originally interpreted as tail drags, may represent sweeping movements of pterodactyloid jaws (Lockley and Wright, 2003; Rodriguez-de la Rosa, 2003).

Several rodents utilize their dentition, as well as their claws, for the excavation of burrows. Good examples have been described from the Late Oligocene and Miocene of Nebraska and Colorado in the United States. Tooth marks of *Palaeocaster fossor* occur in the spiral *Daimonelix* burrows from the late Oligocene-early Miocene of Nebraska (Martin and Bennett, 1977; Yelinek, 2005). Gobetz and Martin (2006) described dentalites of a gopher-like rodent, possibly *Gregorymys*, from the Early Miocene of that state. Late Miocene burrows from Nebraska produced by marmotine ground squirrels contain paired striations, which are common dentalites in rodent burrows (Joeckel and Tucker, 2013). Gobetz (2006) and Hembree and Hasiotis (2008) described other burrows of mylagaulids with dentalites from the late Miocene of the adjacent state of Colorado. One of us (SGL) is describing Pliocene rodent burrows from New Mexico with dentalites.

Geophagy is the consumption of soil or minerals (including salt licks) and is practiced by many Recent animals, principally herbivores, including ungulates, seed-eating birds and human and non-human primates (Jones and Hanson 1985; Gilardi et al., 1999; Izawa, 1993; Pryce, 1994; Abrahams and Parsons, 1996; Mahaney et al., 1996; Diamond et al., 1999; Abrahams, 2003; Tobler et al., 2009). There are multiple potential advantages to geophagy, principally related to mineral supplementation or alleviating gastrointestinal disorders (e.g., adsorb toxins, adjust gut pH, antidiarrhoea, counteract the effects of endoparasites, protect the gastrointestinal lining from biological and chemical damage) (Gilardi et al., 1999; Krishnamani and Mahaney, 2000; Abrahams, 2003). Geophagy should result in dentalites in non-primates, and these could be recognized in the fossil record.

Some Recent terrestrial vertebrates, including bears and raccoons, use mechanical excavation (i.e., digging into the sediment) to feed (Gingras et al., 2007). Currently there is no described fossil record for this behavior.

Plant Substrate

Specialized herbivorous vertebrates date back to the Pennsylvanian (Lucas et al., 2018), and Paleozoic-Cenozoic invertebrate predation on plants has been widely documented (e.g., Scott, 1991; Labandeira, 1998), but there are very few examples of vertebrate dentalites on vegetation, and all are from the Cenozoic. All dentalites are preserved on the more dense portions of plants such as wood and nuts.

There are few well documented Mesozoic examples of dentalites on plant material. However, Lewis (2011) described fossil vines associated with hadrosaur bones from the Late Cretaceous of Texas, USA, with damage indicating that the branches were dominantly removed by shearing consistent with herbivory. In addition, the internal anatomy of the vines shows tracheid-filled false rings that are generally caused by mechanical removal of a portion of the plant during life. Manchester et al. (2010) described palm seeds in the same area associated with bones of juvenile ceratopsian and hadrosaurian dinosaurs and interpreted them as food debris.

Dentalites produced by rodents occur on seeds and nuts from the Eocene to the Pleistocene (Collinson, 1990). Collinson and Hooker (2000) recorded gnaw marks on late Eocene seeds of *Stratiotes* from southern England. Kodaira (1921) and Yoshikawa (2000) described dentalites produced by mice on nuts of *Juglans* spp. from the Pleistocene of Japan. The latter example was attributed to *Apodemus speciosus* (Yoshikawa, 2000). Gregor (1982) described another example of rodent activity in the stripping of Miocene *Aruacaria* cones.

Beavers actively modify woody tissue and produce dentalites. Wood-cutting behavior may date back to the Oligocene, but the earliest dentalites on wood are Pliocene in age (Rybczynski, 2008). Dentalites occur with skeletal remains of *Dipoides* sp. from the early Pliocene on Ellesmere Island in Canada (Harington, 1996; Hutchinson and Harington, 2002; Tedford and Harington, 2003). Both *Dipoides* and the Recent *Castor* employ the same function of their incisors, but the living beaver has a more efficient cutting mechanism (Rybczynski, 2008).

Other Substrates

Dentalites occur, or potentially could occur, on a number of other substrates:

1. Hirsch et al. (1997) described predatory peck marks on fossil eggshells from the Eocene of Colorado, USA.
2. Possible dentalites on dinosaur skin include concave depressions with radiating stress fractures in *Psittacosaurus* (Lingham-Soliar, 2008) and a healed wound in *Edmontosaurus* (Rothschild and Depalma, 2013).
3. Chumakov et al. (2013) erected three new ichospecies, *Machichnus normani*, *M. harlandi* and *M. jeansi,* for scratch marks on phosphorite nodules and pebbles from the Late Cretaceous of England. They are interpreted as scratches that originated from the teeth of fish scraping bacterial or algal film off the surface of nodules that were covered with phosphate gel.
4. Some rocks are gnawed by rodents and other mammals for minerals or to wear down incisors (e.g., Gobetz and Hattin, 2002), although no paleontological specimens have been identified.
5. Jensen et al. (2019) report human chewing of birch pitch for non-nutritional reasons from the Holocene, and similar behavior might be seen in older hominins.

Ichnotaxobases and Ichnotaxonomy

Introduction

Bromley and Jacobsen (2008) outlined research designed to produce an ichnotaxonomy of dentalites. They also noted how few ichnotaxa have been named for trace fossils in bone and recommended the development of rigorous ichnotaxobases and ichnotaxonomy. Currently, there are 19 named ichnotaxa of dentalites on bone and lithic substrates (Table 2).

Ichnotaxobases

Ichnotaxobases are distinctive morphologic features of a trace fossil that display significant and readily detectable variability and are thus important to ichnotaxonomic classifications (e. g., Bromley, 1996; Buatois and Mángano, 2011; Pirrone et al., 2014).

Pirrone et al. (2014) proposed ichnotaxobases for bioerosional structures of all kinds in bone; the following are particular to dentalites.

Substrate

We follow Bertling et al. (2006) in considering substrate as an important ichnotaxobase if it implies a different behavior of the producer. This is clearly the case if the dentalite is in a bone, wood, a coprolite or an invertebrate shell (Lucas, 2016).

Orientation

Virtually all vertebrate teeth/dentitions function (move) vertically (dorso-ventrally), though lateral motion of the teeth/dentitions is also significant in some vertebrate taxa. Thus, dentalites can be divided into those produced by a vertical or lateral impact or a combination of the two. Binford's (1981) influential classification scheme of tooth marks recognized two vertical (punctures, pits) and two lateral tooth strike marks (scores, furrows).

Vertical features include deep (puncture of Binford, 1981; perforation of Fernández-Jalvo and Andrews, 2016) and shallow (pits) penetrations. Binford (1981) suggested the definitions are based on whether there is collapse of surficial layers (in bone, but this could also be applicable to shells), but a simpler differentiation might be whether the depression is deeper than wide. Binford (1981) considered pits to be more typical of gnawing.

Traces produced by lateral impacts of teeth are generally U-shaped (Fiorillo, 1991a, b; Fernández-Jalvo and Andrews, 2016). Binford's (1981) terms scores and furrows distinguish single and repeated jaw action. Some traces represent both vertical and lateral contact. Many of these include a tooth strike that slipped, but others may represent "torsional forces applied against incompletely gripped bones that slip on clasped jaws during side-to-side head thrusting and clockwise to counterclockwise death roll pivots……and are common in crocodile-modified assemblages" (Njau and Gilbert, 2016, p. 5).

Size

Absolute size and size relative to the dimensions of the substrate are important. Small tooth marks on a large bone (or shell) probably denote post-mortem damage, although the opposite is not always the case.

Evidence of tooth structure

Tooth structure can be seen in vertical marks by the cross section of the impression (e.g., Cruickshank, 1986; Rinehart et al., 2006). In lateral marks, serrations can produce lineations (Jacobsen and Bromley, 2009). Grooved incisors of rodents can also produce lineations (Fernández-Jalvo and Andrews, 2016). Bicarinate crocodile teeth produce distinctive marks (Njau and Blumenschine, 2006).

Evidence of dentition

The most useful traces provide not only evidence of behavior but also of the tracemaker's morphology. Bromley and Jacobsen (2008) favored naming bite marks based on the damage of a single tooth and regard multiple tooth marks as compound trace fossils. However, this suggestion fails to recognize the significance of heterodonty and the variation in single dental configurations (arcades). Thus, the ideal ichnotaxobase is the tooth marks of an entire dental arcade, and anything less than that could be regarded as extramorphological variants (Lucas, 2016).

Pattern of occurrence (Pirrone et al., 2014)

Many dentalites are not isolated. Pits often occur in groupings. Multiple lateral marks can be sinuous, arcuate or sub-parallel (Mikuláš et al., 2006; Jacobsen and Bromley, 2009). Gnawing traces are usually sub-parallel (Fernández-Jalvo and Andrews, 2016, figs. A.194-A.201).

Location

Buckland (1822, 1824) recognized that the location of dentalites on the substrate was important to identify the behavior and identity of the tracemaker. Subsequently, the pattern of dentalites on skeletons has been recognized as important in assessing predation and scavenging in animals with and without living analogues (e.g., Binford, 1981; Brain, 1981; Hunt et al., 1994b).

Summary

There are several ichnotaxobases available for dentalites, but the ideal one is based on the tooth marks of an entire dental arcade.

Utility of Dentalites

Dentalites have the potential to document a wide range of behaviors, including: (1) predation, including hunting strategies; (2) bite method and force; (3) dietary selection; (4) feeding; (5) scavenging strategies; (6) methodologies of bone accumulation; (7) trophic patterns; (8) intraspecific (agonistic) interactions; (9) tooth sharpening; and (10) bone and rock utilization for other purposes, including mineral extraction (Binford, 1981; Hunt et al., 1994b; Drumheller-Horton, 2012; Lucas, 2016). They thus are of diverse paleoethological significance.

Conclusions

There have been two centuries of studies of dentalites and abundant records, but with strong biases towards archeology, and towards dinosaurs as a result of the Taxophile Effect. Dentalites have diverse potential in paleoethology. What is now needed is a dentalite ichnology beginning with diverse documentation of the dentalite ichnofossil record, compilation and synthesis of the entire record, rigorous ichnotaxonomy and determination of analytical criteria for establishing inferences about the behaviors archived by tooth-mark ichnofossils (Lucas, 2016).

REGURGITALITES

Introduction

Regurgitalites have the least extensive fossil record among bromalites and are the least studied. This results from both the relative infrequency of regurgitation among vertebrates and the difficulty in identifying these traces.

History of Study

The description and discussion of regurgitalites started about a century after the first work on dentalites, coprolites and consumulites. Götzinger and Becker (1932) described discrete accumulations of small fragments of *Inoceramus* shells from the Upper Cretaceous of Austria. They tentatively interpreted them as coprolites. However, Häntzschel et al. (1968, p. 53) noted that they are "perhaps vomit balls, corresponding to the undigestible matter vomited by birds."

Much of the work on regurgitalites in the second half of the Twentieth Century was conducted by German paleontologists, particularly with regard to the Jurassic Holzmaden and Solnhofen Lagersttäten (Frentzen, 1936; Broili, 1938; Wellnhofer, 1964; Janicke, 1970; Barthel and Janicke, 1970; Janicke and Schairer, 1970; Keller, 1977; Barthel, 1978; Mehl, 1978; Böttcher, 1989, 1990; Jäger, 1991) as well as some other localities (Wetzel, 1953, 1960, 1964; Horstmann and Maier, 1957; Engesser and Storch, 1999). Italian paleontologists also conducted important studies (Pinna et al., 1985; Dalla Vecchia et al., 1989).

The most prominent work in the United States during this time period was Zangerl and Richardson's (1963) meticulous study of the Pennsylvanian Carbondale Formation of Indiana. They recognized numerous regurgitalites and introduced terminology to distinguish different types. However, subsequent actualistic taphonomic studies have demonstrated that many of these specimens represent decayed fish (Elder, 1985; Elder and Smith, 1988). Gawne (1975) described the first convincing strigilite from the Miocene of New Mexico. Other strigilites were noted in the western United States (Walton, 1990; Korth and Emry; Lillegraven et al., 1981). Stewart and Carpenter (1990), Hattin (1996) and Everhart (1999) described the first regurgitalites from the productive Cretaceous chalk of Kansas. Wilson (1977a, b, 1980, 1987) studied Eocene lacustrine regurgitalites of the Western United States and Canada. Hunt (1992) introduced the term regurgitalite in a study of Pennsylvanian bromalites from New Mexico.

Starting in the 1970s there was an increased interest in the origin of microvertebrate fossil accumulations. Much work was focused on strigilites (and other ornithoregurgitalites) as an important source of such accumulations (Dodson, 1973; Dodson and Wexlar, 1979; Mellett, 1975; Mayhew, 1977; Andrews, 1990; Kusmer, 1990; Montalvo and Fernández, 2019).

During the first decade of this century there was intermittent, but diverse, interest in regurgitalites. Aldridge et al. (2006) described the earliest putative regurgitalites from the Late Ordovician, and Sanz et al. (2001) published an influential paper in *Science* on a regurgitalite from the Lower Cretaceous of Spain. There were several reports of avian regurgitalites from the Paleocene of Argentina (Nasif et al., 2009) and the Eocene of the United States (Murphey et al., 2001; Alexander and Burger, 2001) and from non-avian specimens from the Late Cretaceous Nammoûra Lagerstätte of Lebanon (Dalla Vecchia and Chiappe, 2002) and the Jurassic of Germany (Dietl and Schweigert, 2001).

Most recognized vertebrate regurgitalites contain vertebrate remains. Oji et al. (2003) used angular shell debris as a proxy for the prevalence of durophagous predators, including fish, and Salamon et al. (2014) reported Devonian and Mississippian regurgitalites that confirm this hypothesis. Zatoń and co-workers (Zatoń et al., 2007; Zatoń and Salamon, 2008; Salamon et al., 2012) described vertebrate regurgitalites from the Triassic and Jurassic of Poland composed of the remains of diverse invertebrate taxa. Other examples of regurgitalites composed of invertebrate hard parts have also been described in the last two decades from the Mesozoic of Germany and Austria (Neumann, 2000; Stevens et al., 2014; Lukeneder et al., 2020; Lukeneder and Lukeneder, 2021).

In the last decade there has been elevated interest in regurgitalites, which has increased in pace during the past three years. Myhrvold (2011) and Hunt and Lucas (2012a) reviewed terminology and introduced new terms, and several papers have reviewed criteria for the recognition of regurgitalites (Myhrvold, 2011; Thies and Hauff, 2012; Hunt et al., 2015a; Klug and Vallon, 2018; Hoffman et al., 2019; Gordon et al., 2020; Friemuth et al., 2021). Burrow and Turner (2010) described the oldest definitive vertebrate regurgitalite from the Lower Devonian of Scotland. Hunt and collaborators (Hunt et al., 2012e, h-i; Hunt and Lucas, 2021a) described a series of Pennsylvanian ichnofaunas from New Mexico and Montana in the United States and named the first regurgitalite ichnotaxa, *Ostracobromus* and *Conchobromus*. Diverse regurgitalites produced by owls and snakes have been described from the Messel Lagersttäte in Germany (Morlo et al., 2012; Mayr and Schaal, 2016; Schaal, 2016; Gunnell et al., 2018). Everhart has described multiple regurgitalites from the marine Cretaceous of Kansas in the United States (Everhart, 1999, 2003, 2004b, 2017). Lucas et al. (2012) described a spectacular purgolite composed of strigilites from the lower Oligocene of eastern Wyoming, and Freimuth (2020; Friemuth et al., 2021) studied the regurgitalites of a theropod dinosaur from Montana.

Regurgitation

The vomiting reflex is common in vertebrates and is a protective mechanism for the bulk ejection of noxious material (Simms et al., 2000). Habitual regurgitation occurs in a variety of Recent carnivorous, piscivorous and insectivorous species that routinely ingest food with a high proportion of indigestible material that is egested through the mouth (Shäfer, 1972; Myhrvold, 2011). The other principal expulsion mechanism is stomach eversion, which occurs in sharks and rays and, possibly, some amphibians (e.g., Simms et al., 2000; Brunnschweiler et al., 2005). The range of reasons for regurgitation include: (1) eradicating poison; (2) removing mechanically dangerous matter; (3) feeding offspring; (4) removing parasites; (5) eliminating indigestible material; and (6) getting rid of sloughed gastric mucosa and mucus (Gudger, 1949; Beintema, 1991; Sims et al. 2000; Klug and Vallon, 2018; Hoffmann et al., 2019).

Many bony fish and chrondrichthyans regurgitate indigestible material (e.g., Hattin, 1986; Bowman, 1986; Andrews et al., 1998; Zatoń and Salamon, 2008; Aas et al., 2017). Most carnivorous snakes and many lizards egest gastric pellets and other materials such as eggshell fragments (Gans, 1952; Reinhard and Vogel, 1980; Myhrvold, 2011). Long et al. (2010) reported regurgitation in turtles. Varanids produce gastric pellets (Petzold, 1967; Auffenberg, 1981), as do many crocodilians (Dolowy et al., 1960; Scherpner, 1980; Fisher, 1981a,b; Chabreck, 1996; Andrews et al., 2000; Myhrvold, 2011). Virtually all birds that eat invertebrate or vertebrate animals egest pellets, and the majority of birds regurgitate to feed their young (e.g., Rea, 1973; Duke et al., 1976; Andrews, 1990; Zijlstra and Van Eerden, 1995; Myhrvold, 2011). Among mammals, some marine mammals–whales and most pinnipeds–produce gastric pellets (e.g., Fea and Harcourt, 1997; Goodman-Lowe, 1998; Clarke et al., 1998).

Actualistic Studies

Following the recognition that avian regurgitalites are important in the development of microvertebrate accumulations (e. g., Dodson, 1973; Dodson and Wexlar, 1979; Mellett, 1975; Mayhew, 1977), there have been extensive actualistic studies of Recent regurgitations. Peter Andrews has been prominent in this work, with authorship of two comprehensive volumes (Andrews, 1990; Fernández-Jalvo and Andrews, 2016). Recent works that provide access to this large literature include Fernández-Jalvo and Andrews (2016), Fernández-Jalvo et al. (2016), Denys et al. (2018) and Montalvo and Fernández (2019).

Recognition

Hunt (1992; Fig. 3) proposed the encompassing term bromalite in part because it can be difficult to distinguish a regurgitalite from a coprolite. The majority of studies have identified bromalites as either coprolites or regurgitalites, without considering other possibilities (Gordon et al., 2020). And, many regurgitalites may have been mistaken for coprolites (Myrhvold, 2011; Vallon, 2012). Note that Recent raptor pellets can be identified as to originator (e.g., Moon, 1940; Terry, 2007, 2010). Regurgitalites have no single unique characteristics, but they can be recognized on the basis of a suite of features (Wilson, 1987; Myhrvold, 2011; Thies and Hauff, 2012; Hunt et al., 2015a; Klug and Vallon, 2018; Hoffman et al., 2019; Gordon et al., 2020; Freimuth, 2020, Friemuth et al., 2021):

1. Geometry. Putative regurgitalites range from three-dimensional cylindrical or amorphous bodies to splatters of associated organic matter in a discrete area on a bedding plane (e.g., Hunt et al., 2012e, h; Hoffmann et al., 2019; Gordon et al., 2020).
2. Non-biotic content. Regurgitalites contain a relative (to coprolites) lack of phosphatic matrix, and some specimens have none (Hunt et al., 2015a; Klug and Vallon, 2018; Gordon et al., 2020; Freimuth et al., 2021).
3. Biotic content.
    a. Physico-chemical characteristics. The principal inclusions are elements that are not easy to digest, so they may be preferentially evacuated (e.g., vertebrate skeletal elements, invertebrate valves and cuticle, dermal elements – fur and feathers) (Myhrvold, 2011; Hunt et al., 2015a; Hoffman et al., 2019). It is important to note that some hard parts, such as invertebrate shells, can pass through the digestive tracts of durophagous fish and some birds (Cate and Evans, 1994; Zuschin et al., 2003). Nevertheless, the reverse could also be true, and regurgitalites could be characterized by materials that are easy to digest and that would not be present in coprolites (Gordon et al., 2020).
    b. Size. Hard parts are comparably larger and articulated more often in regurgitalites than in coprolites (Hoffmann et al., 2019).
    c. Evidence of digestion. Regurgitalites should demonstrate evidence of digestion but less than coprolites (Bochenski et al., 1993, 1998; Hockett, 1996; Hunt et al., 2015a; Hoffmann et al., 2019; Gordon et al., 2020).
        i. Physical – broken or rounded elements.
        ii. Chemical – etched or pitting.
    d. Dentalites. Evidence of predation is likely to be better preserved in elements in regurgitalites that have low residence time in the digestive tract than in coprolites (Hunt et al., 2015a).
    e. Element composition. Recent and fossil avian pellets can be characterized by a prevalence of skulls, articulated elements and the association of one or more discrete skeletons (Myhrvold, 2011; Hoffman et al., 2019; Freimuth et al., 2021).
    f. Element orientation. Elements are often aligned about their long axes and closely packed (Myhrvold, 2011; Holgado et al., 2015).

Terminology

Hunt (1992) introduced the term regurgitalite to be consonant with coprolite, for bromalites egested through the mouth. Previously, a range of imprecise and inconsistently used terms had been applied to such specimens (see review in Hunt and Lucas, 2012a; Appendix B). Regurgitalite has since been widely used. Darroch et al. (2021) recently used the term “casting“ for fossil rergurgitalites. The verb “to cast“ is often used in Recent ornithology, but the noun “casting“ appears to derive from falconry and is usually only applied to hawks. It is widely accepted that ichnofossils use a different terminology than modern animal traces (Bertling et al., 2006; Hunt and Lucas, 2012a). Myrhvold (2011) coined the term emetolite for fossilized gastric pellets produced by routine vomiting (emesis).

Hunt and Lucas (2012a) introduced the term purgolite for an accumulation of regurgitalites (accretionary, if concentrated by physical processes, and ethological, if by behavior) and others for specific types, including ejectalite (deriving from oral cavity or gastrointestinal tract anterior to the stomach), ekrhexalite (derives from the stomach), ornithoregurgitalite (produced by a bird) and strigilite (fossil owl pellets) (Appendix B). Gordon et al. (2012) rightly pointed out that some of these cannot be readily discriminated in the fossil record.

Fossil Record

The majority of identified regurgitalites occur in marine or lacustrine environments characterized by low energy and fine-grained sediments (Hoffman et al., 2019). Overviews of the fossil record of regurgitalites were provided by Thies and Hauff (2012), Klug and Vallon (2018) and Hoffmann et al. (2019).

Paleozoic

The earliest putative regurgitalites are from the Late Ordovician Soom Shale Lagerstätte of South Africa (Aldridge et al., 2006). Aldridge et al. (2006) described compact, pellet-like clusters of fragmented conodont elements that they tentatively interpreted as regurgitalites produced by conodont animals.

A regurgitalite, likely produced by a nautiloid, occurs in the Silurian of Poland (Brachaniec et al., 2016). This specimen consists of fragmented and intermingled angular and non-abraded mollusc, brachiopod and crinoid remains (Brachaniec et al., 2016).

A definitive vertebrate regurgitalite is from the Early Devonian locality of Duntrune in Scotland (Burrow and Turner 2010). From this locality, Burrow and Turner (2010) described and illustrated a bromalite that includes four tooth whorls, two fin spines, a scapulocoracoid, flank scales, tesserae, and umbellate scales of one individual of the acanthodian fish *Nostolepis scotica*. They also mentioned several hundred similar specimens from the important fish localities at both Duntrune and Tillywhandland, each of which includes elements from a single specimen of *Ischnacanthus gracilis* or *Mesacanthus mitchelli*. Klug and Vallon (2018) reported three regurgitalites containing cephalopods from the latest Devonian of Morocco. They contain dissolved ammonite shell fragments and ?jaws of ?*Mimimitoceras* and are tentatively ascribed to a gnathostome.

Salamon et al. (2014, figs. 6-7) reported one regurgitalite from the Devonian and nine from the Mississippian composed of shell fragments. Angular shell fragment debris may indicate the presence of durophagous fish, so the distribution of such material should parallel that of shell-rich regurgitalites (Oji et al., 2003; Salamon et al., 2014). This seems to be the case in the Devonian to the Mississippian (Salamon et al., 2014, fig. 7). Thus, based on the work of Oji et al. (2003), we predict that there was a rise in such regurgitalites during the Paleogene and a major increase in the Neogene.

Regurgitalites are notable in several Pennsylvanian units of the United States. The Mississippian Bear Gulch Lagerstätte of Montana includes the ostracode-bearing regurgitalite *Ostracobromus snowyensis* (Hunt et al., 2012e), which is probably also present in the Pennsylvanian Hamilton Lagerstätte (Cunningham et al., 1993, p. 230). Zangerl and Richardson (1963) described faunas from the Early Pennsylvanian Carbondale Formation of Indiana. They distinguished two types of regurgitalites based on the degree of processing in the digestive tract – ejected prey (mastication, minor digestion) and gastric residues (more extensive digestion) (Zangerl and Richardson, 1963). However, the putative regurgitalites containing vertebrate material probably mainly represent decayed fish instead of regurgitalites (Elder, 1985; Elder and Smith, 1988). Nevertheless, some of the accumulations of invertebrate debris (e.g., of the bivalve *Myalina*) do probably represent vertebrate regurgitalites (e.g., Zangerl and Richardson, 1963, pl. 44D).

The Missourian Atrasado Formation at the Kinney Brick Quarry and Tinajas Lagerstätten in New Mexico, USA, yields large samples of bromalites, including the regurgitalite *Conchobromus kinneyensis,* which contains abundant conchostracans (Hunt et al., 2012e, h-i; Hunt and Lucas, 2021a). Huber (1992) and Scholtze et al. (2021) suggested that the groupings of conchostracans present in *Conchobromus* were caused by weak swirls of water. However, this seems unlikely since there is no other evidence for swirling currents at the Kinney Brick Quarry, and no other fossil specimens occur in such groupings in this Lagerstätte.

Mesozoic

Salamon et al. (2012) described a number of putative regurgitalites from the Middle Triassic Gogolin Formation in southern Poland. These are discrete accumulations composed primarily of angular bivalve shell fragments with sharp, non-abraded margins and crinoid ossicles with many breaks. They are interpreted to represent regurgitalites of durophagous vertebrates, including sharks, colobodontid fish, placodonts and pachypleurosaurs or sauropterygian reptiles (Salamon et al., 2012). Another possible regurgitalite from the same formation is fusiform in shape, composed of fragmented bivalve shells and, based on its size, is attributed to the sharks *Acrodus* or *Palaeobates* (Niedźwiedzki et al., 2021). These regurgitalites suggest that the "Mesozoic Marine Revolution" may have begun by the Middle Triassic and thus was a far more prolonged evolutionary event than its name implies (Salamon et al., 2012).

The Reingraben Shales in Austria yield a Late Triassic (early Carnian) Konservat-Lagerstätte that contains regurgitalites (Lukeneder et al., 2020; Lukeneder and Lukeneder, 2021). These specimens are large (> 40 mm long) and consist of flat ovoids with closely packed invertebrate debris, no matrix and evidence of acid etching (Lukeneder et al., 2020). The constituents are entire shells and fragments of the ammonoid *Austrotrachyceras* and rare teuthid arm hooks, and buccal cartilage of *Phragmoteuthis* (Lukeneder et al., 2020). The regurgitalites are attributed to durophagous sharks such as *Acrodus* (Lukeneder et al., 2020; Lukeneder and Lukeneder, 2021).

Dalla Vecchia et al. (1989) described a regurgitalite from the Late Triassic of northern Italy as containing pterosaur skeletal elements, but they were subsequently re-interpreted as pertaining to a protorosaurian similar to *Langobardisaurus* (Holgado et al., 2015). The producer is hypothesized to be a large fish such as *Saurichthys*, *Birgeria* or a coelacanthiform (Holgado et al., 2015). Gordon et al. (2020) described another Late Triassic regurgitalite from Arizona that is composed of a compact mass of skeletal material of the pseudosuchian archosaur *Revueltosaurus*. They interpret the producer as a phytosaur, rauisuchid, or temnospondyl.

The Lower Jurassic Posidonia Shale of South Germany yields a number of regurgitalites. Keller (1977; also see Vallon, 2012) considered a coiled-up skeleton of an 1.6-m-long specimen of the ichthyosaur *Stenopterygius quadriscissus* as a regurgitalite produced by the large predatory ichthyosaur, *Temnodontosaurus* (= *Leptopterygius*). Jäger (2001) interpreted disarticulated bones of a small ichthyosaur to be another regurgitalite produced by *Temnodontosaurus*. The type specimen of the small ornithischian *Emausaurus ernsti* may also represent a regurgitalite produced by a large ichthyosaur or marine crocodile (Haubold, 1990; Thies and Hauff, 2012). Thies and Hauff (2012) described a fourth regurgitalite that contains the remains of four specimens of the actinopterygian *Dapedium* sp. and a lower jaw of *Lepidotes* sp. It may have been produced by a chondrichthyan (*Hybodus*), actinopterygians (pachycormiforms) or by marine reptiles (crocodilians, ichthyosaurs, plesiosaurs). Hoffmann et al. (2019) regarded the "Seeball" described by Jäger (1991), which is composed of spines of the echinoid *Diademopsis,* to be a regurgitalite. Böttcher (1989, 1990) also noted regurgitalites from Holzmaden, and Frentzen (1936) described the ammonite *Amaltheus* from what he considered to be a fish consumulite, but it is more likely a regurgitalite. Pinna et al. (1985) and Garassino and Donovan (2000) described regurgitalites from the Early Jurassic of Italy containing fish centra and scales and coleoid hooks and ascribed them to thylacocephalan crustaceans, but they could pertain to vertebrates.

Zatoń and co-workers (Zatoń et al., 2007; Zatoń and Salamon, 2008) described regurgitalites from the Middle Jurassic of Poland. Nine specimens are composed of molluscs (scaphopods, gastropods, bivalves, ammonites and belemnites), articulate brachiopods and echinoderms (asteroids, crinoids and echinoids), and the probable producers are palaeospinacid sharks, although other vertebrates such as durophagous pycnodontiform fish, cannot be excluded (Zatoń et al., 2007). Zatoń and Salamon (2008) described another 11 specimens that contain remains of diverse taxa, including gastropods, scaphopods, bivalves, belemnites, ammonites, brachiopods, bryozoan, crinoids, echinoids, ophiuroids and even wood, which they interpreted to have been produced by an opportunistic generalist, most likely a fish.

The Middle Jurassic of the Bielefeld area of northern Germany has yielded possible regurgitalites of marine reptiles (Wetzel, 1953, 1964; Horstmann and Maier, 1957). These contain juvenile ammonites, belemnites, cephalopods, echinoderms, scaphopods and foraminiferans with smaller quantities of fish scales, crustacean limbs and reptile teeth (Wetzel, 1953, 1964; Horstmann and Maier, 1957).

The majority of regurgitalites from the Late Jurassic derive from the Nusplingen and Solnhofen Lagerstätten of Germany. Stevens et al. (2014) described four closely associated belemnites from Nusplingen that they interpreted as a regurgitalite produced by an elasmobranch, holocephalan, or marine reptile. Other Nusplingen regurgitalites contain echinoid (*Pseudodiadema, Nenoticidaris, Plegiocidaris*) and sea star (*Sphaeraster*) remains that do not occur elsewhere in these limestones, and they are attributed to the pycnodont fish *Gyrodus* (Dietl and Schweigert, 2001). Dietl and Schweigert (2001; Fig. 9) and Schweigert et al. (2001) reported a regurgitalite that contained bones of the pterosaur *Rhamphorhynchus*, possibly produced by a crocodile, *Cricosaurus* (*Geosaurus*) or *Dakosaurus*, or large predatory fish such as *Caturus* (Hoffmann et al., 2019) or possibly *Aspidorhynchus* (Frey and Tischlinger, 2012). Other Nusplingen regurgitalites contain the echinoid *Plegiocidaris* and the fishes *Tharsisdubius* and *Caturus* (Grawe-Baumeister et al., 2000; Vallon, 2012; Albersdörfer and Häckel, 2015; Viohl, 2015; Hoffmann et al., 2019).

Six coiled vertebral columns of the actinopterygian *Leptolepis sprattiformis* from the Solnhofen Lagerstätte represent

FIGURE 9. Regurgitalite from the Upper Jurassic Nusplingen Lithographic Limestone of Germany. The bromalite (SMNS Inv. Nr. 63990) contains bones of a pterosaur, probably *Rhamphorhynchus,* and is interpreted as having been produced by a large fish or a marine crocodile (Schweigert et al., 2001). The regurgitalite is approximately 4 cm tall. Image courtesy of Günter Schweigert.

a regurgitalite (Janicke and Schairer, 1970). Janicke (1970) and Barthel (1978) described regurgitalites from Solnhofen containing the actinopterygian *Caturus* and interpreted them as produced by a large fish or crocodile. Hoffman et al. (2019) listed other fish regurgitalites from the Solnhofen strata, including: (1) multiple mollusks, among them ammonites, from *Lepidotes* (Wellnhofer, 1964; Barthel and Janicke, 1970); (2) lamellaptychi from sharks (Barthel and Janicke, 1970); and (3) lamellaptychi from Holostei, Amiiformes (e.g., *Caturus*) or Aspidorhynchiformes (Mehl, 1978).

There are two Solnhofen pterosaurs associated with possible regurgitalites. The first is represented by a loose spiral of an articulated vertebral column of *Leptolepides* preserved adjacent to the mandibular tip of a specimen of *Scaphognathus crassirostris* (Bennett, 2014). This fish skeleton may have been a regurgitalite, or it may have been ejected from the animal during the decay process (Bennett, 2014). The second is a specimen of "*Pterodactylus propinquus*" from the Upper Jurassic of Germany (now lost) that preserves disarticulated fish debris around the gular pouch, which could have been regurgitated from the gut (Broili, 1938; Wellnhofer, 1970; Witton, 2018).

Sanz et al. (2001) described a regurgitated pellet from the Early Cretaceous Los Hoyas Lagerstätte in Spain. This bromalite consists of partial skeletons of four juvenile birds that may have derived from a non-avian theropod or a pterosaur (Sanz et al., 2001). Pellets occur in several birds from the Jehol Lagerstätte in China (Wang et al., 2016; O'Connor, 2019). All appear to be incorporeal pelletites and not egested. Probable regurgitalites composed of fish scales and bones also occur with three specimens of the Jehol troodontid *Anchiornis huxleyi* (Zheng et al., 2018b).

The majority of Late Cretaceous regurgitalites contain vertebrate elements, but Neumann (2000) described subrounded or elliptical lenses consisting of densely packed asteroid ossicles and/or other echinoderm remains from chalk in Germany. These pellets are interpreted as possible regurgitalites produced by bony fishes or sharks (Neumann, 2000). Similar bromalites have been found in the Late Cretaceous and Danian of northern Europe, although some have been attributed to large asteroideans (Wright and Wright, 1940; Rasmusseen, 1950; Müller, 1953; Gale, 1987; Neumann, 2000).

Wetzel (1960, 1964) described possible regurgitalites from the Late Cretaceous of Chile. They contain ammonite larvae and adult *Baculites* as well as bivalves and plankton, and he ascribed them to plesiosaurs.

Hattin (1996) described a regurgitalite from the chalk of Kansas in the United States. This bromalite includes not only bone, but also cirriped plates and coccoliths and is attributed to the chondrichthyan *Ptychodus*. Capasso (2019b) described a regurgitalite just exterior to the oral cavity of the pycnodont *Acrorhinichthys poyato*i from the Middle Cenomanian of Lebanon.

Everhart (2017) noted the occurrence of similar bromalites in the Kansas Cretaceous. Marine deposits of the Late Cretaceous of the Western Interior Seaway have yielded a variety of other regurgitalites. Bishop (1975) illustrated two regurgitalites, one containing disarticulated fragments of the crab *Dakoticancer* and the other of the mud shrimp *Callianassa*. Regurgitalites from Kansas include heavily-pitted bones of fish, marine reptiles (several mosasaurs, one plesiosaur) and the dinosaur *Niobrarasaurus* (Everhart, 1999, 2003, 2004b, 2017). A regurgitalite consisting of the front part of a juvenile mosasaur skull has teeth that are eroded down to the roots (Everhart, 2017, fig. 4.3). An isolated mandible of the ornithocheiroid *Pteranodon* preserves a pellet between the mandibular rami, probably held in place by throat tissues before burial (Brown, 1943; Bennett, 2001; Witten, 2018). This specimen preserves several fish vertebrae (Bennett, 2001). Stewart and Carpenter (1990) noted two other possible regurgitalites from Kansas: (1) a juvenile specimen of the ammonite ?*Clioscaphites choteauensis* with apatitic matrix in the outer whorl; and (2) a mass of teleost bones, batoid denticles and fragments of a teuthidid gladius. Martin and Tate (1976) described associated material with *Baptornis advenus* that could represent a regurgitalite (or a coprolite or evisceralite).

Dalla Vecchia and Chiappe (2002) described a bird from the Late Cretaceous Nammoûra Lagerstätte of Lebanon. This skeleton is preserved in a ball-like mass of powdered bone mixed with carbonized feathers and represents a regurgitalite (Dalla Vecchia and Chiappe, 2002; Myrhvold, 2011).

Three multi-individual aggregates of mammalian skeletons from the Late Cretaceous nesting locality of Egg Mountain in the United States represent regurgitalites (Freimuth, 2020; Friemuth et al., 2021). One yields two individuals of the multituberculate *Filikomys primaevus,* and the other two are composed of three and 11 individuals, primarily of the marsupialiform *Alphadon halleyi*. These regurgitalites are interpreted as being produced by *Troodon formosus* on the basis of abundant shed teeth and nesting evidence, and this would be consistent with previous inferences of this predator as having a diet of small-bodied prey, manipulating prey during feeding, heightened metabolic processes, and potential nocturnality (Freimuth et al., 2021).

Cenozoic

The only described regurgitalite from the Paleocene is an ornithoregurgitalte (*sensu* Hunt and Lucas, 2012a) from the Salamanca Formation of Argentina at Punta Peligro (Muzzopappa et al., 2021). This orithoregurgitalite contains a single skeleton of the anuran *Calyptocephalella sabrosa*.

Eocene regurgitalites occur in shallow lacustrine facies of the western United States and Canada. Wilson (1977a, b, 1980, 1987) studied middle Eocene freshwater vertebrate fossils from the interior of British Columbia and northern Washington (Wilson, 1980). In 25 vertebrate fossil assemblages, he noted that up to 69% of fish remains occurred in pellets (fish-bone coprolites), which were interpreted as principally avian regurgitalites (Wilson, 1987). Buskirk et al. (2015) described several morphotypes of bromalites from the Middle Eocene

Florissant Formation of Colorado, including regurgitalites that are ovoid (rarely sinusoidal) in shape with little to no groundmass and with a high content of crushed invertebrate shells—these are likely regurgitalites.

The Eocene Messel Lagerstätte in Germany yielded three regurgitalites that resemble Recent owl pellets and are considered to be strigilites (Mayr and Schaal, 2016). They contain various broken bird bones and may have been produced by the Messel owl *Palaeoglaux artophoron*, which would make it the oldest owl pellet identified so far. The two other gastric pellets with bird remains have more elongate shapes and probably derive from snakes or other squamates (Mayr and Schaal, 2016; Gunnell et al., 2018). Another regurgitalite reported from Messel includes a skeleton of the hyaenodontid mammal *Lesmesodon edingeri* and was likely produced by a large boid snake, probably *Palaeopython* (Morlo et al., 2012; Schaal, 2016; Gunnell et al., 2018). This specimen is deformed to a slender carcass with the forelimbs pressed against the body and contains a consumulite consisting of teeth, jaws and bone fragments of an amphibian or reptile and an insectivore (Morlo et al., 2012; Schaal, 2016; Gunnell et al 2018). Lastly, Messel yielded a skeleton of the gecko *Ornatocephalus metzleri* that is partially disarticulated, missing the pelvis, hind limbs and tail, and with the bone surfaces corroded. This is probably the regurgitalite of a raptor (Smith et al., 2018).

The Eocene *Omomys* Quarry in Wyoming in the United States consists almost exclusively of bones of the eponymous primate as well as bones of birds, including owls. It may be a strigilite purgolite (Murphey et al., 2001; Alexander and Burger, 2001).

A specimen of the owl *Stihanus* from the latest Eocene Peanut Peak Member of the Chadron Formation in South Dakota is a possible strigilte (Hunt and Lucas, 2007a). Lucas et al. (2012; Fig. 10) described a purgolite composed of strigilites from the early Oligocene of eastern Wyoming, first mentioned by Walton (1990) and Korth and Emry (1991). The strigilites are preserved as calcareous nodules full of fossil mammal bones and yielded the type specimens of the sciurid rodent *Cedromus wilsoni* and the todid bird *Palaeotodus emryi*. The strigilite assemblage also includes the skeletons, bearing skulls, of at least three individual owls, which strongly reinforces the interpretation of these small masses of bone as owl pellets (Lucas et al., 2012). Other possible Oligocene occurrences from Wyoming include a skeleton of the insectivore *Centenodon chadronensis* that exhibits features suggestive of it originating in a strigilite (Lillegraven et al., 1981), and pellets and possible owl bones from another locality (Walton, 1990). The late Oligocene of Germany also preserves presumed strigilites that contain rodent specimens (Engesser and Storch, 1999; Smith and Wuttke, 2015).

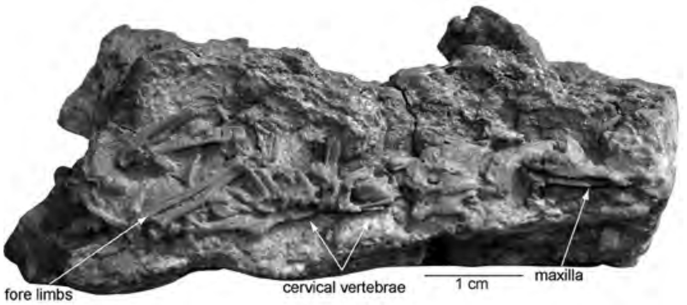


FIGURE 10. Strigilite (regurgitalite) with anterior portion of skeleton of a small rodent from the Orella Member of the White River Formation (early Oligocene), Wyoming, USA (Lucas et al., 2012, fig. 4A).

Gawne (1975) distinguished a strigilite from the early Miocene of central New Mexico. This specimen is a small pellet containing tightly-packed cranial and postcranial specimens of two rodents (*Proheteromys cejanus* and *P.* aff. *P. floridanus*) (Gawne, 1975).

Two fossil regurgitalites from the Andalhuala Formation (Upper Miocene), Santa María of Argentina, are composed of articulated and disassociated bones and teeth of octodontid and cricetid rodents that show evidence of corrosion (Nasif et al., 2009). Nasif et al. (2009) interpreted these as ornithoregurgitalites *(sensu* Hunt and Lucas, 2012a) of "terror birds" (Phorusrhacidae, Psilopterinae). This is the oldest record of a cricetid rodent in South America.

An early Miocene lake in eastern Spain yields "abundant clumps of scales and bones" of unidentified teleosts (Álvarez-Parra et al. 2021, p. 10). These specimens are flat accumulations that lack phosphatic matrix. Álvarez-Parra et al. (2021) recognized them as bromalites, and they clearly represent regurgitalites.

The best example of Pliocene strigilites is a putative purgolite of slightly disaggregated strigilites from Arizona in the United States (Walton, 1990; Czaplewski, 2011). A less well documented occurrence occurs in the adjacent state of New Mexico (Walton, 1990). Many Pleistocene cave deposits and some archeological sites yield bone accumulations derived from raptor, notably owl, regurgitations (e.g., Andrews, 1990; Hunt and Lucas, 2007a). Rodents from Pleistocene cave deposits in Poland may derive from strigilites (Kowalski, 1960; Sulimski, 1964).

There are very few convincing examples, prior to the Pleistocene, of paleontological microvertebrate accumulations that comprise bones derived from raptor regurgitations (Lucas et al., 2012). However, many Pleistocene cave deposits and some archeological sites yield bone accumulations derived from raptor, notably owl, regurgitations (e.g., Andrews, 1990; Hunt and Lucas, 2007a; Montalvo et al., 2012). Indirect evidence of strigilites (or other ornithoregurgitalites) is based on analysis of microvertebrate accumulations (e.g., Mellett, 1975; Mayhew, 1977; Kusmer, 1990). There is strong evidence that some cave microvertebrate accumulations, particularly of bats and lizards, resulted from accumulation by owls (e.g., Williams, 1952; Morgan, 1994).

Cenozoic marine regurgitalites are rare. Milner (in Hunt and Lucas, 2007a) noted fish regurgitalites from the Late Pleistocene calcareous concretions from the Champlain Sea Clays of eastern Canada. Baldanza et al. (2013) described fossil ambergris from the Pleistocene of Italy, but this is probably fecal in origin (Clarke, 2006).

Ichnotaxobases and Ichnotaxonomy

Currently, there are only two named regurgitalite ichnotaxa, both from the Carboniferous of the United States - *Ostracobromus snowyensis* and *Conchobromus kinneyensis* (Hunt et al., 2012e, h). However, there is great potential to construct an ichnotaxonomy of regurgitalites that will further the study of these traces. Ichnotaxobases would include:

1. Composition
    a. Biologic
        i. Taxonomy of inclusions
        ii. Physical or chemical modification of inclusions
    b. Non-biologic
        i. Volume of matrix
        ii. Composition of matrix
2. Morphology
    a. Geometry
    b. Size

Utility

Regurgitalites have diverse utility, including:

1. Providing evidence of the evolution of predation and digestion.
2. Analysis of taphonomy and sedimentary environments.
3. Proxy for the presence of biotaxa.
4. Loci for exceptional preservation (Gordon et al., 2020).
5. Biogeographic studies (Darroch et al., 2021).
6. Evaluating digestive processes of producer (Gordon et al., 2020).
7. Evidence of the evolution of durophagy.

Conclusions

Regurgitalites are not only the least studied bromalites, but they can also be the most difficult to identify. Bromalite pellets can represent coprolites or regurgitalites, and two-dimensional examples could be taphonomic artifacts (decayed specimens or physical concentrations). Many identified vertebrate regurgitalites were produced by fish or birds and are preserved in a limited range of environmental settings (e. g., aquatic low energy). Thus, the fossil record of regurgitalites is strongly controlled by both taxonomic and taphonomic factors.

CONSUMULITES

Introduction

Hunt and Lucas (2012a) introduced the term consumulite to refer to material ingested and preserved within the gastrointestinal tract of a fossil vertebrate. We have attempted to compile data on all recorded specimens of consumulites older than Pleistocene. However, most published references to consumulites, particularly in the older literature, are within publications that have a different focus, so we recognize that the compilation is likely incomplete. The volume of literature on Pleistocene consumulites precludes a complete review, so we have only included representative examples. Previously, the "Extant Phylogenetic Bracket" approach was often utilized to reconstruct the digestive tract of extinct vertebrates (e.g., Bryant and Russell, 1992; Witmer, 1995), but consumulites can provide direct evidence of the structure.

History of Study

In 1829, William Buckland introduced the term coprolites for fossil feces (Buckland, 1829; Hunt and Lucas, 2012a). However**,** it is not generally appreciated that Buckland utilized the term coprolite in three different senses (Hunt and Lucas, 2012a):

1. Evacuated fecal material, as that term is now universally used.

2. Un-evacuated, dispersed and un-pelletized material preserved within the gastro-intestinal tract–Buckland (1830, p. 23) noted that "in many of the entire skeletons of Ichthyosauri……….coprolites are seen within the ribs and near the pelvis." Further, Buckland (1836, p. 149) stated that "the certainty of the origin of these coprolites is established by their frequent presence in the abdominal region of fossil skeletons of Ichthyosauri… One of the most remarkable of these is represented in Pl. 13." Buckland (1836, pls. 13 and 14) illustrated two skeletons of ichthyosaurs with dispersed, digested/partially digested material almost filling the extent of the rib cage in each case.

3. Infilled gastro-intestinal tract–Buckland (1829, p. 142) introduced the term "Ichthyo-coprus" for food material preserved within the body cavity of a fish (later Ichthyocoprus: Buckland, 1835, p. 230). Subsequently, he named a variety of this form of coprolite as "Amia [sic]-coprus" (Buckland, 1830, p. 24) that clearly represents an infilled segment of a gastro-intestinal tract (see Duffin, 2009, fig. 14). Thus, Buckland was the first to recognize material ingested and preserved within the gastrointestinal tract of a fossil vertebrate, which Hunt and Lucas (2012a) later termed consumulites.

Here we also introduce the term aspirationalite for consumulites that preserve prey in the oral cavity with a significant portion extending exteriorly (Fig. 11). Aspiration is the medical term for breathing in a foreign object/sucking food into the airway. Grande (2013, p. 396) utilized the term "aspiration specimens" for "fossil fishes with other animals preserved in their mouth or stomach." Aspirationalites occur in many large samples of articulated fish (e.g., Eocene Green River Formation, USA: Jepsen, 1967; Grande, 2013, figs. 64 upper, 85 upper) and some tetrapods such as the pterosaur *Rhamphorhynchus* (Frey and Tischlinger, 2012).

During the 19th Century, there was sporadic interest in consumulites of Mesozoic marine reptiles (e.g., Moore, 1856) and of Mesozoic (e.g., von Münster, 1842; Huxley, 1866; Davis, 1887; Stewart, 1899) and of Paleogene fish (Agassiz, 1833-1845a,b). Increased collection and study of mosasaurs later in that century, notably in western North America, resulted in more reports (e.g., Dollo, 1887a,b; Williston, 1898, 1899).

The earliest described nonmarine consumulite was Pleistocene plant debris of *Ephedra* sp. and *Salix* sp. in the oral cavity of a frozen woolly rhinoceros (*Coelodonta antiquitatis)* from Russia (Ukraintseva, 1993). In 1900, the first complete frozen mammoth with a preserved gastrointestinal tract was found (Gerts, 1902). Subsequently, numerous frozen Pleistocene specimens of mammoths, bison and horse have yielded consumulites, principally in Russia, but also in North America (e.g., Ukraintseva, 1981, 1993; Guthrie, 1990; Boeskorov et al., 2014).

There were relatively few reports of consumulites for the first nine decades of the 20th Century, and the majority were just noted in the context of morphological and taxonomic descriptions (e.g., Brown, 1900; Eastman, 1911, Cockerill, 1915; Neumayer, 1929; Weiler, 1934; Broili, 1938; Camp, 1942; Arambourg, 1954; Nybelin, 1958; Eaton, 1964; Pollard, 1968; Sorbini, 1972; Špinar, 1972; Wellnhofer, 1975a,b; Patterson and Rosen, 1977; Richter, 1981; Milner, 1982; Werneburg, 1988). Boucot's (1990) influential compendium on the paleobiology of behavior and coevolution includes numerous references to consumulites and includes important review papers on consumulities in fish by Williams (1990) and Viohl (1990). In the past three decades, there has been increasing mention of consumulites, in general, and publications in which the main focus is these bromalites, in particular (e.g., Massare and Young, 2005; Wahl, 2012). Everhart and others have described a large number of consumulites from the Late Cretaceous of the Western Interior of North America (see Everhart, 2017). Another principal area of focus in the 21st Century has been the consumulites from the Early Cretaceous Jehol Lagerstätte of China, principally in theropods and birds, but also in a mammal, frog and choristodere (Hu et al., 2005; Wang et al., 2005; O'Connor, 2019; Xing et al., 2019; O'Connor and Zhou, 2020; Table A.9).

FIGURE 11. Aspirationalite from the early Eocene of Wyoming, USA. *Mioplosus labracoides* swallowing *Knightia eocaena.* The specimen is approximately 50 cm long. Photograph courtesy of Vincent Santucci, National Park Service.

Actualistic Studies

Preservation of consumulites is favored by a longer gut retention time and a lower digestive acidity (Miller and Pittman, 2021). Gut retention times are influenced by overall ecology and short-term behaviours in birds (Miller and Pittman, 2021). In Recent birds, fully terrestrial species tend to have much longer gut retention times than flying taxa, with the most active having the lowest time (Jackson, 1992; Hilton et al., 1999; Caviedes-Vidal et al., 2007; Frei et al., 2014). Gut retention is also related to aspects of diet including fiber content, lipid content, particle size and energy density (Balch and Campling, 1965; Warner, 1981; Hilton et al., 1998, 2000a; McWhorter and Martínez del Rio, 2000; Levey and Del Rio, 2001). Short-term behavioral changes affecting retention include dietary switching (Hilton et al., 2000b), migration (McWilliams et al., 1999), and raising young (Thouzeau et al., 2004). Stomach acidities vary among Recent raptors, with less bone remaining in the pellets of raptors with lower stomach pH (Duke et al., 1975; Duke, 1997; Miller and Pittman, 2021).

Recognition

Demalites are biogenic material putatively preserved within the body cavity of an animal that does not pertain to that animal (Hunt and Lucas, 2012a). They can have five principal sources: (1) apparent preservation as the result of stacked carcasses with parts of one skeleton seeming to be within the body outline of a superposed specimen, as has been proposed for specimens of the Late Triassic theropod dinosaur *Coelophysis* (Rinehart et al., 2009); (2) gignolites, such as embryos or eggs; (3) postmortem utilization of the carcass (e.g., shed carnivore teeth); (4) material introduced by sedimentological processes; and (5) true consumulites. Thus, consumulites are a subset of demalites referring specifically to fossilized, ingested food material preserved within the body cavity (Hunt and Lucas, 2012a). In much of the vertebrate paleontological literature, consumulites are referred to informally as "stomach contents" or "gut contents."

Consumulites, with the notable exception of evisceralites, cannot be unambiguously recognized unless they occur within an articulated or at least substantially complete skeleton. Voss et al. (2019) adapted identification criteria proposed for the recognition of gastroliths by Wings (2004) to apply to stomach contents, but these criteria are potentially relevant to all consumulites:

1. In association with the skeleton of "an appropriate consumer" – this can be useful, but some consumulites preserve prey that would be unexpected in the consumer (e.g., a fish within the apparently terrestrial theropod dinosaur *Baryonyx*: Charig and Milner, 1986, 1997) or an absence of expected prey (e.g., no insects within the pangolin *Eomanis,* a putative anteater: von Koenigswald et al., 1981; Richter, 1988).
2. In an anatomically correct position – there are definitely exceptions related to rupture or displacement of the gastrointestinal tract (e.g., Eocene *Amia*: Boreske, 1974; Grande, 1980).
3. Discrete clusters of bromalitic material – often the case, but it can be disseminated, e.g., clustered and separated by distance from other such clusters, and, in some cases, the putative consumulite could be an associated concretion (e.g., fish associated with *Elasmosaurus*: Everhart, 2017).
4. Found in a low-energy depositional setting in sediment finer in clast size than in the consumulite.
5. Dentalites present – dentalites are actually rarely reported in consumulites (an exception is the consumulite of *Postosuchus alisonae*: Sues et al., 2003; Peyer et al., 2008), and their absence can provide evidence of prey swallowed whole (e.g., conchostracan valves in the salamander *Jeholotriton*: Dong et al., 2012).
6. A further criterion is evidence of mechanical or chemical processing, which is relatively uncommon (e.g., etched headshield of *Cephalapis* in *Ptomacanthus*: Denison, 1956; Allen and Tarlo, 1963; Miles, 1973).

Terminology

Consumulites are the bromalites with the most complicated terminological history (Table 1, Appendix B; Hunt and Lucas, 2012a). Hunt and Lucas (2012a) reviewed the long history of terms applied to bromalites preserved within the body cavity and introduced the term consumulite to encompass all such trace fossils. They also redefined existing terms and introduced new ones to provide a refined terminology for all consumulites, including oralite (wholly or partially within the oral cavity), esophogalite (in the gastrointestinal tract anterior to the stomach), gastrolite (in the stomach), cololite (in the gastrointestinal tract posterior to the stomach), intestinelite (cololite in intestines), enterospira (cololite in a spiral valve) and incorporeal pelletite (pelletite preserved within the body cavity) (Hunt and Lucas 2012a) (Fig. 3; Table 1). An evisceralite is a cololite that is a preserved segment of infilled fossilized intestines preserved independent of, or exterior to, a carcass.

Fossil Record

Introduction

Vertebrate consumulites have an extensive fossil record, which is compiled here for the first time (Fig. 12; Tables A.6-11). They occur in diverse environments, starting in the Devonian. Consumulites are principally associated with, or at least recognized in the context of, articulated skeletons (Hunt and Lucas, 2020b). The majority of articulated skeletons are from aquatic environments, as thus are many consumulites. Articulated skeletons thus are common in Lagerstätten that preserve vertebrate fossils (Hunt and Lucas, 2020b). Thus, the record of consumulites is biased towards Lagerstätten such as the Cleveland Shale (Devonian), Holzmaden (Jurassic), Solnhofen (Jurassic), Jehol (Cretaceous), Messel (Eocene), and Green River (Eocene). Beyond Lagerstätten, consumulites are most common in fine-grained deposits of low energy environments (Hunt and Lucas, 2020b). The vast majority of consumulites represent carnivorous animals because plant material is usually finely macerated during digestion, and it is much easier to recognize a bone as a foreign object than carbonaceous debris (Hunt and Lucas, 2020b).

Large body size favors the recognition of consumulites. The combination of large body size and an aquatic lifestyle results in an extensive record of consumulites in large Mesozoic marine vertebrates, notably ichthyosaurs, plesiosaurs and mosasaurs.

We will review the fossil record of consumulites, as with dentalites, by era and environment. Evisceralites are considered separately because of their limited fossil record. Significant sources of data on consumulites include Massare (1987), Boucot (1990), Viohl (1990), Cicimurri and Everhart (2001), Konuki (2008), Boucot and Poinar (2010), Naish (2014), Everhart (2017) and O'Connor (2019).

Evisceralites

Agassiz (1833-1845a, b, p. 676) introduced the term cololite to refer to the fossilized "more or less stuffed intestines of fish." He used the term in relation to both infilled intestines preserved within a body cavity and also those preserved in isolation and not directly associated with a body cavity; the latter are now termed evisceralites (Hunt and Lucas, 2012a). A cited example of the latter was *Lumbricaria,* an enigmatic ichnotaxon common in the Upper Jurassic Solnhofen Limestone of Germany and now recognized as ammonite coprolites (e.g., von Münster, 1831; Muller, 1969; Janicke, 1970; Barthel et al., 1990; Knaust and Hoffman, 2021). *Lumbricaria* is not found associated with fish

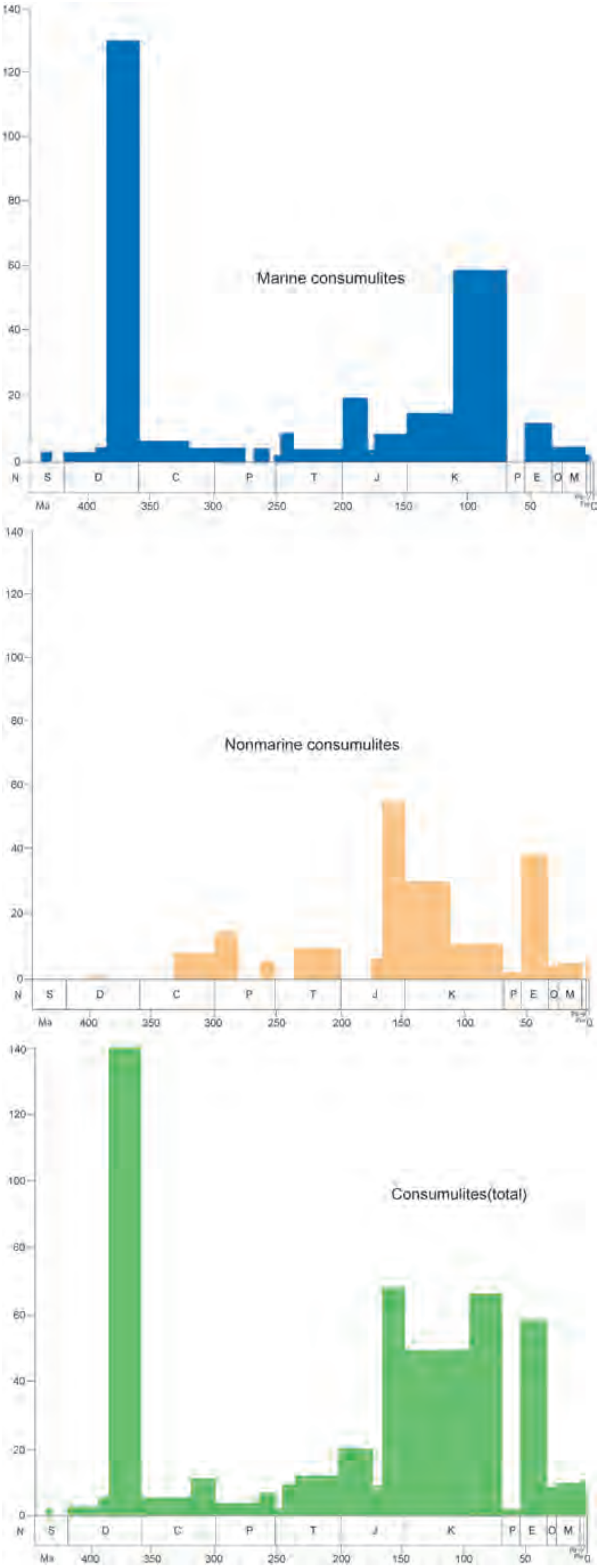


FIGURE 12. Temporal distribution of reports of consumulites. Sources are in the text; also see Tables A.6-11.

skeletons, but "M. Agassiz has ingeniously explained this fact by observing the process of decomposition of dead fishes in the lakes of Switzerland. The dead fish floats on the surface with its belly upwards, until the abdomen is so distended with putrid gas, that it bursts: through the aperture thus formed the bowels come forth into the water, still adhering together in their natural state of convolution" (Buckland, 1835, p. 156). The best evidence for this type of preservation may derive from the Middle Jurassic (late Callovian) fish fauna of the Luciano Mesa Member of the Todilto Formation in eastern New Mexico, USA (Koerner, 1930; Schaeffer and Patterson, 1984; Lucas et al., 1985). Multiple specimens of the holostean fish *Todiltia schoewei* preserve consumulites, and the surrounding matrix also preserves isolated sections of intestinal tract (Schaeffer and Patterson, 1984; Lucas et al., 1985; Hunt and Lucas, 2014b; Fig.13). We term this type of evisceralite, in which a portion of the gastrointestinal tract is physically removed from a carcass, as dislocational.

Buckland (1835, 1836) recognized that spiral coprolites were derived from fish with valvular intestines. Fritsch (1895) and Neumayer (1904) considered that some of the spiral bromalites actually represented fossilized valvular intestines rather than coprolites. Subsequently, Hoernes (1904) and Fritsch (1907) introduced terms for bromalites that represent infilled spiral-valved intestines, enterolite and enterospira, respectively. Hunt and Lucas (2012a) accepted the term enterospira over enterolite because of widespread usage. The idea that spiral bromalites represent infilled intestines has been re-examined several times (e.g., Williams, 1972; McAllister, 1985; Ward et al., 2020). A 300 to 500 µm separation between whorls could represent a thin mucusoal membrane and be used as a criterion to distinguish intestinal infillings (Ward et al., 2020).

There are few other recorded examples of dislocational evisceralites. Clark (1989) described the earliest such evisceralite from the Late Mississippian (Serpukhovian) of Bearsden, Scotland.

A second type of evisceralite results from preferential fossilization of the gastrointestinal tract, and we term this preservational. Some geologists of the U. S. Geological Survey and others first described unusual sideritic specimens from the Paleocene of North Dakota and the Miocene of Washington (Amstutz, 1958; Roberts, 1958; Brown, 1962). Subsequently, similar specimens were described from the Permian of China and the Late Cretaceous of Canada and Madagascar (Broughton et al., 1977; Broughton, 1981; Seilacher et al., 2001; Hunt and Lucas, 2016b). They were variously interpreted as coprolites, pseudofossils, or casts of internal organs (Amstutz, 1958; Broughton et al., 1977, 1978; Broughton, 1981; Schmitz and Benda, 1991; Spencer, 1993; Mustoe, 2000; Seilacher et al., 2001). Seilacher (Seilacher et al., 2001; Seilacher, 2002) convincingly argued that they are both ichnofossils and cololites. Thus, they are interpreted as evisceralites prefossilized by bacterial activity and later transformed into siderite. All occurrences are in fluvial overbank deposits with no other vertebrate remains. The absence of skeletal fossils may be due to aquifer roll-fronts that destroyed phosphatic bones and teeth but favored siderite precipitation (Seilacher et al., 2001). Hunt et al. (2012b) designated one of the preservational evisceralites from North Dakota as the holotype of *Hiabromus seilacheri.* Broughton (2017) proposed an *ad hoc* hypothesis that multi-decimeter-long specimens may be evisceralites of an unknown taxon of giant terrestrial earthworm (Oligochaeta) that existed from the Late Cretaceous to the Neogene. We consider this unlikely.

Paleozoic

Marine

The earliest vertebrates were jawless, so they are considered to have been primarily filter feeders. Thus, it is not surprising that

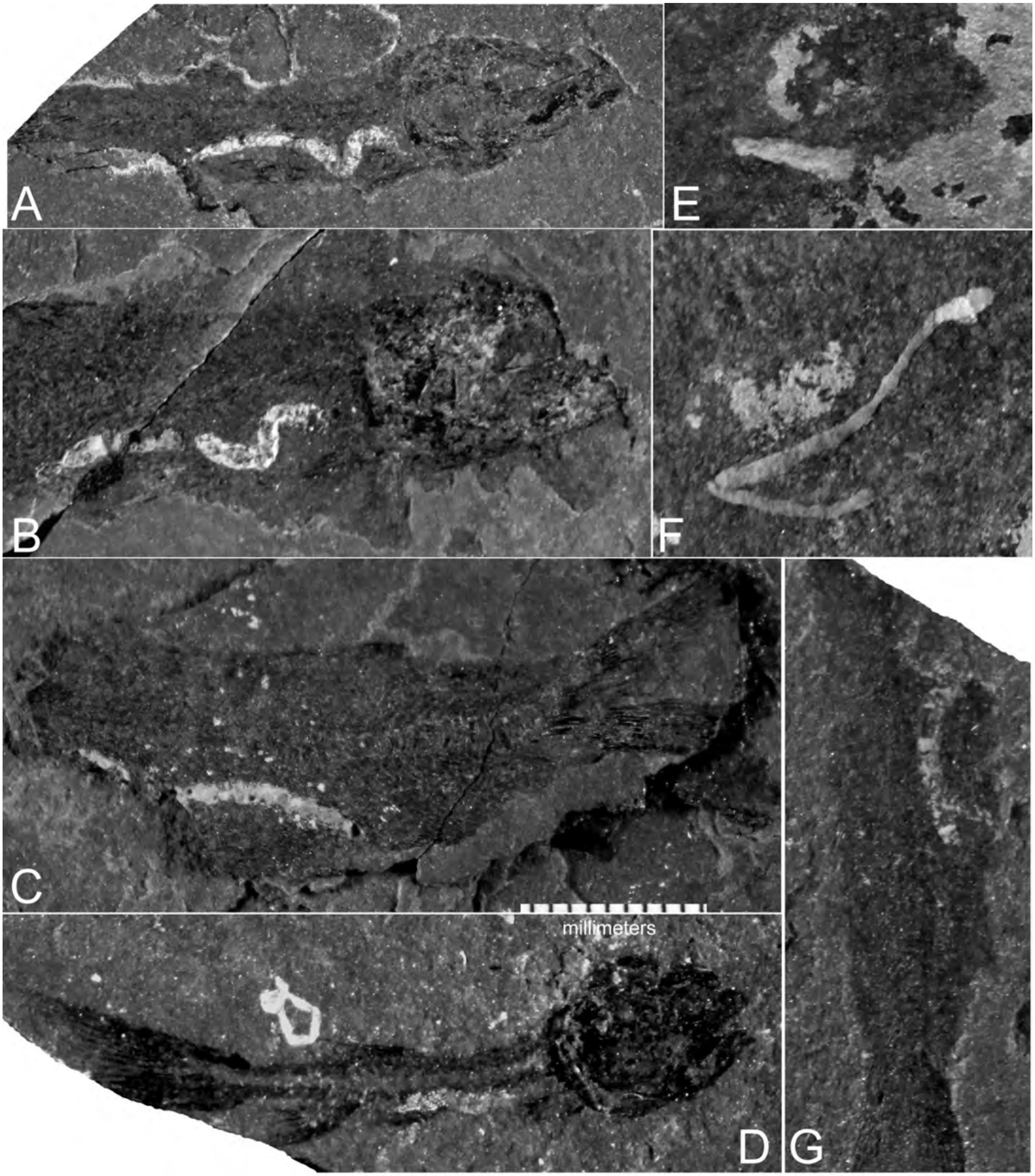


FIGURE 13. Middle Jurassic consumulites and evisceralites in "holostean" fishes from the Luciano Mesa Member of the Todilto Formation at NMMNH locality L-1476, Bull Canyon (A-D, G), and NMMNH locality L-3520, Warm Springs (E-F) in New Mexico, USA. **A,** NMMNH P-32715, *Todiltia schoewei* in lateral view with consumulite. **B,** NMMNH P-32713, *Todiltia schoewei* in lateral view with consumulite. **C,** NMMNH P-32718, *Todiltia schoewei* in lateral view with consumulite. **D,** NMMNH P-32714, *Todiltia schoewei* in lateral view with adjacent evisceralite. **E,** NMMNH P-28700, evisceralite in lateral view. **F,** NMMNH P-28700, evisceralite in lateral view. **G,** NMMNH P-32712, *Todiltia schoewei* in lateral view with consumulite. All to same scale (Hunt and Lucas, 2014b, fig. 12).

the earliest consumulite known consists of a gastrolite infilled by sediment within the furcacaudiform thelodont *Pezopallichthys ritchie* from the Middle Silurian of Canada (Wilson and Caldwell, 1993, 1998). This strongly suggest that stomachs evolved before jaws in early vertebrates (Wilson and Caldwell, 1993). Other furcacaudiforms from the Early Devonian of Canda have similar arenaceous consumulites (Wilson and Caldwell, 1993, 1998), as do the endeiolepidiform *Endeiolepis aneri* and the euphanerid *Euphanerops longaevus,* both from the Late Devonian of Canada (Stensiö, 1939; Arsenault and Janvier, 1991; Janvier, 1996a, b; Janvier and Arsenault, 2007).

The oldest known consumulites that contain recognizable prey are from the Early Devonian of England and include a *Cephalaspis* head shield within the shark *Ptomacanthus* and a small ostracoderm within an acanthodian (Denison, 1956; Allen and Tarlo, 1963; Miles, 1973; Table A.6). Middle Devonian examples from Scotland occur in several specimens of *Coccosteus* and *Glyptolepis* as well as in acanthodians, actinopterygians and placoderms (Heintz, 1938; Miles and Westoll, 1968; Ahlberg, 1992; Davidson and Trewin, 2005). One *Glyptolepis* contains a small *Glyptolepis* (Ahlberg, 1992). This is both the earliest record of cannibalism and the first to demonstrate a fish swallowing another head first. This orientation of prey acquisition is prevalent in gape-limited predatory fish throughout the Phanerozoic. Swallowing prey head-first significantly reduces: (1) esophageal abrasion; (2) escape rate of the prey; and (3) the prey manipulation period (Reimchen, 1999). These advantages diminish with small prey. Head-first prey acquisition also occurs in most, but not all (e.g. Braz and Marques, 2016) snakes and squamates. A significant literature demonstrates analagous causation: (1) reduce the resistance offered by the appendages and body covering of the prey; (2) reduce the prey-handling time, which decreases the period of vulnerability to other predators; and (3) advantageous to ophiophagous snakes because it decreases the resistance from posteriorly projecting overlapping ventral scales (Diefenbach and Emslie, 1971; Loop and Bailey, 1972; Loop, 1974; Greene, 1976; Queiroz and de Queiroz 1987; Wiseman et al., 2019). As with fish the probability of head first ingestion increases with increasing prey size (Queiroz and de Queiroz, 1987).

The geographic distribution and volume of consumulite specimens increases substantially in the Late Devonian (Fig. 12; Table A.6). More than 50 fish from the Cleveland Shale in Ohio, USA, preserve consumulites (Williams, 1990). These include more than 40 sharks representing four species of *Cladoselache*, *Ctenacanthus compressus* and unidentified taxa. The majority of consumulites consist of paleoniscoid debris, but they also include a couple of complete fish (*Kentuckia blavini*), several contain arthropods and four yield conodonts. Three specimens contain the crustacean *Concavicaris* cf. *C. bradleyi*, which were swallowed tail first (Williams, 1990). Whereas most fish are swallowed head first, most invertebrates with appendages in the Devonian and later are swallowed tail first, presumably to avoid damage to the predator during ingestion. Other Late Devonian consumulites are from Russia (Zakharenko, 2008), Latvia (Upeniece, 2001, 2011), Canada (Arsenault, 1982; Janvier, 1996b; Chevrinais et al., 2017) and Australia (Dennis and Miles, 1981; Long, 1991, 1995; Choo et al., 2009).

Notably fewer records of consumulites come from the later Paleozoic (Fig. 12). There are reports of specimens from the early Carboniferous of England and Scotland (Traquair, 1879; Watson, 1937; Viohl, 1990; Coates and Sequeira, 2001). The selachian *Akmonistan zangerli* from Scotland preserves the oldest incorporeal pelletite (*Chondripilula zideki*), and a second occurs in another shark (*Cobelodus aculeatus)* from the Late Pennsylvanian of the United States (Coates and Sequeira, 2001; Hunt, 1992; Hunt et al., 2012h; Hunt and Lucas, 2021a). *Typhloesus wellsi* from the Bear Gulch Lagerstätte in the Lower Mississippian of Montana, USA, is a rare example of an invertebrate that preserves consumulites of vertebrates (fish) as well as conodont apparatuses and worm teeth (Conway Morris, 1976, 1990).

Most Permian consumulites derive from Germany (Table A.6). Three specimens are known from the late Permian Kupferschiefer (Weigelt, 1928a, b, 1930a, b; Malzahn, 1968; Schaumberg, 1979), and the remainder are from earlier in the period (Heidtke, 2007; Kriwet et al., 2008). Lohmann and Sachs (2001) reported on consumulites through four ontogenetic stages of the temnospondyl amphibian *Sclerocephalus haeuseri*. The only reptilian consumulites from the marine Paleozoic pertain to the mesosaur *Brazilosaurus sanpauloensis* from the lower Permian of Brazil and include crustacean fragments and bones of very young mesosaurids (Silva et al., 2017).

Nonmarine

The pattern of nonmarine Paleozoic consumulites is a mirror image of that of the marine, but with increasing numbers through time (Fig. 12; Table A.7). There are no Devonian examples. Carboniferous specimens are currently only known from two Lagerstätten in the United States, Mazon Creek in Illinois (Richardson and Johnson, 1971; Richardson, 1980; Milner, 1982; Viohl, 1990; Godfrey, 1997) and the Kinney Brick Quarry in New Mexico (Hunt, 1992; Hunt et al., 2012h; Werneburg et al., 2013, 2021). One host is a shark, but all the remaining pertain to small amphibians (body lengths less than 50 mm). The "branchiosaur" *Milnerpeton huberi* from New Mexico and an unidentified amphibian from Illinois each have ostracods as consumulites. The dvinosaurian *Bermanerpeton kinneyi* from Kinney preserves syncarid arthropods (*Uronectes* cf. *U. kinniensis, Aenigmacaris* cf. *A. minima)*, spines of *Acanthodes* cf. *A. kinneyi,* actinopterygian scales and ribs and neural arches of amphibians in consumulites. Hunt and Lucas (2021a) named the ostracod-bearing consumulite *Werneburgichnus kinneyensis*, and that containing more diverse content is named *W. varius. Chondripilula zideki* is a pelletal body preserved within the posterior intestines of sharks (Hunt and Lucas, 2021a). No identifiable food items occur in the specimens from Mazon Creek (Godfrey, 1997).

Small "branchiosaur" amphibians from the lower Permian of Germany preserve a variety of consumulites that range from conchostracans to other amphibians (e.g., Werneburg, 1986, 1988, 1989, 2020; Witzmann, 2009). These strata also yielded the first consumulite within a consumulite, which is the shark *Triodus sessilis,* which ingested two amphibians, *Archegaurus decheni* and *Cheliderpeton latirostre*; the latter had swallowed a specimen of *Acanthodes bronni*. Two early Permian reptile skeletons from the United States contain oralites. A specimen of the captorhinimorph *Romeria* sp. from Texas contains a smaller skull and partial skeleton of probably the same species (Case, 1911; Eaton, 1964). Two skulls of the parareptile *Delorhynchus priscus* from Oklahoma preserve fragments of arthropod cuticle between the palatal teeth (Modesto et al., 2009; Reisz et al., 2014).

Late Permian reptile skeletons with consumulites occur in Tanzania and Germany (Table A.7). A specimen of the gorgonopsid *"Aelurognathus" parringtoni* from Tanzania includes a mandibular symphysis of the dicynodont *Katumbia parringtoni* as a gastrolite (Maisch, 2009). Both Weigelt (1928a) and Munk and Sues (1993) described ovules of the conifer *Ullmannia frumentaria* associated with different specimens of the early archosauromorph reptile *Protorosaurus speneri* from Germany. The first report had been regarded with skepticism (e.g., Haubold and Schaumberg, 1985) because the plant material was scattered within a disarticulated skeleton, but the latter demonstrated the presence of plant material within an articulated ribcage. Munk and Sues (1993) also described coarse clastics with interspersed carbonized material (that they interpreted as macerated plant matter) in a consumulite of the pareisaurian parareptile *Parasaurus geinitzi.*

Mesozoic

Marine

The Mesozoic marine record of consumulites is extensive and dominated by sharks, bony fish and the three main clades of marine reptiles (ichthyosaurs, plesiosaurs and mosasaurs). The frequency of occurrences increases through the Mesozoic and reaches its maximum during the Late Cretaceous (Fig. 12; Table A.8).

An Early Triassic specimen of the ray-finned fish *Birgeria* from Madagascar yields conspecifics as a demalite. This was originally interpreted as an example of ovoviparity by Beltan (1977), but these specimens more likely represent a consumulite (Viohl, 1990). Middle Triassic fish consumulites occur in specimens of *Saurichthys* in China and in the Monte San Giorgio Lagerstätte in Switzerland (Wu et al., 2015; Argyriou et al., 2016). Monte San Giorgio also yields consumulites in a nothosaur and a pachypleurosaur (Tschanz, 1989; Diedrich, 2015). Ichthyosaur consumulites occur not only at this Swiss locality (Rieber, 1970; Brinkmann, 2004) but also in the Early Triassic of Norway (Buchy et al., 2004) and the Late Triassic of China (Cheng et al., 2006) and the United States (Camp, 1930; Druckenmiller et al., 2014). The gastrointestinal tracts of Early and Middle Triassic ichthyosaurs yield only cephalopod hooklets, but the Late Triassic examples include both vertebrate remains and mollusk shell fragments (Rieber, 1970; Camp, 1980; Brinkmann, 2004; Buchy et al., 2004; Cheng et al., 2006; Druckenmiller et al., 2014).

The Early Jurassic Holzmaden Lagerstätte of Germany has produced many specimens of consumulites (Table A.8). These records include about 250 belemnite guards in a specimen of the shark *Hybodus* (Brown, 1900; Pollard, 1990; Doyle and McDonald, 1993) and coleoid remains in the bony fishes *Saurostomus* and *Pachycormus* (Urlichs et al., 1994; Přikryl et al., 2012). Mateer (1974) documented an indeterminate organic area above the sacral area in a specimen of the marine crocodylomorph *Steneosaurus bollensis*. However, the majority of consumulites from the Jurassic Posidonienschiefer pertain to ichthyosaurs. These include more than 35 specimens found in skeletons of *Stenopterygius* spp. and *Leptopterygius* spp. (von Wurstemberger, 1876; Keller, 1976; Massare, 1987; Böttcher, 1989; Bürgin, 2000). These consumulites principally contain cephalopod hooklets, but also include an actinopterygian fish, juvenile *Stenopterygius* and rare wood fragments (e.g., Keller, 1976; Massare, 1987; Böttcher, 1989; Bürgin, 2000). Dick et al. (2016) studied a large sample of consumulites in *Stenopterygius quadriscissus* and demonstrated that ontogenetic shifts in the size and shape of the dentition coincide with dietary changes. The smallest specimens fed on small, burst-swimming fishes, with a progressive shift with increasing body size towards consuming faster moving fish and, ultimately, cephalopods.

Ichthyosaur consumulites also occur in the Lower Jurassic of England in several species of *Ichthyosaurus* (Buckland, 1858; Pollard, 1968; Lomax et al., 2019; Fig. 14). The majority of specimens yield only cephalopod hooklets, but Buckland (1858) reported some *Pholidophorus* fish scales and spines. Middle Jurassic consumulites also derive from England from the Oxford Clay. They include cephalopods in the plesiosaurs *Simolestes vorax* and *Peloneustes* sp. (Andrews, 1910; Martill, 1992; Cicimurri and Everhart, 2001) and the crocodyliform *Metriorhynchus* sp. (Martill, 1985a).

Late Jurassic consumulites are more geographically widespread but are not numerous (Fig. 12). They include amorphous gut contents in the fish *Allothrissops* in Europe (Patterson and Rosen, 1977) and cephalopod remains in the ichthyosaurs *Pantosaurus striatus* and *Ophthalmosaurus natans* from the United States (Massare and Young, 2005; Wahl, 2012). One American plesiosaur (cf. *Pantosaurus striatus)* has ichthyosaur embryos in its digestive tract (O'Keefe et al., 2009), and another (cf. *Tatenectes laramiensis)* contains hybodont shark teeth, spines and denticles in addition to coleoid cephalopod hooklets (Wahl, 1998; Cicimurri and Everhart, 2001). Late Jurassic plesiosaur skeletons in Russia and England also contain consumulites with hooklets as well as fish (Zhuravlev, 1943a, b; Gekker and Gekker, 1955; Tarlo, 1959). Two skeletons of Metriorhynchidae from Germany preserve consumulites (Spindler et al., 2021). Taylor et al. (1993) described a specimen of *Pliosaurus brachyspondylus* that contains ornithischian dinosaur osteoderms, the oldest example of clearly terrestrial vertebrate remains in a marine consumulite.

Consumulites are geographically widespread in the Lower Cretaceous, but the majority of the specimens come from two countries, Brazil and Australia (Table A.8). The Aptian Santana Formation of Brazil yields at least 10 examples of fish consumulites that contain identifiable fish that were ingested head first (Patterson and Rosen, 1977; Case, 1982; Viohl, 1990; Wilby and Martill, 1992; Maisey, 1994, 1996; Mulder, 2013). The Early Cretaceous of Australia has produced consumulites in the turtle cf. *Notochelone* sp. (inoceramids), the ichthyosaur *Platypterygius longmani* (turtle, bird, fish), two specimens of the pliosaur *Kronosaurus* (fish, turtle, elasmosaur) and two elasmosaurs (principally invertebrates) (Kear et al., 2003; McHenry et al., 2005; Kear, 2006; McHenry, 2009). The plesiosaur *Nichollsia borealis* from Canada contains fish in a consumulite (Druckenmiller and Russell, 2009).

The very extensive record of Late Cretaceous consumulites is heavily biased toward the well excavated and researched vertebrate fauna of the Western Interior seaway of North America, notably in the United States, and particularly the state of Kansas (Table A.8). There are six occurrences of shark consumulites from the United States, and one each from Italy and Lebanon, which preserve a wide range of prey including fish, turtle, plesiosaur and mosasaur (Sternberg, 1917; Martin and Rothschild, 1989; Viohl, 1990; Druckenmiller et al., 1993; Shimada, 1997; Everhart, 2003; Amalfitano et al., 2017).

Arguably the most famous consumulite is the *Gillicus arcuatus* swallowed by *Xiphactinus audax* (Fig. 15), the "fish within a fish" from Kansas that is on display at the Sternberg Museum of Natural History (e.g., Walker, 2006; Everhart, 2017, fig. 5.1). The Kansas chalk yields at least half a dozen more specimens of *Xiphactinus* with consumulites as well as several other bony fishes that exhibit similar examples (Table A.8; see discussions and/or listings in Bardack, 1965; Konuki, 2008; Everhart, 2017). There is also a significant record of osteicthyans with consumulites from Lebanon (Davis, 1887; Woodward, 1901; Viohl, 1990; Konuki, 2008; Amalfitano et al., 2017). Other examples are known from Brazil (Viohl, 1990), Morocco (Arambourg, 1954; Cavin, 1999), France (Poplin, 1986) and Germany (Diedrich, 2012b).

A large number of mosasaur skeletons preserve consumulites (Table A.8). Most examples are from the United States (e.g., Konuki, 2008; Everhart, 2017), but specimens also occur in Canada (Konishi et al., 2011, 2014), Belgium (Dollo, 1887a, b, 1913) and Angola (Strganac et al., 2015). Mosasaur consumulites contain a large range of vertebrate prey items, including turtles (Dollo, 1887a,b; Konishi et al., 2011), sharks (Martin and Bjork, 1987), bony fishes (Williston, 1899, 1914; Camp, 1942; Martin and Bjork, 1987; Konishi et al., 2014; Everhart, 2017), plesiosaurs (Everhart, 2004c), mosasaurs (Martin and Bjork, 1987; Bell and Barnes, 2007; Strganac et al., 2015) and birds (Martin and Bjork, 1987). The invertebrate content of mosasaur consumulites includes belemnites (Dollo, 1913), echinoids (Dollo, 1913) and bivalves (Martin and Fox,

FIGURE 14. Consumulites in ichthyosaur skeletons from the Lower Lias (Hettangian-Lower Pliensbachian) of Lyme Regis, UK. **A,** Consumulite in lateral view (OUM J10320). **B,** Consumulite in lateral view (OUM J13593), also see Buckland, 1836, pl. 14).

2004).

Late Cretaceous plesiosaur consumulites occur in the United States (Cope, 1868, 1872; Brown, 1904; Martin and Kennedy, 1988; Storrs, 1999; Cicimurri and Everhart, 2001), Canada (Nicholls, 1988) and Japan (Matsumoto et al., 1982; Sato and Tanabe, 1998; Sato and Storrs, 2000). Most of these consumulites contain cephalopods (Brown, 1904; Sato and Tanabe, 1998; Sato and Storrs, 2000; Cicimurri and Everhart, 2001), fishes (Cope, 1868; Brown, 1904; Martin and Kennedy, 1988; Nicholls, 1988; Cicimurri and Everhart, 2001), mosasaurs (Cope, 1872; Storrs, 1999) and pterosaurs (Brown, 1904).

There is a single example of a Cretaceous pterosaur consumulite. This bromalite occurs in the throat of *Pteranodon* sp. and includes partially digested fish material, so it may be a regurgitalitic mass in the process of being egested (Brown, 1943; Bennett, 2001).

Nonmarine

There are many instances of Mesozoic nonmarine consumulites, but a large percentage are associated with two Lagerstätten, the Late Jurassic Solnhofen Limestone of Germany, which is dominated by fish, and the Early Cretaceous Jehol biota of China in which most bromalites occur in tetrapods (Fig. 12; Table A.9). Hunt et al. (2018) reviewed the consumulite record from the Late Triassic.

There are no reported Early or Middle Triassic consumulites. There are eight Late Triassic examples in terrestrial reptiles and one in a pterosaur. Three phytosaurs from the United States

FIGURE 15. *Xiphactinus audax* (FHSM VP-333) from the Upper Cretaceous Smoky Hill Chalk of Kansas, USA, with a consumulite of *Gillicus arcuatus* (Everhart, 2017, fig. 5.1). Length of *Xiphactinus* is approximately 4 m long and *Gillicus* is 1.8 m long. Photograph courtesy of Michael Everhart.

and India preserve consumulites that indicate consumption of a range of tetrapods, including the metoposaurid *Apachesarus* and reptiles, including *Vancleavea, Trilophosaurus* (=*Malerisaurus*: Spielmann et al., 2006), a phytosaur and a rhynchosaur (Chatterjee, 1978, 1980; Hunt, 1991, 1994, 2001; Hunt and Lucas, 2014b). The paracrocodylomorph *Postosuchus alisonae* from the eastern United States contains a gastrolite with a diverse assortment of prey, including a partial skeleton of a small aetosaur (cf. *Aetosaurus*), a snout, left coracoid, and left humerus of the traversodont cynodont *Plinthogomophodon herpetairus*, two articulated phalanges of a large dicynodont, and a fragment of an unidentified ?temnospondyl bone. Some of the bones have dentalites, and others display periosteal erosion likely caused by digestion (Sues et al., 2003; Peyer et al., 2008).

Specimens of the Late Triassic theropod *Coelophysis bauri* from the western United States contain oralites, incorporeal dentalites and a gastrolite with a specimen of *Hesperosuchus* (Nesbitt et al., 2006; Rinehart et al., 2009; Hunt and Lucas, 2014b). The Italian theropod *Notatesseraeraptor frickensis* has a consumulite that includes a maxilla of the rhynchocephalian *Clevosaurus* (Unterrassner, 2009).

There are no reported Early Jurassic consumulites, but Middle Jurassic specimens include fish, amphibians and a dinosaur (Fig. 12; Table A.9). Many specimens of the bony fish *Todiltia schoewei* and a few of *Hulettia americana* from a Middle Jurassic Todilto Formation in New Mexico contain gastrolites and intestinilites (Lucas et al., 1985b; Hunt and Lucas, 2014b; Fig. 13). Post-Paleozoic amphibian consumulites are rare, but there are three examples from the Middle Jurassic of China, including *Jeholotriton paradoxus* and *Chunperpeton tianyiensis*, which contain conchostracans, and a specimen of *C. tianyiensis* that yields insects (Gao and Shubin, 2003; Dong et al., 2012). The theropod *Poekilopleuron bucklandii* from France contains a tooth of the hybodont shark *Polyacrodus* sp. and bone fragments that resemble skeletal elements of cartilaginous fishes (Eudes-Deslongchamps, 1838).

There are more than 120 consumulites from the Upper Jurassic of the Solnhofen area in Germany (including the Ettling Lagerstätte of Ebert et al., 2015), which principally relate to fish and pterosaur skeletons. More than 110 fish skeletons representing more than 20 taxa yield consumulites that contain fishes (Table A.9: e.g., Viohl, 1990; Ebert et al., 2015). The coelacanth *Undina penicillata* is the only taxon from Solnhofen to have undoubtedly ingested a conspecific, and this was initially interpreted as evidence of ovoviparity but more recently of predation (Watson, 1927; Schultze, 1972). Five specimens of the pterosaurs *Rhamphorhynchus* and two of *Pterodactylus* contain consumulites composed of fish material (Broili, 1938; Wellnhofer, 1970, 1975a, b; Kellner, 2006; Frey and Tischlinger, 2012; Witton, 2013, 2018; Hone et al., 2013, 2015). The holotype of the theropod *Compsognathus longipes* contains a skeleton of the lepidosaur *Bavarisaurus* cf. *B. macrodactylus* (Ostrom, 1978). Outside of Solnhofen, there are four Late Jurassic fishes and a turtle that also contain consumulites (Eastman, 1911; De Saint Seine, 1949; Joyce et al., 2021).

The majority of consumulites from the Lower Cretaceous derive from the Jehol Lagerstätte in northeastern China and include specimens from a frog, a choristodere, nine theropods, 13 birds, a pterosaur and a mammal (Table A.9). The frog *Genibatrachus baoshanensis* contains as a consumulite a skeleton of a salamander, cf. *Nuominerpeton* (Xing et al., 2019). Seven juvenile skulls of the choristodere *Monjurosuchus splendens* were found within the skeleton of an adult, indicating cannibalism in this taxon (Wang et al., 2005). The diversity of small, derived theropods and birds and their consumulites from Jehol provides important information about the development of the crop, proventriculus and ventriculus (O'Connor et al., 2019) discussed below. We introduce the term cropalite for preserved contents of the crop, and the term proventrilite for contents of the proventriculus. Mayr et al. (2021) demonstrated that several putative ovarian follicles in some Jehol birds actually represent propagules assignable to *Carpolithes multiseminalis*: (1) carbonaceous or originally carbonaceous; (2) putative follicles have similar dimensions in differently sized birds; (3) simultaneous maturing of multiple follicles unlikely; (4) no evidence of medullary bones; and (5) unlikely in specimens with little or no soft tissue preservation. We follow O'Connor (2019) and O'Connor and Zhou (2019) in the recognition of other paravian consumulites from Jehol (Table A.9). The gastrolite of the mammal *Repenomamus robustus* is significant in that it provides direct evidence of predation on dinosaurs, as it contains remains of a juvenile of the ceratopsian *Psittacosaurus* (Hu et al., 2005). Surprisingly, Ji et al. (2016) reported fish remains in the presumably herbivorous ankylosaur *Liaoningosaurus paradoxus*.

A salamander and a bird from the Early Cretaceous of Spain yield consumulites (Sanz et al., 1996; Evans, 2016; O'Connor, 2019). Two theropods contain consumulites, the large English theropod *Baryonyx walkeri* contains fish and *Iguanodon* bones, and the Italian *Scipionyx samniticus* yields fish and lepidosaurian bones (Charig and Milner, 1986, 1997; Dal Sasso and Signore, 1998; Dal Sasso and Maganuco, 2011). The ornithischian ankylosaur *Mimni* sp. from Australia contains a consumulite with plant debris and seeds (Molnar and Clifford, 2000, 2001). *Ludodactylus sibbicki* is a pterosaur from Brazil with the unusual oralite of a leaf between mandibular rami (Frey et al., 2003; Witton, 2018).

There are less than a dozen reports of consumulites from the Late Cretaceous, and they all represent tetrapods (Fig. 12; Table A.9). The two examples that do not pertain to dinosaurs or birds are both from Brazil. These are an unidentified frog and the baurusuchid crocodyliform *Aplestosuchus sordidus* (Leal and Martill, 2007; Godoy et al., 2014). Theropods are represented by three specimens from Mongolia and the United States. The American example is acid-etched vertebrae and a fragmentary dentary from a juvenile hadrosaur found in association with *Daspletosaurus* sp. (Varricchio, 2001). The Mongolian (Hone et al., 2012; Lee et al., 2014), or putative Mongolian (Sereno et al., 2009; Fowler et al., 2011), specimens are *Deinocheirus mirificus* (fish), the enigmatic ?*Raptorex kreigsteini* (*Lycoptera* or Ellimmichthyiformes) and *Velociraptor mongoliensis* (azhdarchid pterosaur). At least four hadrosaurs from Canada and the United States contain plant debris that has been interpreted as consumulites (Kräusel, 1922; Ostrom, 1964; Taggert and Cross, 1997; Currie et al., 1995; Tweet et al., 2008, 2016). The sole Late Cretaceous bird consumulite of *Enantiophoenix electrophyla* is from Lebanon and is interesting because blebs of amber were interpreted to be evidence of feeding on sap (Dalla Vecchia and Chiappe, 2002; Cau and Arduini, 2008).

Cenozoic

Marine

There are relatively few consumulite reports from the Paleogene-Quaternary. The majority pertain to fish, with four examples from whales and one from a bird (Fig. 12; Table A.10).

The early Eocene Pesciara di Bolca Konservat–Lagerstätte in Italy has yielded nine examples of consumulites from fish– two from sharks and the remainder from bony fish (Table A.10; Agassiz, 1833-1845a, b; Sorbini, 1972; Fanti et al., 2016; Friedman and Carnevale, 2018). The presence of remains of the barracuda *Sphyraena bolcensis* within the shark *Galeorhinus cuvieri* is interesting because there is a predator: prey relationship between these genera in modern reef systems (Fanti et al., 2016). Other consumulite examples occur in a Miocene shark and a whale from Peru (Lambert et al., 2015; Collareta et al., 2017c) and bony fish in the Oligocene of Germany (Weiler, 1934) and Romania (Paucă, M., 1933), the Miocene of Algeria (Carnevale and Pietsch, 2006), Peru (Collareta et al., 2017c) and the United States (Crane, 1996) and the Pliocene of Italy (Sorbibi in Boucot, 1990; Viohl, 1990).

Three late Eocene whales from Egypt contain consumulites. *Basilosaurus isis* yields bones of a juvenile whale (*Durodon atrox*) and large fishes (*Pycnodus mokattamensis*), *B. cetoides* contains fishes and sharks, and *D. atrox* contains fishes (Swift and Barnes, 1996; Uhen, 2004; Voss et al., 2019). Martínez-Cáceres et al. (2017) describe another example from Peru. An undescribed late Miocene whale contains bones of the sardine *Sardinops*, which provides the first evidence of piscivory in an edentulous mysticete (Collareta et al., 2015). Lambert et al. (2015) described specimens of the clupeiform *Sardinops* sp. cf. *S. sagax* in the odontocete *Messapicetus gregarius* from the same strata in Peru. An early Oligocene loon (?*Colymboides metzleri*) from Germany has a gastrolite consisting of fragments of small fish (Mayr, 2004).

Nonmarine

The consumulite record from nonmarine Cenozoic rocks is skewed by large samples from several Lagerstätten, notably the Eocene Green River Formation of the United States and the Middle Eocene Messel Lagerstätte of Germany (Fig. 12; Table A.11). The Paleocene Menat Lagerstätte in France yields the oldest Cenozoic consumulites, with a fish within a crocodylomorph and a gastrolite within an insectivore (Guth, 1962; Wedmann et al., 2018).

The lacustrine Green River Formation includes a number of fish consumulites (Jepsen, 1967; Boreske, 1974; Ulrich, 1978 – cited by Boucot, 1990; Grande, 1980). A notable specimen is an example of a consumulite within a consumulite – *Amia uintaensis* consumed *Diplomystus,* which, in turn, had consumed *Knightia* (Boreske, 1974; Grande, 1980).

The Middle Eocene of Messel has yielded many consumulites, notably from multiple mammals (Franzen, 1976, 1977, 1984, 1985; Richter and Storch, 1980; von Koenigswald et al., 1981, 1992; Maier et al., 1986; Richter, 1988; Collinson, 1990; Storch, 2001) and birds (Mayr and Peters, 1998; Mayr and Mourer-Cauvré, 2000; Mayr, 2002, 2009, 2013; Mayr et al., 2004, 2006; Morlo, 2004; Mayr and Richter, 2011; Table A.11). These consumulites pertain to both carnivores and herbivores. Multiple specimens of *Rhenanoperca minuta* and *Thaumaturus intermedius* yield insects, crustaceans and fish (Richter and Baszio, 2001a, 2006). Two lizards and two snakes contain gastrolites (Greene, 1983; Schall, 2004;Weber, 2004; Smith and Scanferia, 2016; Scanferia and Smith, 2020). One specimen of *Eoconstrictor fisheri* has the lizard *Geiseltaliellus maarius* in its stomach that in turn contains an insect in its digestive tract (Smith and Scanferia, 2016). This is only the second example of a consumulite within a consumulite. Five specimens of the putative pangolin *Eomanis waldi* have gastrolites of coarse sand and plant debris rather than the insects that might be expected (von Koenigswald et al., 1981; Richter, 1988).

Other terrestrial mammals from Messel with consumulites represent nine families (Pantolestidae, Dichobunidae, Equidae, Gliridae, Ischyromyidae, Choeropotamidae, Adapidae, Proviverridae and Amphilemuridae). The bat *Palaeochiropteryx tupaiodon* principally yields lepidopteran wings but also some hair that presumably was derived from grooming (Richter and Storch, 1980; Richter, 1988). Other bats contain moths, caddis flies and beetles (Habersetzer et al., 1994). Several birds yield consumulites. Eleven taxa of birds yield gastrolites and cropalites (Mayr and Peters, 1998; (Mayr and Mourier-Chauviré, 2000; Mayr, 2002, 2009, 2013, 2015; Morlo, 2004; Mayr et al., 2006; Mayr and Richter, 2011; Mayr and Wilde, 2014). For example, the mousebird *Masillacolius brevidactylus* yields a large seed (Mayr, 2015).

Alexander and Burger (2001) described a crocodilian, *Pristiochampsus vorax*, from the middle Eocene of the United States, which had ingested a hindlimb of the perissodactyl *Helaletes* sp. Oligocene specimens include the frog *Palaeobatrachus* sp. from Germany with ingested fish (Wuttke and Poschmann, 2010), tadpoles of *Pelobates decheni* and *Eopelobates anthracinus* from Germany with granular gut contents, the tortoises *Stylemys* sp. and *Stylemys nebrascensis* from the United States with hackberry seeds (Marron and Moore, 2013) and the bird *Oligocolius psittacocephalon* from Germany with fruit stones in its crop (Mayr, 2013).

Miocene consumulites include the fish *Lepidocottus* from Germany, which fed on planorbid snails (Wuttke and Poschmann, 2010), and *Rama pueyoi* frogs and their tadpoles from Spain, respectively, which preserve gastrolites composed of gastropod shells (with rarer plants, arthropods and larval anurans) and fine debris that includes diatoms (McNamara et al., 2009, 2010; Wuttke and Poschmann, 2010). The only recorded Miocene mammalian consumulite is from the canid *Carpocyon* from the United States, which ingested the rabbit *Hypolagus* and other small mammals (Green, 1948; Stirton, 1959; Tedford in Boucot, 1990). We have found no records of Pliocene consumulites.

There are many examples of Pleistocene consumulites. The frozen mummies of large herbivores that contain consumulites, notably *Mammuthus*, *Coelodonta*, *Equus* and *Bison,* have been extensively studied (Ukraintseva, 1981, 1993; Guthrie, 1990; Harington, 2007; van Geel et al., 2008; Boeskorov et al., 2011, 2014; Kosintsev et al., 2012). Several studies confusingly use the terms "feces" and "dung" to refer to fragments of consumulites of *M. primigenius* (e.g., Van Geel et al., 2004, 2011; Mol et al., 2006).

Ichnotaxobases and Ichnotaxonomy

There are currently only four named consumulites, three preserved within the body cavity, *Werneburgichnus kinneyensis, W. varius* and *Chondripilula zideki* (Hunt and Lucas, 2021a), and the evisceralite *Hiabromus seilacheri* (Hunt et al., 2012b). Evisceralites are discrete bodies, so ichnotaxobases include shape, size, content, composition and surface texture. However, there are distinct morphologies and content that should allow the erection of other ichnotaxa of consumulites preserved within body cavities. Bromalite content representing different diets would represent different ichnotaxa because they represent different behaviors. Potential ichnotaxobases include: (1) location of bromalite in digestive tract; (2) morphology, e.g., pellet, infilling that follows form of digestive tract; (3) nature of contents and inclusions (including taxonomic identification of inclusions); and (4) degree of mechanical and biochemical processing.

Utility

Consumulites provide the most compelling evidence of diet, as they are direct evidence of what a vertebrate animal consumed. However, the study of consumulites is in an early stage of development, though they also have great potential to provide direct evidence of aspects of patterns of digestion, such as:

1. Assessing the chemistry of digestive systems by examining the etching and erosion of consumulite materials (e.g., degradation of bones within mosasaurs: Strganac et al., 2015)
2. Studying the evolution of the components of the digestive system, as has been done so successfully with early birds (e.g., O'Connor et al., 2019) and also with fish (Janvier and Arsenault, 2007).
3. Analyzing dietary changes through ontogeny, as has been done with "branchiosaurs" (e.g., Werneburg et al., 2007) and ichthyosaurs (Dick et al., 2016).
4. Evaluating the evolution of diets within clades (e.g., ichthyosaurs: Druckenmiller et al., 2014).
5. Identifying environmental tolerances (e.g., nonmarine ostracods in larval amphibians indicate that the amphibians were not marine: Werneburg et al., 2021).

Consumulites preserve a wide range of organic elements with a poor fossil record, ranging from lepidopteran wings to hair (Richter and Storch, 1980; Richter, 1988) to embryos (O'Keefe et al., 2009) and thus can be Lagerstätten as first proposed by Wilby and Martill (1992). In addition, consumulites can also preserve tissues of the gastrointestinal tract (Wilby and Martill, 1992). The systematic study of consumulites will undoubtedly yield significant records of contained fossils as has the recent focus on the content of coprolites.

Conclusions

This review demonstrates that there is an extensive and under appreciated fossil record of consumulites. This record provides the most direct evidence of who was eating who in the past and has substantial potential to address a number of evolutionary and paleoecological issues, notably the evolution of digestive systems, including the function and location of organs, the evolution of diets within clades and the ontogeny of species.

GASTROLITHS

Terminology

We use the term gastrolith to refer to sand and/or gravel swallowed by an animal and retained in the digestive tract. Wings (2004, 2007) provided a detailed review of some of the terminology of gastroliths. We reprise that review here and discuss additional terminological issues not covered by Wings. Thus, our focus is on these terms: gastrolith, geophagy, lithophagy, gizzard, grit and stone.

Though its first use apparently was by Mayne in 1854 (Baker, 1956), the term gastrolith (Greek *gastros*, stomach and *lithos*, stone) has only been in frequent use since the early 1900s. In some of the literature, particularly that dealing with extant animals, the terms "stomach stone" and "gizzard stone" are used interchangeably with gastrolith. In dictionaries of geological terms, gastroliths are usually referred to as "stomach stones" used as "an aid to digestion" (Whitten and Brooks, 1983, p. 198, 428; Currie, 1997), and some note that "such stones acquire a rounding and polish" (Allaby and Allaby, 1991, p. 152). Thus, AGI (1960, p. 119; 1974, p. 201) defines gastroliths (in 1960) and stomach stones (in 1974) as "highly polished, well-rounded pebbles associated with saurian skeletons," even though gastroliths are often associated with many non-reptilian (non-"saurian") tetrapods.

"Gastrolith" has also been applied in an extensive literature to calcic/phosphatic accretions that form inside the bodies of some decapod crustaceans (lobster and crayfish) just before molting (ecdysis) (Huxley, 1880). The crustaceans remove $CaCO_3$ from their exoskeletons to form these "gastroliths" and usually reabsorb them after molting (Tucker and Tucker, 2018). Found as fossils in the Eocene of Texas and Louisiana, these "gastroliths" have received the taxonomic name *Wechesia pontis* (Frizzell and Exline, 1958; Frizzell and Horton, 1961). Frizzell and Exline (1958) noted that, to avoid confusion, these structures should be referred to as "crustacean gastroliths." Importantly, they should be regarded as part of the body (a derivative of the exoskeleton) of the crustaceans that produced them, not as trace fossils.

Skoczylas (1978) referred to gastroliths as "pebbles, stones and gravel residing in the alimentary tract." Johnston and Enter (1999, p. 507) stated that gastroliths are "usually made of silicates and are rounded, highly polished and have a waxy feel." Schmeisser and Gillette (2009, p. 453) presented a simple definition of gastrolith: "gastroliths are stones ingested by extant and extinct animals that are retained in the digestive tract." Schmeisser and Flood (2008, p. 72) defined "paleogastrolith" as "stomach stones associated exclusively with extinct animals." However, we do not make such a distinction, as the gastroliths of extinct animals are, in principle, the same as those of extant animals in terms of origin and function (actualism).

Wings (2007, p. 2) defined gastrolith as "a hard object of no caloric value (e.g., a stone, a natural or pathological concretion) which is, or was, retained in the digestive tract of an animal." This brings the "crustacean gastroliths," pathological concretions that form in some mammal's stomachs ("Bezoar stones:" DeBakey and Ochsner, 1939; Tomassini et al., 2019; Rothschild and Biehler-Gomez, 2021) and swallowed "stones" (sand/gravel) together under the single term gastrolith. So, it refers to objects formed by three very different processes. We do not endorse that definition, as it groups together three kinds of objects with different origins and function, so we prefer to restrict the term gastrolith to sand and/or gravel swallowed by an animal and retained in the digestive tract.

Because Wings (2007) grouped objects with different origins under the single term gastrolith, he proposed to add prefixes to the word gastrolith to create terms that identified their different origins: "bio-gastrolith" for the calcareous concretions formed in the bodies of some crustaceans; "patho-gastrolith" for concretions formed in the stomach pathologically; and "geo-gastroliths" for swallowed rock particles. These terms are unnecessary if gastrolith is restricted to the meaning we advocate, which is the same as Wing's "geo-gastrolith."

Wings (2007) also advocated using the term "exolith" for "stones" that might be gastroliths but lack a convincing skeletal association. This term, however, enshrines the widespread misconception that highly polished "stones" are gastroliths, regardless of any skeletal association (see later discussion). It also lacks specificity, as any polished "stone" anywhere could be called an exolith. Thus, we do not use the term exolith.

The terms lithophagy and geophagy have also been applied by some to refer to the process of acquiring gastroliths, and some use them interchangeably (e. g., Sokol, 1971; Skoczylas, 1978). Lithophagy has a standard definition as the ingesting of "stones" to aid in digestion. But, geophagy refers to eating earth, particularly chalk or clay, and especially by humans, though some nonhuman animals (such as some bats) do engage in geophagy (e.g., Abrahams, 2003). The consumption of earth is either as a dietary supplement or is an eating disorder (Geophagia). Geophagy should not be used in reference to the ingestion of "stones," which is correctly called lithophagy.

When Brown (1904) suggested that plesiosaur gastroliths resided in a "gizzard-like arrangement," Eastman (1904) rebuked him, stating that only birds have gizzards (see below). In birds, the gizzard (ventriculus or muscular stomach: Figs. 16-17) is an anatomical structure separate from and posterior to the stomach (Romer and Parsons, 1977, figs. 272C, 273E). Other vertebrates lack such a structure. Nevertheless, the term gizzard (or "pyloric gizzard") has been applied by some workers to a distinct muscular compartment of the posterior portion of the stomach in crocodiles (e.g., Pernkopf, 1929; Sokol, 1971; Romer and Parsons 1977; Luppa, 1978; Skoczylas, 1978; Parson and Cameron, 1997; Schwenk and Rubega, 2005). This is because the crocodilian stomach has two chambers, fundus and pyloris, and the pyloric part is sometimes called a gizzard (Varrichio, 2001, argued that such a two-part stomach is a synapomorphy of archosaurs).

Sokol (1971, p. 70) stated that in crocodiles "the posterior end of the stomach [is] modified to form a distinct gizzard." This "pyloric gizzard" of crocodiles may be homologous with the true gizzard of birds, but there are real questions about whether the primary function of gastroliths in crocodiles is to grind food, as it is in the birds (see below). Therefore, we would rather not say that crocodilians have (had) a gizzard, but simply say that they retain gravel in a posterior part of the stomach.

The term grit is widely used to refer to the rock particles swallowed by birds (e.g., Gionfriddo and Best, 1999). However, grit, generally defined as a hard and sharp (rock) granule, has no size specificity except in industrial applications (sandpaper, etc.). If we follow the Wentworth scale used by most geologists for particle size, gastroliths in living birds, which are about 1-10 mm in size range, are very fine to coarse sand to granules and pebbles (Fig. 18). Gastroliths of plesiosaurs and some dinosaurs are larger, as large as cobbles on the Wentworth scale. Thus, we do not advocate continued use of the imprecise term "grit" in reference to avian gastroliths.

Stone is another imprecise term widely used in the gastrolith literature. It has vernacular definitions such as a hard, solid, nonmetallic mineral matter that rocks are made of, or a hard earthen substance. As the definitions of gastrolith given above indicate, the terms gastrolith and stone are often used interchangeably. However, like grit, stone has no specific size limits, and the sand particles that comprise many gastroliths, particularly in birds, would not be called stones. Thus, we abandon the imprecise term stone when referring to gastroliths and replace it with clast, or with more precise terms based on the Wentworth scale, namely sand, granules, pebbles or cobbles (Fig. 18).

We do not consider uroliths (bladder stones, kidney stones), gallstones or bezoars herein since they are pathologic in origin and thus are not technically trace fossils (sensu Bertling et al., 2006). However, they could be confused with gastroliths (Rothschild and Biehler-Gomez, 2021).

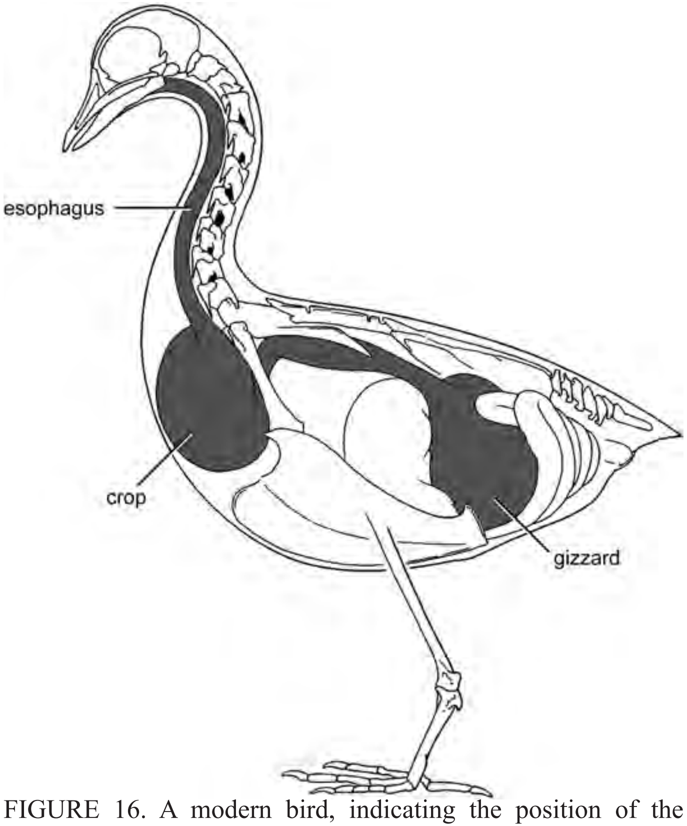


FIGURE 16. A modern bird, indicating the position of the esophagus, crop and the gizzard (modified from Zheng et al., 2011).

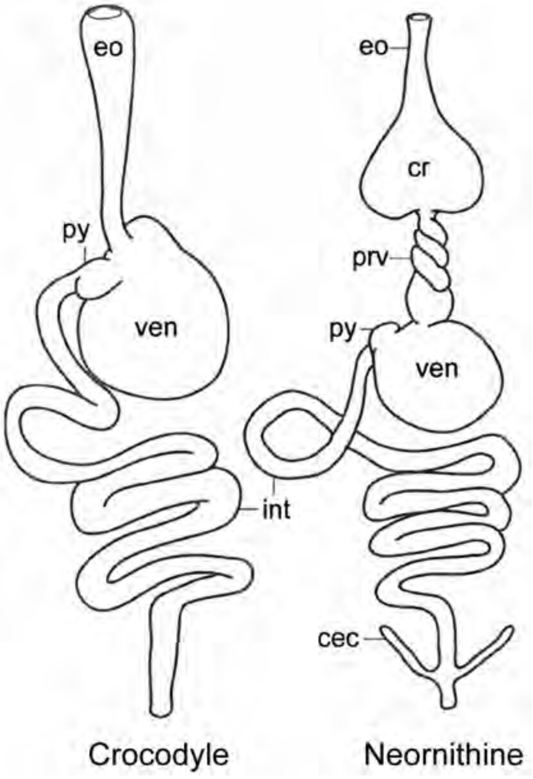
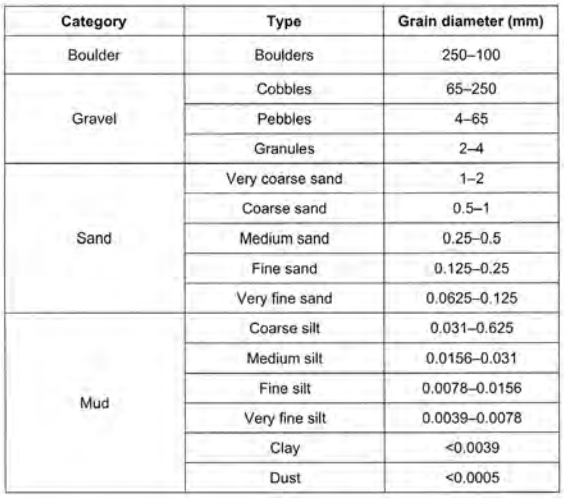


FIGURE 17. Comparison of crocodile and bird alimentary tracts (modified from O'Connor, 2019). Abbreviations are: cec = ceca; cr = crop; eo = esophagus; int = intestines; prv = proventriculus; py = pyloric chamber; ven = ventriculus.



Category	Type	Grain diameter (mm)
Boulder	Boulders	250–100
Gravel	Cobbles	65–250
	Pebbles	4–65
	Granules	2–4
Sand	Very coarse sand	1–2
	Coarse sand	0.5–1
	Medium sand	0.25–0.5
	Fine sand	0.125–0.25
	Very fine sand	0.0625–0.125
Mud	Coarse silt	0.031–0.625
	Medium silt	0.0156–0.031
	Fine silt	0.0078–0.0156
	Very fine silt	0.0039–0.0078
	Clay	<0.0039
	Dust	<0.0005

FIGURE 18. Wentworth scale for size of sedimentary particles.

Some History

According to Skoczylas (1978), in 1668 the German natural philosopher Henry Oldenburg (1619-1677) described "stomach stones" in an extant crocodile. This report by Oldenburg (1668) was actually of observations of gastroliths in a caiman made by a Dr. Stubbes. Wings (2004) notes that Spallanzini (1785) described gastrolith use by birds. Baker (1956) stated that Mayne (1854) first used the term *Gastrolithus* to refer to a "stone or calculus in the stomach." Lequat (1708) may be the oldest published reference to gastroliths in an extinct vertebrate. He noted their presence in a recently extinct (within historical times) bird, the solitaire (*Pezophaps*) from the Island of Rodrigues, east of Madagascar in the Indian Ocean (also see Caldwell, 1875).

Seeley (1877, p. 546) reported gastroliths in a British Cretaceous elasmosaur, suggesting that "a structure analogous to a gizzard, or the stomach of an edentate, may have used these pebbles to assist in breaking up or crushing the food on which this saurian lived." Mudge (1877) made similar observations on American plesiosaur gastroliths, though the first American plesiosaur skeletal material associated with gastroliths was likely collected in the 1860s (Everhart, 2005e).

Real discussion of gastroliths in extinct vertebrates began in the early 1900s. Thus, Brown (1904, p. 185) briefly commented on stones associated with plesiosaur skeletons in the Cretaceous of Kansas, USA, and stated that they had formed a "gizzard-like arrangement" used to aid digestion. As noted above, Eastman (1904) countered Brown's idea, arguing that a gizzard is a feature exclusive to birds. In contrast, Henderson (1906) stated that similar stones are swallowed by extant sea lions and held in the stomach, concluding that the diets of plesiosaurs were similar to those of the sea lions. Williston (1904), replying to Brown (1904), noted that stones are common in the abdominal regions of both European and North American plesiosaur skeletons, and that the British paleontologist Seeley (1877) had first suggested their use in digestion in a "gizzard." Williston (1904), however, did not believe the plesiosaurs swallowed stones to aid in digestion, but instead used them as ballast to regulate buoyancy.

Williston (1906) noted that Mudge (1877) and Williston (1891) had described siliceous pebbles associated with elasmosaurs from the Upper Cretaceous of Kansas and Wyoming. He concluded that "the plesiosaurs had a real, muscular bird-like gizzard, which utilized the pebbles in whatever way the crocodiles may use them" (Williston, 1906, p. 227).

Wieland (1906, p. 820) joined the discussion, "coining" the term gastrolith: "stomach stones, or *gastroliths*, as I shall conveniently call them." (note that Johnston and Enter, 1999, erroneously attributed the term to Brown, 1907). Wieland noted polished stones associated with a "sauropod" bone from the Upper Jurassic of the northern Bighorn Mountains in Wyoming-Montana, USA. Wieland (1920) later referred to these as "pebbles of a singular smoothness." Nevertheless, Wieland (1906, p. 821) initially regarded the highly polished surfaces as primary (polished before they were ingested), not polish produced after swallowing, identifying "secondary or gastral wear" as producing a roughened surface.

Cannon (1906) stated that such pebbles were associated with Morrison Formation sauropod fossils from Colorado. Eastman (1906) expressed further skepticism. In rejoinder, Wieland (1907, p. 66), contrary to his earlier opinion, stated that in dinosaurian gastroliths "their entire surface may exhibit a higher polish than wind or water ever produces." Brown (1907) endorsed the idea of high polish characterizing gastroliths, but he expressed doubt about the identity of the dinosaur gastroliths described by Wieland.

This discussion between Brown, Williston, Wieland and Eastman set up three ideas about gastroliths that have been much discussed in later studies: (1) plesiosaurs had gastroliths that were used either for diet or buoyancy control; (2) sauropod dinosaurs had gastroliths; and (3) high polish is characteristic of gastroliths. What followed for about one century is a diffuse literature that has documented gastroliths in various fossil vertebrates (particularly plesiosaurs) and a less extensive literature that has debated their function. Particularly important was the work of Bryan (1931), who cogently argued that high polish does not character gastroliths, a conclusion ignored by many subsequent workers.

Much literature has focused on dinosaur gastroliths, in particular, identifying clasts without skeletal associations or with very loose skeletal associations as gastroliths, simply because they are highly polished. Archeologists have followed suit, identifying polished sand/pebbles at archaeological sites as bird gastroliths, although they lack any association with avian bones. And, some geologists have identified dropstones and other exotic clasts as gastroliths.

Wings (2004) undertook the first extensive study of gastroliths in extinct vertebrates, and his results seem not to have been fully appreciated yet. Thus, his work supports the concept that high polish does not characterize gastroliths and reinforces earlier conclusions that without a plausible skeletal association (i.e., mass of stones in the abdominal cavity), no sand/gravel can be verified as gastroliths.

Actualistic Basis

Overview

Extensive reviews of gastroliths in extant vertebrates have been published (Wickes, 1908; Baker, 1956; Taylor, 1993; Whittle and Everhart, 2000; Wings, 2004, 2007), obviating the need for a detailed review here. Gastroliths are rare among living fishes (a handful of osteichthyans swallow sand and/or gravel to grind food, and possible gastroliths in Devonian placoderms are discussed by Long and Trinajstic, 2010), and none are known among extant amphibians. Among mammals, some pinnipeds swallow gravel, likely for buoyancy control (Emery, 1941; Fleming, 1951; Taylor, 1993; Wings, 2007). Modern pangolins have a muscular stomach and swallow fine gravel that is retained in the stomach (e.g., Walker, 1968). In contrast, many living reptile and bird species swallow sand and/or gravel. Thus, some living turtles, snakes, lizards and crocodilians (see more below) swallow sand/gravel, mostly to grind food (Sokol, 1971), and many birds (in particular, most herbivorous and omnivorous birds) use gastroliths to aid digestion.

Nevertheless, the distribution of gastroliths is very irregular

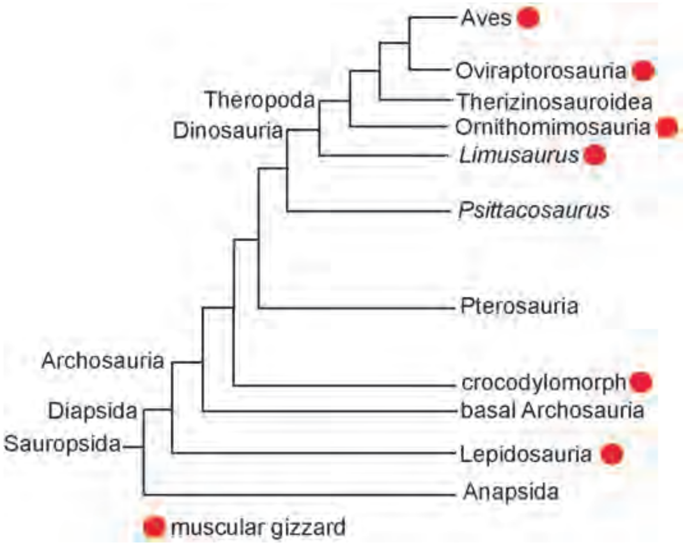


FIGURE 19. Simplified vertebrate phylogeny showing the distribution of the muscular gizzard (after O'Connor, 2019).

in extant vertebrates and is often related to the presence of a muscular gizzard (Fig. 19). For example, a few species of crocodilians swallow gravel, whereas others do not, and, in a population of crocodilians that swallow gravel, some individuals apparently do not. As Whittle and Everhart (2000, p. 77) well observed, "lithophagy in extant turtles, lizards and marine Mesozoic diapsids appears to be species-specific." We would add that the literature suggests that swallowing or not swallowing sand/gravel can be specific to some individuals within a species as well. The literature on extant crocodilian and bird gastroliths is most extensive, so we discuss these two taxa separately.

Crocodilia

Most of the scientific literature on gastroliths in extant reptiles focuses on crocodilians, especially the Nile crocodile (*Crocodilus niloticus*) and American alligator (*Alligator mississippiensis*), two species long known to have gastroliths (e.g., Cott, 1961; Neill, 1971). Nevertheless, there has long been disagreement over the function of the gastroliths in extant crocodilians, divided into those who see them as used in digestion to grind food (e.g., Pooley and Gans, 1976) and those who advocate that crocodilians use the gastroliths to control buoyancy (Cott, 1961).

In a much cited and highly influential article, Cott (1961) argued that the gastroliths of living crocodilians were not used in digestion but instead increased stability while in water. However, Henderson (2003) undertook three-dimensional computer modeling of the effects of gastroliths on a crocodilian to conclude that they would have little to no effect on buoyancy or stability while in water. Thus, the gastroliths in his model represent less than 4% of body mass and had much less effect on depth of immersion or inclination than did the crocodile simply inflating/deflating the lungs.

Platt et al. (2006) documented that gastroliths are present in all of the growth stages (from hatchlings to adults) of at least one crocodilian species, and argued that this indicates they are not for buoyancy control. Platt et al. (2006) concluded that the gastroliths are used to break down ingested prey.

Nevertheless, the idea of buoyancy control by crocodiles using gastroliths has had, and continues to have, wide support (e.g., Cott, 1961; Seymour, 1982; Grigg and Kirshner, 2015; Uriona et al., 2018). Particularly compelling were experiments by Uriona et al. (2018) on dive duration by juvenile American alligators. As little as 2.5% of body weight in gastroliths increased the duration of dives by 88-117%. The reasoning is that the gastroliths increase specific gravity, thus allowing a greater lung volume in order to prolong the dive. This increases the time of submersion and may also be important to the Nile crocodile, which normally drowns prey items while submerged (Cott, 1961). It may also be consistent with the modeling of Henderson (2003), as his model indicates the interplay between gastrolith mass and lung volume. Furthermore, there seems to be little if any direct evidence that extant crocodiles use their gastroliths in digestion (see Wings, 2004), so their use in buoyancy by crocodiles may be the most well supported function.

Aves

Most of the extant species of vertebrates that swallow sand/gravel are birds, who use them in a gizzard to aid digestion, particularly herbivorous birds (e.g., Pough et al., 2002). After birds swallow food, if necessary, they store it in the crop, a chamber connected to the esophagus (a ventral pouch anterior to the furcula) (Figs. 16, 17). They then pass food into the gizzard (ventriculus or muscular stomach) where it can be ground by sand/gravel that has been swallowed and stored in that chamber. Once processed in the gizzard, the food is passed to the true stomach. This differs from crocodilians, whose swallowed pebbles go directly to the stomach and, if retained, are then stored in the posterior (pyloric) portion of the stomach (see above).

A diverse literature on the gastroliths of living birds exists, much of it summarized by Gionfriddo and Best (1999), who concluded: (1) most birds swallow sand/gravel to mechanically grind and pulverize food in their gizzards, though some sand/gravel is swallowed for mineral extraction (especially calcium) or to stimulate/facilitate digestion; (2) the size of the swallowed clasts correlates to body size and ranges in diameter from < 0.1 mm to > 25 mm (in ostriches: Meinertzhagen, 1954); (3) the larger the sand/gravel swallowed, the harder and coarser the diet; (4) most birds selectively swallow rough and angular sand/gravel that can become more rounded in the gizzard; and (5) some birds prefer sand/gravel of a certain color (also see Milton et al., 1994; Tryon, 2002).

As noted above, in the ornithological literature, the clasts swallowed by birds are usually referred to as "grit." However, on the Wentworth size scale they are very fine sand to gravel (Fig. 18).

Fritz et al. (2011) demonstrated that gizzard-based reduction in particle size in herbivorous birds is as efficient as mastication by herbivorous mammals (also see Moore, 1999). Thus, the evolution of the avian gizzard presents a solution for birds to the problem of how to grind vegetation to produce more effective digestion (and secondarily compensating for the loss of teeth).

Function of Gastroliths

A variety of functions have been suggested for gastroliths, only two of which are of significance: use in digestion to grind, pulverize and/or disintegrate food or use as ballast for buoyancy control (see Wings, 2004, 2007, for a thorough review). Some gastroliths are swallowed while feeding, either by accident (mostly by herbivores browsing close to the ground) or incidentally as the gastroliths inside of a prey item that was consumed.

The function of gastroliths in terrestrial tetrapods seems clear–they are used in digestion. But, in aquatic tetrapods, a digestive function and/or use as ballast for buoyancy control have been advocated and have long been a source of disagreement.

Taylor (1993, 1994) studied the distribution of gastroliths in extant and extinct aquatic tetrapods to conclude that the stones were swallowed as ballast for buoyancy control. Thus, his analysis indicated no correlation between the possession of gastroliths and diet among marine tetrapods. However, according to Taylor, the gastroliths do correlate with a mode of locomotion called "underwater flying," employed by the Mesozoic plesiosaurs, and now by sea lions and penguins. Taylor noted that crocodiles may also swallow stones for ballast (see above), but aquatic tetrapods that use the hind limbs or caudal fin for propulsion (ichthyosaurs, mosasaurs, some pinnipeds and cetaceans) do not swallow stones. Taylor reasoned that the stones are much denser than bone, so they provide an efficient way to take on ballast that can also be released by vomiting and thus provide for rapid regulation of buoyancy.

Nevertheless, gastroliths have been recognized in swimmers that are/were not underwater flyers, including some cetaceans and seals (see review by Wings, 2007). This contradicts the correlation between gastroliths and a specific mode of locomotion (underwater flying) in marine tetrapods, and thus undermines Taylor's (1993, 1994) conclusion that these gastroliths were used only for buoyancy control (Wings, 2007). Indeed, as discussed further below, the case for plesiosaurs using gastroliths for buoyancy control is a weak one. It seems likely that some crocodiles and marine mammals use/used gastroliths for buoyancy control, but all other gastrolith-bearing vertebrates appear to have used them in digestion.

Does High Polish Characterize Gastroliths?

Identification of fossil gastroliths is only certain when the sand/gravel are found as a concentrated mass in an anatomically plausible position within the abdominal region of a fossil skeleton. This conclusion has long been advocated by various authors (e.g., Bryan, 1931; Dorr, 1966; Lucas, 2000; Wings, 2004, 2007; Schmeisser and Flood, 2008). Nevertheless, many pebbles and granules are identified as gastroliths that lack such a skeletal association.

The idea that high polish characterizes gastroliths, first articulated by Wieland (1906) and Brown (1907), has dominated the quest to recognize gastroliths that lack a skeletal association. Indeed, many authors state a priori that gastroliths are highly polished. For example, Johnston et al. (1994, p. 159), who asserted that "a particularly striking characteristic of gastroliths is that they are highly polished." This, despite the fact that the gastroliths of living birds are not highly polished nor are most bona fide fossil gastroliths, especially those of plesiosaurs.

In a classic review of ventifacts, Bryan (1931) stated that the high polish of so-called gastroliths from the Upper Jurassic Morrison Formation in the western USA must have been acquired after the pebbles left the gastrointestinal tracts of the dinosaurs. He based this argument on the observation that quartz pebbles from the gizzard of an extant turkey are not polished, but instead have a "matte" or "frosted" surface texture of numerous conchoidal fractures produced by the impact of the pebbles against each other. As Bryan (1931, p. 36) noted, "the pebbles in a bird's gizzard click together and are abraded by impact" and that "they attained a smooth but not polished surface…formed by innumerable impact fractures." Bryan (1931) concluded that most so-called gastroliths are actually wind-polished stones (ventifacts).

Dorr (1966, p. 272) concurred with Bryan and stated that "no smooth, rounded, or even highly polished stones can be identified as gastroliths unless they are found within the fossilized skeleton of an animal in an area formerly occupied by the digestive tract." Miller (1987) also agreed, noting that many polished and rounded ventifacts from the Pleistocene of New Jersey are identical to so-called gastroliths. And, Schmeisser and Flood (2008, p. 72) well observed that "conclusive identification of paleogastroliths not associated with skeletal remains continues to be problematic."

Actualistic studies convinced Wings and Sander (2007, p. 637) that "natural stones taken up by a bird will not develop any polish in its gastric mill." Indeed, Wings (2009) simulated an avian gastric mill, and it did not polish stones. This is contrary to Hoskin et al. (1970), who claimed, without analysis, that the longer the stones are in a bird's gizzard the more rounded and polished they become. Rounded, yes (see Gionfriddo and Best, 1999), but polished, no.

Despite these conclusions, the literature abounds in diverse identifications of polished "stones" as gastroliths where there is no skeletal association. Particularly striking are identification of dinosaurian gastroliths in Cretaceous strata of Kansas and Minnesota, USA, hundreds of kilometers from the nearest coeval dinosaur bones (Schaffner, 1928; Stauffer, 1945).

Various studies of gravel clasts from the Upper Jurassic Morrison Formation that lack a skeletal association have claimed that particular types or a high degree of polish characterize gastroliths (Kemp, 1936; Minor, 1937; Frison, 1939; Brown, 1941; Salo, 1942; Greene, 1956; Sperry, 1957). These clasts are usually seen as out of sedimentological context–granules, pebbles or cobbles in fine-grained sediments. They are mostly siliceous (quartz, chert, quartzite) and highly polished (Fig. 20). Stokes (1942) first expressed skepticism about these Morrison Formation "gastroliths," suggesting that they are actually stream or pediment gravels polished by the wind (ventifacts). He based this largely on their lack of association with dinosaur skeletons, and the fact that they are not coextensive geographically or stratigraphically with the Morrison Formation (they tend to be concentrated in the upper part of the formation).

Stokes (1964) later reported a Morrison Formation sauropod skeleton from Utah with "stomach contents," though the identification of the stomach contents is open to question (Hunt and Lucas, 2014). He noted that "here and there are small rounded pebbles of amorphous siliceous material that may have been ingested as lumps of clay" (Stokes, 1964, p. 576) but no gastroliths. Nevertheless, Stokes (1987) subsequently changed his mind about polished siliceous pebbles of the Morrison Formation, accepting their origin as gastroliths, though he noted that there are no gastroliths in the extensive Cleveland-Lloyd dinosaur bonebed in Utah (nor are they present in abundance in any of the extensive Morrison bonebeds: Lucas, 2000; Wings and Sander, 2007; Wings, 2015b). Petrographically, according to Stokes, these pebbles had an origin to the west of the Morrison depositional basin.

The most recent addition to the analysis of such Morrison "gastroliths" is Malone et al. (2019, 2021). They examined three red quartzite pebbles from the Morrison Formation in Utah that lack any skeletal association, but identified them as dinosaur gastroliths. According to Malone et al. (2019, 2021), the detrital zircons in these pebbles are most similar to Neoproterozoic red quartzite from the Lake Superior region (well to the east of the Morrison depositional basin), though they do note that there is Neoproterozoic red quartzite in the Cordilleran belt from California to Idaho. In contrast, we regard as questionable identifying three isolated quartzite pebbles as gastroliths. Furthermore, the sample size is too small to identify what seems a highly unlikely source area for these pebbles hundreds of kilometers east of the Morrison depositional basin, in which paleoflow was mostly to the east.

Highly polished stones without any skeletal association from the Lower Cretaceous Cloverly Formation of Wyoming-Montana have also been called gastroliths (Hares, 1917; Stokes, 1942, 1944, 1952, 1987). But, various workers (e.g., Moberly, 1960; Mirsky, 1962; Ostrom, 1970) doubted that attribution. Relatively recently, Zaleha and Wiesemann (2005) argued that the highly polished siliceous clasts in the Cloverly Formation were simply polished by transport in ash-laden hyperconcentrated flows. Given the volume of volcanic detritus in the Morrison Formation, and the similarities between the Morrison and the Cloverly fluvial systems, it seems likely that transport in ash-

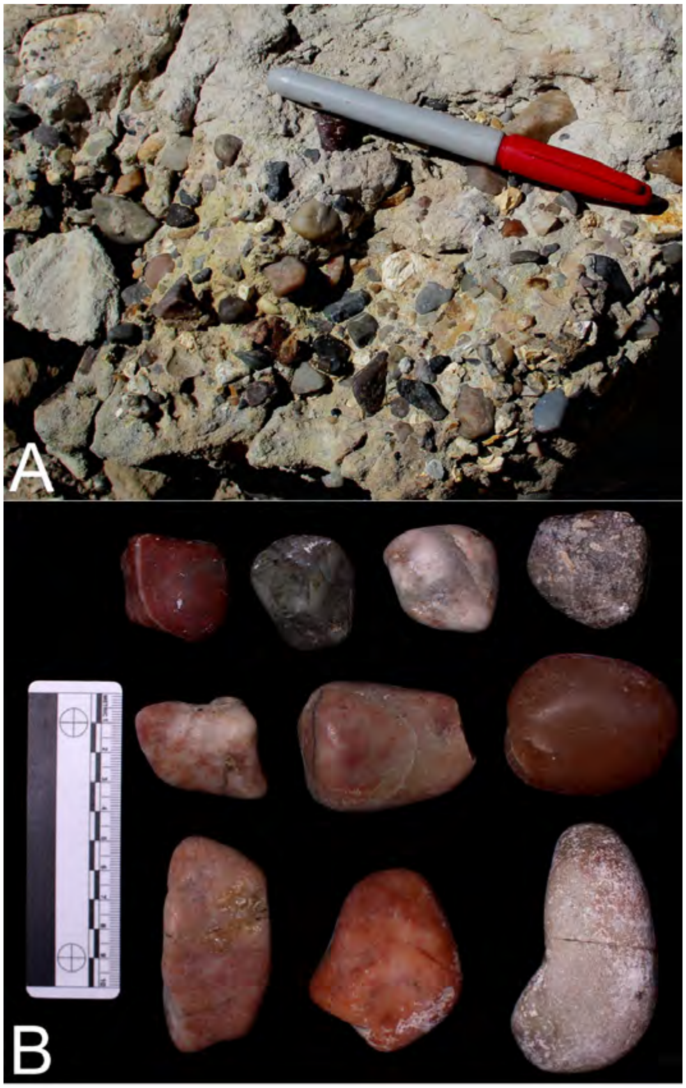


FIGURE 20. **A**, Siliceous fluvially-transported pebbles (conglomerate) in sandstone, Jackpile Member of Morrison Formation (Upper Jurassic), central New Mexico. **B**, Some of the supposed gastroliths of the Morrison sauropod dinosaur "*Seismosaurus*" from the Brushy Basin Member of the Morrison Formation (Upper Jurassic), central New Mexico.

laden hyperconcentrated flows could also have polished many of the "gastroliths" from the Morrison Formation.

Two methods have been used to document and/or quantify the polish of supposed gastroliths: high magnification of surface textures by SEM and measuring reflectance. The SEM examination has brought inconsistent results. Thus, Chatelain (1991, 1993) studied the surface texture of more than 400 Morrison formation "gastroliths" to conclude they show a "diagnostic, grid-like pattern of shallow, fine scratches on the highly polished surfaces," which could be duplicated by tumbling similar stones with conifer and cycad foliage. Unfortunately, his work was only published in two abstracts and not further documented.

Whittle and Onorato (2000) concluded that gastroliths show pronounced pitting and rill-like features at 50 x magnification. Schmeisser and Flood (2004, 2008) treated the pebbles associated with the partial skeleton of the Late Jurassic sauropod dinosaur "*Seismosaurus*" as bona fide gastroliths (but see Lucas, 2000) and concluded that ostrich gastroliths are highly pitted, lapidary stones have deep gouges, fluvially polished stones have rough textures and multiple cresentric gouges, and the *Seismosaurus* "gastroliths" have curved and parallel polish grooves. They argued that small particles and stomach muscle movement produced the polish grooves. Schmeisser and Flood (2004, 2008) concluded that such "polish grooves" diagnose gastroliths, in contrast to the results of Chatelain (1991, 1993) and Whittle and Onorato (2000).

Johnston et al. (1990, 1994), Manley (1989, 1991a, b, 1993) and Cox (1994, 1997, 1998) used video and laser instruments to scatter light from known gastroliths, suspected gastroliths and other "stones" to quantify surface polish (concentrated reflectance = high polish). Manley (1991b) argued that pebbles not associated with bones can be identified as gastroliths if they: (1) have high polish; (2) come from stratigraphic units with fossils of known "stone" swallowers; and (3) the "stones" are not in their perceived lithologic or sedimentological context. She quantified polish using a profilometer and laser light scattering. The profilometer measures smoothness, whereas laser light scattering measures light reflectance.

However, the methodology of all of these studies is questionable. For example, Schmeisser and Flood (2004, 2008) did not control for rock type in their comparisons. And, Lucas (2000) noted that Manley's (1991b, 1993) analysis needs to be repeated with unquestioned gastroliths, and the gastroliths should be compared to fluvial clasts of identical petrology. Significantly, none of the researchers who claim that high polish characterizes gastroliths actually compared the polish on bona fide gastroliths to the polish on bona fide ventifacts.

Darby and Ojakangas (1980, p 549) expressed skepticism about the diagnostic utility of high polish and used the term "gastromyth" to refer to stones thought to be gastroliths of uncertain origin (also see Lucas, 2000). Everhart (2005c, fig. 7.8; 2017, fig. 7.13; also see Cicimurri and Everhart, 2001) documented plesiosaur gastroliths with conchoidal fractures that he inferred were formed by the stones hitting one another while in the plesiosaur's digestive tract (Fig. 21). Again, Wings (2009) simulated a bird gastric mill, and it did not polish stones.

Gastroliths have also been invoked as a possible biogenic source of dropstones (lonestones), but we are not aware of any specific cases of a dropstone being definitively identified as a gastrolith (e. g., Hawkes, 1951; Bennett et al., 1996; Ahlberg et al., 2002). In the Lower Cretaceous Wessex Formation of England, a Late Jurassic ammonite steinkern was considered to be a regurgitated gastrolith by Martill and Baker (2000). Other polished stones in the British Lower Cretaceous have also been identified as dropstones or gastroliths (Radley, 1993, 1994, 2005; Sweetman and Underwood, 2006). However, identification of

FIGURE 21. A plesiosaur gastrolith showing scratch marks inferred to have been made by adjoining gastroliths while the clasts were in the alimentary tract of the plesiosaur. Photograph courtesy of Mike Everhart.

these clasts as gastroliths is primarily based on their high polish, not on any skeletal association, so their identity as gastroliths is open to question.

Ernst et al. (1996) identified the stones in a Cenomanian pebble bed from the Saxony basin in Germany as scattered gastroliths, largely because they are highly polished (also see Wilmsen and Nieburh, 2002; Kruger, 2003). Bartholommäus et al. (2004) interpreted these stones as plesiosaur gastroliths that came from sources about 300 km distant. However, these stones lack a skeletal association, so we are skeptical of their origin as gastroliths.

The important point, echoing Bryan (1931), is that there are various ways to polish stones, notably by the wind to make them ventifacts (there is even tectonic polish: Clifton, 1965). Polished clasts identified as gastroliths are siliceous, mostly quartz or chert. These clasts could have been polished by wind and/or water, both before ingestion by an animal and/or after excretion or other removal from an animal's digestive tract. Furthermore, how a stomach or gizzard would polish siliceous clasts (which are very hard) is also unclear, and such polishing does not occur in extant birds. Only a small minority of bona fide gastroliths, particularly those of plesiosaurs, are highly polished (also see Rothschild and Biehler-Gomez, 2021, especially their figure 9). M. Everhart (written commun., 2021) notes that plesiosaur gastroliths are only temporary in the plesiosaur, being ground down by use until the remaining clasts are small enough to pass out of the gut. Thus, the gastroliths would need to be periodically replaced, and an accumulation of gastroliths inside a plesiosaur specimen would have included a mixture of material of various ages.

There is thus an inability to establish when and where the clasts were polished, and inferring that they acquired their polish while gastroliths is not supported by actualistic studies of gastroliths. The idea that any highly polished clast is a gastrolith needs to be abandoned.

Gastroliths in Fossil Vertebrates

Introduction

Diverse fossil vertebrates of late Permian to Pleistocene age are associated with gastroliths. The most extensive and well documented record comes from plesiosaurs, the long-necked marine reptiles of the Mesozoic. Though there are relatively few bona fide gastrolith-dinosaur associations, a diverse literature has been published on dinosaur gastroliths, a good example of the Taxophile Effect. Some fossil birds have gastroliths, and, importantly, exceptionally preserved specimens from China document that both the crop and the gizzard had already evolved in birds during the Early Cretaceous.

Plesiosaur gastroliths

Plesiosaurs have the most extensive and unambiguous gastrolith record of any fossil vertebrates (Fig. 22). Since the 1870s (e.g., Seeley, 1877; Mudge, 1877), numerous articulated or semi-articulated skeletons have been collected with closely associated clasts of granule to cobble size, often aggregated as masses in the abdominal cavity. O'Gorman et al. (2014) also noted that several plesiosaurs have been documented with sand in their abdominal cavities, indicating that not just gravel was being swallowed (e.g., Andrews, 1910; O'Keefe et al., 2009).

FIGURE 22. Two masses of gastroliths from Cretaceous elasmosaurids. Photographs courtesy of Mike Everhart.

Indeed, more than a century ago, Williston (1904) stated that he knew of at least 30 plesiosaur skeletons from Europe and North America with gastroliths, and many more have been described since. There is now an extensive literature on plesiosaur gastroliths, mostly from the long-necked elasmosaurids (e. g., Riggs, 1939; Welles and Bump, 1949; Shuler, 1950; Storrs, 1981; Nicholls, 1988; Chatterjee and Small, 1989; Matsumoto et al., 1982; Nakaya, 1989; Stewart and Martin, 1993; Ludvigsen and Beard, 1994, 1997; Cicimurri and Everhart, 2001; Everhart, 2000, 2005e-f; Whittle and Everhart, 2000; Everhart, 2004a; Schumacher and Everhart, 2005; McHenry et al., 2005; Thompson et al., 2007; Liggett, 2005; Sato et al., 2006; Druckenmiller and Russell, 2008; Cerda and Salgado, 2008; O'Gorman et al., 2012, 2013, 2019), but also from the short-necked forms (e.g., Andrews, 1910; Fraas, 1910; Zhuravlev, 1943a, b; Ritchie, 1991; Taylor, 1992; Sato and Storrs, 2000; Schumacher, 2007; Smith, 2007; Druckenmiller and Russell, 2009; O'Keefe et al., 2009; Schmeisser and Gillette, 2009; Kear, 2016). Gastroliths have thus been documented in the plesiosaur families Pliosauridae, Rhomaleosauridae, Elasmosauridae and Polycotylidae. Clearly, there are more elasmosaurid records than of other families, but the pattern of gastrolith possession in plesiosaurs is complex, as it is in other tetrapod groups. Space prevents a review of all of these examples, most of which are very well documented, so we add texture by detailing a few here.

Riggs (1939, fig. 113) described an elasmosaurid specimen from the Upper Cretaceous of southeastern Montana that had 206 granitic clasts, 20-102 mm in diameter, scattered around the coracoids and paddles. He described them as "rounded and smooth, but in no case do they have a high polish" (Riggs, 1939, p. 390).

Welles and Bump (1949) described a skeleton of an elasmosaurid from the Upper Cretaceous of South Dakota that had 254 siliceous clasts massed in an area of 194 cm^2 and 18 cm deep immediately anterior to the pelvis and ventral to some dorsal vertebrae. These clasts (Welles and Bump, 1949, p. 523, fig. 2) were mostly quartzite, 11-128 mm in diameter and had "no luster or polish."

Shuler (1950, p. 18, figs. 11, 14) described an elasmosaurid skeleton from the Upper Cretaceous of Texas that, within the rib cage, contained at least 70 siliceous clasts that "range in size from well-worn, rounded and highly polished pebbles, half an inch [12.7 mm] in section, to a large rectangular block of flint–2 by 4 inches [50 x 100 mm] and weighing almost a pound–with a rough unaltered surface." Shuler (1950, p. 18) claimed that "an alternating rhythmic squeeze of great gizzard muscles gave the flints their beautiful polish." He also observed that "close association with an actual skeleton is the only direct proof" that such clasts are gastroliths. Darby and Ojakangas (1980) documented the 197 gastroliths associated with an elasmosaurid skeleton from the Upper Cretaceous of Montana. They noted that among these gastroliths, which they concluded resemble river cobbles, sphericity decreases with size. These gastroliths were mostly quartzite with a dull finish.

Cicimurri and Everhart (2001) documented an elasmosaurid with a mixture of fish bones and gastroliths posterior to the pectoral girdle. These are 95 gastroliths up to 151 mm in diameter, and they are shaped as disks, spheres or cylinders. Those made of chert were polished, but those made of quartzite had a dull, pitted texture. They concluded that the association of food and stones demonstrates a dietary function for the gastroliths.

In a polycotylid plesiosaur skeleton from the Upper Cretaceous of Utah, Schmeisser and Gillette (2009) reported 289 pebbles up to 34.5 mm diameter with varied degrees of polish. However, we note that these pebbles were scattered, not concentrated in a mass inside the abdominal cavity, so it is not certain that they are gastroliths.

From these details and a review of the other literature on plesiosaur gastroliths, we can conclude that: (1) many plesiosaurs used gastroliths, especially elasmosaurids; (2) plesiosaur gastroliths are numerous in one individual (usually 50-200 pebbles, but as many as 793 in one individual: O'Gorman et al., 2014), show a wide range in size (up to 170 mm maximum diameter: Everhart, 2005c) and are mostly siliceous pebbles of varied shapes; (3) most plesiosaur gastroliths are *not* highly polished; and (4) plesiosaur gastroliths are mostly found in the posterior part of the abdominal region, but it is not certain whether the plesiosaur held them in a separate structure ("gizzard") or in the posterior region of the stomach, like modern crocodiles.

Gastroliths have provided important inferences about plesiosaur behavior. Thus, in the American Late Cretaceous, plesiosaurs generally swam above muddy or chalky sea floors that offered no clasts of the same lithology as their gastroliths. Analysis indicates that such clasts as bedrock were often hundreds of km (maximum estimate = 600 km: Cicimurri and Everhart, 2001) distant from the location of the plesiosaur fossil skeleton with gastroliths (e.g., Cicimurri and Everhart, 2001; Everhart, 2005e; McHenry et al., 2005; and see Vincent et al., 2017 for a Jurassic example). Furthermore, as was first noted by Darby and Ojakangas (1980), the gastroliths of plesiosaurs resemble river cobbles. Thus, O'Gorman et al. (2013, 2014) demonstrated that the sphericity metrics of plesiosaur gastroliths (Darby and Ojakangas, 1980; Everhart, 2000; Cerda and Salgado, 2008; O'Gorman et al., 2012) show a close similarity to fluvial pebbles (cf. Dobkins and Folk, 1970). This, and the fact that many plesiosaur skeletons with gastroliths are found in marine shale and chalk units that are hundreds of km from a possible source of pebbles, indicate that plesiosaurs were prodigious swimmers that likely went very close to shore or ashore to swallow stones in estuaries or along river courses. As O'Gorman et al. (2014) noted, this also suggests that habitat partitioning by adult (deep offshore) and juvenile (shallow nearshore) plesiosaurs (advocated by Wiffen and Moisley, 1986; Wiffen et al., 1995) could only have happened part of the time.

Less clear has been the function of plesiosaur gastroliths. As already noted, the first observers (Seeley, 1877; Mudge, 1877) inferred that plesiosaur gastroliths were used as an aid to digestion (also see Martin and Kennedy, 1988). But, as already discussed, Taylor (1993, 1994; also see Sander et al., 1997; Lingham-Soliar, 2000) argued for their use as ballast for buoyancy control. Nevertheless, Reiss and Frey (1991) reviewed underwater flight in plesiosaurs and concluded that ballasting was not needed for buoyancy control. Storrs (1993, p. 74) stated that plesiosaur gastroliths were ballast "needed to maintain a neutrally buoyant position within the water column" but suggested they may also have had a digestive function.

Cicimurri and Everhart (2001) made the very cogent observation that the gastroliths of plesiosaurs represent only 1-2% of total body mass, so their function in buoyancy control seems unlikely (also see Everhart, 2005e). Henderson (2006) undertook three-dimensional modelling of plesiosaur swimming and rejected a role for gastroliths in buoyancy control. Henderson (2006) thus documented that if the gastroliths amount to less than 10% of the body mass of the plesiosaur (which is always the case), they would have had a negligible effect on buoyancy. Yet, he did find that the gastroliths suppressed the dorso-ventral oscillation of the head and neck in floating elasmosaurids.

The function of plesiosaur gastroliths has been debated for more than a century. The current "consensus" favors their use in digestion, not in buoyancy control. However, most other tetrapods (especially birds) that use gastroliths for dietary purposes are herbivores. Plesiosaurs, like crocodiles, were not herbivorous, so whether or not these predatory marine reptiles would use gastroliths to grind their food is not above discussion. As suggested by Storrs (1993), the possibility that plesiosaurs used gastroliths for both digestion and some amount of buoyancy control remains plausible. More research is needed here.

Dinosaur gastroliths

An extensive literature has been published on dinosaur gastroliths, even though there are relatively few records of bona fide dinosaurian gastroliths; indeed, only a few taxa of dinosaurs had demonstrable gastroliths. These taxa are some prosauropods, sauropods, theropods, an ornithopod and some members of the ceratopsian genera *Yinlong* and *Psittacosaurus*.

Most impressive are the gastroliths found in the skeletons of some prosauropod dinosaurs, notably *Massospondylus* from the Lower Jurassic of southern Africa (Bond, 1955; Raath, 1974; Cooper, 1981). Thus, Raath (1974, p. 4) described as many as 50 subrounded "more or less polished" stones inside the rib cages of articulated skeletons of *Massospondylus*. According to Raath, these were composed of quartz, quartzite and chalcedony, used to grind food and were stream pebbles chosen by the prosauropod. These gastroliths have been viewed as forming "gastric mills" for pulverizing and disintegrating the vegetation eaten by the herbivorous prosauropods (Galton, 1976, 1985, 1986).

Nevertheless, prosauropods are a group of dinosaurs with a Pangea-wide distribution during part of the Late Triassic-Early Jurassic, and few had demonstrable gastroliths. Weems et al. (2007) argued that stones without any skeletal association from the Upper Triassic of Virginia, USA, were likely prosauropod gastroliths. These were mostly quartzite with moderate to high polish, up to 105 mm diameter and unlike nearby fluvial conglomerate pebbles. But, given the lack of any skeletal association, we see this as a problematic record.

The case for gastroliths in sauropod dinosaurs is a weak one, despite the fact that a diverse literature identifies gastroliths in these, the largest of all terrestrial tetrapod herbivores (see, for example, Christiansen, 1996). Calvo (1994) first drew attention to this, noting that Wieland's (1907) original report of sauropod gastroliths was actually of clasts near a stegosaur skeleton (Brown, 1907). Calvo (1994, p. 206) concluded that the evidence of gastroliths associated with sauropod bones is "very restricted to fragmentary sauropod remains; thus, these evidences should be interpreted with caution" (also see Lucas, 2000).

Wings and Sander (2007) accepted that some sauropods had gastroliths but argued that these dinosaurs lacked a gastric mill as is found in birds. They thus noted that in examples that they considered bona fide gastroliths in sauropods ("*Seismosaurus,*" *Cedarosaurus, Dinheirosaurus*) the stones are much less than 0.1% of body mass, whereas in herbivorous birds they are 1% of body mass. They also noted that autochthonous sauropod bone beds lack gastroliths, as did Calvo (1994), Lucas (2000) and Wings (2015b).

Wings (2015b) reviewed the classic dinosaur bonebeds in the Upper Jurassic Morrison Formation (Bone Cabin quarry, Cleveland-Lloyd quarry, Como Bluff, Dinosaur National Monument, Dry Mesa quarry, Howe quarry) and stressed the almost total lack of any evidence of sauropod gastroliths, even from articulated/semi-articulated sauropod skeletons in these bonebeds. Indeed, once you eliminate the taphonomic possibilities for gastrolith removal, these quarries generally lack gastroliths.

We should note, however, that the case for gastroliths in "*Seismosaurus*" is unconvincing (Lucas, 2000, and see below). *Dinheirosaurus* has a convincing record of gastroliths according to Wings and Sander (2007), but no gastroliths are mentioned in the original description by Bonaparte and Mateus (1999), and they have not been otherwise documented.

Galton (1986) and Farlow (1987b) accepted a gastric mill in sauropods based on the reports of Janensch (1929), Cannon (1906) and Brown (1941), although these are unconvincing records of one or a few polished stones associated with a sauropod fossil (see below). Bakker (1971, 1980, 1986), like Galton and Farlow, argued that sauropod heads and dentitions were so small that they needed a gastric mill to digest the vast amounts of vegetation such behemoths consumed (also see Weishampel and Norman, 1989; Taggart and Cross, 1997; Upchurch and Barrett, 2000). This found its fullest expression in Bakker (1986, p. 126-138), who presented a lengthy argument for gastroliths in sauropods largely based on his idea that they were endothermic and lacked the masticatory apparatus to process the large quantities of vegetation they ate. He envisioned huge gizzards in sauropods but admitted that direct evidence of sauropod gastroliths was sparse. Indeed, sauropods likely used fermentation to process large amounts of consumed vegetation according to Wings and Sander (2007), as the ability to process vegetation in the mouth was minimal, and there is no compelling evidence of a gastric mill in any sauropod.

Cannon's (1906) claim of sauropod gastroliths was never documented. Janensch (1929) described supposed "gastroliths" (German: Magensteine) associated with some of the Jurassic sauropod bones at the famous East African dinosaur locality Tendaguru. These were composed of gneiss or quartz, rounded, not polished and up to 60 mm in diameter. However, all were isolated clasts found in proximity to vertebrae, so their identification as gastroliths is questionable.

Bird (1985, p. 65) published a photograph of about 64 polished siliceous cobbles between the pelvis and ribs of one sauropod skeleton at the Howe quarry in the Upper Jurassic Morrison Formation in Wyoming, USA. Farlow (1985) and Schwartz et al. (2007) accepted this as a record of sauropod gastroliths, and it may be the first published substantiation of gastroliths in a sauropod skeleton, though this is difficult to confirm without additional documentation.

Calvo (1994) mentioned a complete skeleton of *Rebbachisaurus* from the Cretaceous of Argentina associated with six igneous rocks that he identified as likely gastroliths. Calvo and Salgado (1995, p. 27) described this fossil but only provided minimal information about the gastroliths, namely that the igneous rocks "have roughened and rugose surfaces." We regard this supposed gastrolith record as questionable.

Gillette (1990, 1991, 1994, 1995) reported 240 pebbles/cobbles as gastroliths associated with the partial skeleton of the Late Jurassic sauropod **"***Seismosaurus***"** (= Diplodocus: Lucas et al., 2006). Artwork in Gillette (1995, p. 113) shows both a crop and gizzard in this sauropod. However, Lucas (2000) argued that there is no clear skeletal association of these stones– they do not define a crop or gizzard in a plausible abdominal position surrounded by articulated bones. Instead, the sizes, shapes, textures and orientations of the stones are consistent with their origin as stream-deposited cobbles of a channel-lag deposit according to Lucas (2000). The fact that some of these clasts were imbricated along trough crossbeds (Lucas, 2000, fig. 4) provides compelling evidence of concentration by fluvial processes. These supposed gastroliths of *"Seismosaurus"* show a wide range of polish matched by similar clasts from the Morrison Formation that are not associated with bones (Fig. 20).

Dantas et al. (1998) stated that more than 100 gastroliths were located in a "crop" near the anterior dorsal and posterior cervical vertebrae of a skeleton of the sauropod *Lourinhasaurus*. They described these as mostly well-polished quartz pebbles, 56-217 mm in diameter that had variable shapes, mostly discoidal or spheroidal. These may be gastroliths, but we question the identification of a "crop" in a sauropod dinosaur. Jennings and Hasiotis (2006) identified as gastroliths 14 polished quartz clasts 10-130 mm in diameter between the ischia and caudal vertebrae of an incomplete skeleton of *Camarasaurus*. However, we regard this as a problematic record because of the location of the stones outside of the abdominal cavity.

The only compelling and well documented example of a sauropod skeleton with gastroliths is that of *Cedarosaurus* from the Lower Cretaceous of Utah, USA (Sanders and Carpenter, 1998; Sanders et al., 2001; Myers, 2004). A mass of 115 stones was located in the abdominal cavity (posterior to the coracoid, ventral to dorsal vertebrae) of the skeleton of this sauropod. These pebbles were mostly highly polished chert and quartzite up to 165 mm in diameter, and range in shape from oblate spheroids to blades and cylinders.

Among theropod dinosaurs, gastroliths are most common among the Maniraptorifirmes, which are the theropods closest to bird ancestry. However, there are some reports from other kinds of theropods: (1) a single clast near the skeleton of *Baryonyx* judged (we believe questionably) to be a gastrolith by Milner and Charig (1997); (2) a skeleton of *Pokilopleuron* with stomach contents that include 10 small, rounded pebbles interpreted to be gastroliths among fish bones (Eudes-Deslongchamps, 1838; Allain, 2005); (3) a skeleton with gastroliths in the abdominal cavity of the Jurassic ceratosaur *Limusaurus*, which is a beaked theropod (Xu et al., 2009); (4) in a partially articulated skeleton of *Nqwebasaurus*, 12 scattered pebbles were present that are 5.2-14.5 mm in diameter and are mostly polished quartzite (De Klerk et al., 2000), a problematic record; and (5) Mateus (1998) described a very incomplete skeleton of an allosaurid that had 32 clasts and impressions of 3 more in the rib cage below the 11th dorsal vertebra. These were associated with bone fragments he interpreted as food remains.

As noted above, the theropods closest to bird ancestry have an impressive record of gastroliths that indicates that the crop and gizzard had evolved in some dinosaurs during the Early Cretaceous. Pebbles form a crop and a gizzard in the theropod *Caudipteryx* (Fig. 23; Ji et al., 1998; Zhou et al., 2000; Zhou and Wang, 2000; Zhang, 2001). Twelve ornithomimind skeletons (*Sinornithomimus*) with crops that contain small siliceous grains were documented by Kobayashi et al. (1999; Kobayashi and Lü, 2003; also see Varrichio et al., 2008). A skeleton of the Lower Cretaceous ornithomimosaur *Shenzhusaurus* has concentrated pebbles in the abdomen anterior to the gastral basket that are smooth to pockmarked, and rounded to angular (Ji et al., 2003).

FIGURE 23. Skeleton of the maniraptoriform theropod dinosaur *Caudipteryx*, with a large mass of gastroliths in its abdominal area. Skeleton of *Caudipteryx* is about 1 meter long. Photograph courtesy of the late Stephen Czerkas.

Indeed, Zanno and Makovicky (2011) indicated that gastroliths provide important evidence of herbivory in some coelurosaurs, notably the toothless ornithomimosaurs and oviraptorosaurs.

There are relatively few records of gastroliths in ornithischian dinosaurs. Carpenter (1987, 1990) reported gastroliths in one specimen of the Late Cretaceous ankylosaur *Panoplosaurus*, but these have not been described. K. Carpenter (written commun., 2020) has informed us that these stones were catalogued (presumably collected) with the fossil, but there are no records of their original association in the sediment. Thus, this is a problematic record. A skeleton of *Minmi paravertebra* from the Upper Cretaceous of Australia has an extensive cololite but no gastroliths (Molnar and Clifford, 2001). However, Brown et al. (2020) recently documented bona fide gastroliths in an ankylosaur from the Early Cretaceous of Canada.

Early reports of gastroliths associated with the hadrosaur *Edmontosaurus* ("*Claosaurus*") by Brown (1907) and with *Iguanodon* by Rivett (1956) are not of a mass of gastroliths in the abdominal region and thus are problematic (Wings, 2004). Cerda (2008), nevertheless, published a bona fide gastrolith record in an ornithopod dinosaur. These are clusters of pebbles in the abdominal regions of three articulated skeletons of *Gasparinsaura* from the Upper Cretaceous of Argentina. Up to 17 mm in diameter, these pebbles are mostly of igneous rocks, subrounded and not polished.

Xu (1997) well described gastroliths from a skeleton of the Early Cretaceous ceratopsian *Psittacosaurus* (also see Brown, 1907; Osborn, 1924; Sereno, 1990). At least 36 pebbles up to 20 mm diameter were preserved as a mass around the sacral vertebrate. They range in shape to include spheroids, disks, blades and cylinders. Some other specimens of *Psittacosaurus* have gastroliths (You and Dodson, 2004), as does the Jurassic ceratopsian *Yinlong* (Xu et al., 2006).

Fossil birds

The fossil record of birds is mostly of isolated and/or incomplete bones, not complete skeletons. This likely explains why there are relatively few documented cases of fossil avian gastroliths. These are mainly of late Cenozoic age (e. g., Stirling and Zietz, 1900; Lambrecht, 1931; Voorhies, 1980; Yeh, 1981; Yang and Yang, 1994). Notable among this is the extensive subfossil record of moas, extinct giant birds from New Zealand, the skeletons of which famously contain many gastroliths that are mostly semi-round, white quartz pebbles (Chapman, 1884; Forbes, 1892; Navás, 1922; Duff, 1949; Baker, 1956; Burrows et al., 1981; Anderson, 1989; Johnston et al., 1994). These clasts range in size from "gravel" to 100 mm in diameter. Importantly, the clasts are all of lithologies local to the skeletons that contain them. This suggests that moas were localized, only moving tens of kms during their lifetimes, not the long distances travelled by some other large, flightless birds, such as ostriches (Anderson, 1989).

Importantly, the spectacular record of fossil birds from the Early Cretaceous strata of northeastern China demonstrates that the avian crop and gizzard had already evolved in the Early Cretaceous. Thus, Zheng et al. (2011) documented Early Cretaceous birds from China with masses of fossilized seeds in the region of the crop. Many Early Cretaceous birds with gizzards have been documented, and these birds are therefore thought to have been herbivorous.

Zhou et al. (2004) described some specimens of the Early Cretaceous bird *Yanornis* with fine sand- and gravel-sized particles that are quartz grains 0.2-2.7 mm diameter and subangular to subrounded. To explain the presence of gastroliths in some specimens of *Yanornis* and their absence in others, Zhou et al. (2004) suggested "gizzard plasticity," which is seen in some modern birds due to seasonal changes in diet (Starck, 1999a, b). This kind of phenotypic flexibility of the gastrointestinal tract in response to changes in diet or organismal demand is seen in some extant birds and mammals and generally indicates fluctuating environments (Starck, 1999a, b). Zhou et al. (2004) aptly observed that the distribution of gastroliths in *Yanornis* may indicate that such phenotypic plasticity had evolved early in the Cretaceous.

Zhou and Zhang (2003), Zheng et al. (2011) and O'Connor (2019) described the gastroliths of *Sapeornis*. Zheng et al. (2011) argued that the evolution of the gizzard in birds likely preceded the evolution of the crop. Furthermore, the presence of the crop in Early Cretaceous birds indicates seed eating, and the development of the crop may have facilitated the loss of teeth in beaked birds.

Wang et al. (2016) described an entantiornithine bird with a gizzard. Wang et al. (2018; also see Zhou and Zhang, 2003; Zhou et al., 2013; Wang and Zhou, 2016) documented multiple specimens of the stem bird *Archaeorhynchus* from the Lower Cretaceous of China that have gastroliths clustered in the abdominal cavity (~ 100 gastroliths in one specimen). Gastroliths in the ornithuromorph *Hongshanornis* were described by Chiappe et al. (2014). On one of the specimens they described, the gastroliths are located in a ventral position, consistent with the location of the ventriculus in the abdominal cavity. O'Connor et al. (2018) documented gastroliths in *Jeholornis*. Possible gastroliths in the enantiornithine bird *Bohaiornis* were studied in some detail, but were demonstrated to be mineral precipitates, not gastroliths (Liu et al., 2021).

We note that the avian gizzard could have been inherited from non-avian theropods or evolved independently. Thus, the phylogenetic bracket of theropods with gastroliths (see above) suggests birds inherited it from dinosaurian ancestors, but note that the oldest bird, Late Jurassic *Archaeopteryx*, lacks gastroliths.

Louchart and Viriot (2011) stated that during the Jurassic-Cretaceous, dental reduction occurred at least six times independently among Aves. They concluded that the horny beak (rhamphotheca) and gizzard replaced the dentition, so the loss of teeth in birds is correlated to the evolution of a muscular gizzard (also see Dilger, 1957).

O'Connor (2019) regarded fossil birds with gizzards as herbivores, and those with crops as granivores (but see Miller and Pittman, 2021 for a different analysis of the diets of early birds). She also noted that the role of gizzards in the tooth loss of birds is complicated by the presence of gastroliths in some toothed birds (*Jeholornis*, *Sapeornis*). So, tooth loss and gastrolith acquisition are not clearly correlated according to O'Connor (2019).

Other fossil vertebrates

Various records of gastroliths in fossil vertebrates other than plesiosaurs, dinosaurs and birds are mostly single reports, many of which are problematic. Trewin (1986) documented a placoderm fish (*Coccosteus*) from the Old Red Sandstone with pebbles in the visceral area.

Moodie (1912), Shimada (1997) and Everhart (2000) discussed a large lamniform shark with apparent black chert gastroliths, and Sternberg (1922) and Everhart (2004c) described a mosasaur with apparent gastroliths. Everhart (2005e) stated that both the shark and the mosasaur likely acquired the gastroliths from preying on plesiosaurs.

The only claim of gastroliths in a fossil amphibian is of the temnospondyl *Acerastea* from the Lower Triassic of Australia. Warren and Hutchinson (1987) stated that the holotype partial skeleton had 10 angular, polished pebbles immediately posterior to the skull that are 20-60 mm in diameter. These pebbles were metamorphic mudstone (5 pebbles), sandstone (2 pebbles), quartz (1 pebble) and mudstone (2 pebbles). But, given their size, composition and location with respect to the fossil bones, these pebbles are highly unlikely to have been gastroliths.

The oldest published tetrapod gastroliths are in a late Permian pareiasaur from Germany (Munk and Sues, 1993). The abdominal cavity of this pareiasaur had a mass of unsorted granules and pebbles of quartz and chert of varied roundness up to 10 mm in diameter interspersed with carbonized particles that Munk and Sues interpreted as macerated organic matter. They suggested that herbivorous pareiasaurs may have ingested the stones while foraging close to the ground.

Cheng et al. (2006) documented gastroliths in a Triassic ichthyosaur from China. Given that few other known ichthyosaurs have gastroliths (e.g., Keller, 1976; Long et al., 2006), they concluded that this specimen represents an example of accidental ingestion. Silva et al. (2017) suggested that a few quartz grains and other mineral clasts in some mesosaur skeletons may be gastroliths.

Many skeletons of tangasaurid eosuchians (aquatic reptiles from the upper Permian of Madagascar) have masses of gravel in their abdominal regions (Piveteau, 1926; Haughton, 1930; Currie, 1981) (Fig. 24). The most extensive analysis of these pebbles by Currie (1981, p. 115-12, figs. 3, 5-7) led him to conclude that they were used for buoyancy control. These clasts in *Hovasaurus* are of two sizes, large pebbles and gravel up to 200 mm in diameter and much smaller sand and granules that are 0.5-2.0 mm in diameter. They are mostly quartz and not polished. These clasts are located between the ribs and gastralia of multiple specimens of different body sizes, though two articulated specimens lack any gastroliths.

Currie (1981) argued that these gastroliths were too far posterior to have been held in the stomach, though Haughton (1930) saw the pebbles as having a digestive function. Currie (1981, p. 119) further concluded that they were stored in a "blind sac" in the abdominal cavity that shifted the center of gravity backward to maximize the tail-based propulsion of the tangasaur, and we regard this as reasonable speculation. Estimating the weight of the specimen illustrated here (Fig. 24) as about 300-500 grams, and the weight of the pebbles as ~ 25 grams, Currie noted that this would raise the tangasaur's specific gravity by 5-10%, to a value within the range of the specific gravity of aquatic turtles (Zug, 1971).

Fossil crocodiles have a diverse but not prolific record of gastroliths. These include a few records in nonmarine crocodilians (e.g., Berckheimer, 1928; Hölder, 1955; Keller and Schaal, 1992; Vasconcellos et al., 2008; Nascimiento and Zaher, 2010) and marine crocodiles (e. g., Westphal, 1962; Kobatake and Kamei, 1966; Buffetaut, 1979, 1982; Martill, 1986; Walkden et al., 1987; Keupp and Kohring, 1993; Denton et al., 1997). However, we question the gastrolith identity of some of these records. For example, we doubt Keupp and Kohring (1993), who identified as a gastrolith a single stone in a concretion found near some bones of an Early Jurassic crocodilian.

There are a few records of gastroliths in coprolites, presumably excreted by the animal that swallowed the gastroliths. These are records primarily in fossil crocodile coprolites (Weigelt, 1927; Walter and Weigelt, 1932; Young, 1964; Wings, 2012).

Codorniú et al. (2013) reported gastroliths from a specimen of the pterosaur *Pterodaustro* from the Lower Cretaceous of Argentina. These comprised fine gravel up to 8.4 mm in diameter in an area of 24 cm^2 just in front of the pelvis surrounded by gastralia and ribs. Most of the gastroliths were angular, abraded metaquartzite. They noted the rarity of gastroliths in pterosaurs (many complete skeletons lack gastroliths) and suggested that this pterosaur used the gastroliths to break up hard-shelled crustaceans in its food.

Gastrolith records in fossil mammals are almost unknown. The only record we are aware of is a skeleton of an Eocene pangolin, *Eomanis*, from Germany that had coarse sand in the visceral area (von Koenigswald et al., 1981). Extant pangolins similarly swallow sand and gravel as an aid to digestion (e. g., Walker, 1968).

Gastroliths in Archeology and Pedology

Although our focus is on paleontology, it is worth noting that there is a diverse literature on supposed gastroliths in archeological sites and in very young loessic paleosols, often in an archeological context (Lucas and Hunt, 2021).

The archeological literature is very biased by the notion that high polish characterizes gastroliths, so that any highly polished, "out-of-place" stone can be called a gastrolith, even though it lacks any avian skeletal association (Lucas and Hunt, 2021). The archeological analyses are largely focused on identifying gastroliths as evidence of the consumption of birds by humans (e.g., Hardcastle, 1889; Young, 1967; Hoskin et al., 1970; Powers et al., 1983; Powers and Hoffecker, 1989; Gautier, 1993, but see Thorson and Hamilton, 1977; Tryon, 2002). It ranges from simply calling any polished stone at an archeological site a gastrolith (e. g., Bottema, 1975) to more nuanced treatments at hunting camps where the harvesting of birds finds evidence beyond their supposed gastroliths (e. g., Brooks et al., 2012).

Pebbles that lack any osteological association in loessic soils of late Pleistocene age have also been identified as gastroliths.

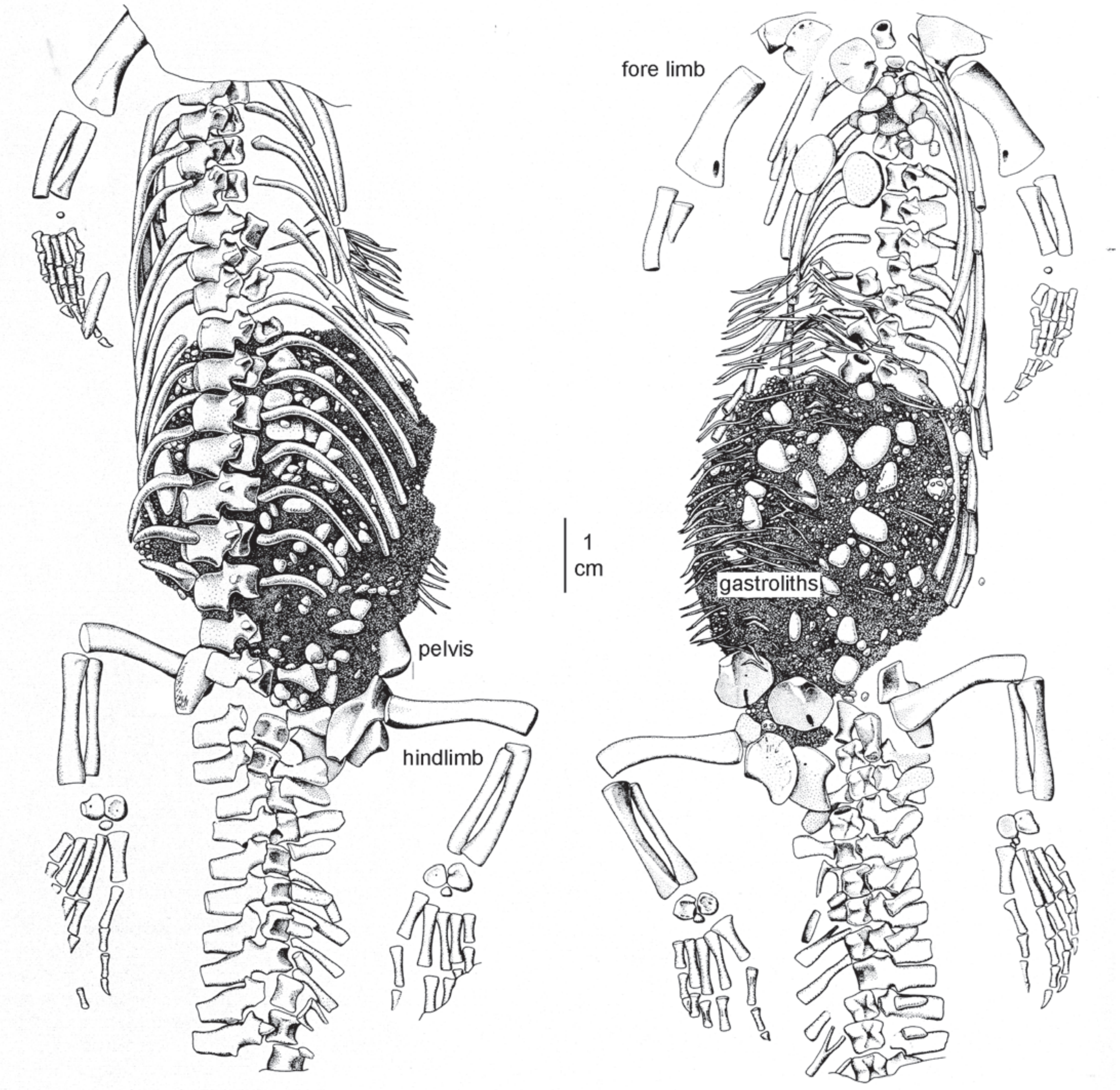


FIGURE 24. Dorsal (left) and ventral (right) views of the abdominal region of the tangasaurid *Hovasaurus* showing gastroliths (modified from Currie, 1981).

Particularly interesting is the work of Cox (1994, 1997, 1998), who identified pebbles 4 to 64 mm in diameter as avian gastroliths that are buried in "stone lines" in Pleistocene loessic soils in Illinois and Mississippi, USA. Cox accepted the conclusions of Johnston et al. (1990, 1994) and Manley (1991b, 1993) that high polish diagnoses gastroliths. He concluded that the pebbles in these stone lines were avian gastroliths that had been moved downward to their current stratigraphic positions by invertebrate bioturbation in the loess. However, identification of the loessic pebbles as gastroliths rested totally on the unsubstantiated idea that high polish identifies gastroliths.

To determine polish, Cox (1994) used the methods of Johnston et al. (1990, 1994) and Manley (1991b, 1993), by which the reflectance of light (which is an indicator of the degree of polish) scattered from the pebbles is quantified. However, the data of Cox (1994, table 4.1) show, as other workers have demonstrated, that most of the gastroliths of extant birds are not highly polished (an average of 16% of gastrolith pebbles from the modern birds Cox listed are highly polished). Because most of the loessic pebbles studied by Cox are not highly polished (only 8.8% to 21% of the pebbles in the populations of loess pebbles he studied are highly polished), Cox concluded that these loessic pebbles are gastroliths. But, if high polish diagnoses gastroliths fide Cox, then only a small minority of the pebbles he studied could be gastroliths by his own stated criterion.

Cox's (1994) idea that invertebrate bioturbation moved the gastroliths to stratigraphic levels that are within loessic paleosols (they are in A, E and upper B horizons of the paleosols), instead of at levels that were paleoland surfaces, is also open to question. Cox (1994) argued that if the stones are gastroliths, they must have been regurgitated, defecated or otherwise left on the paleoland surface by Pleistocene birds (the "gastrolith rain" of Van Nest, 2002), and moved stratigraphically downward later. But, he presents no evidence that invertebrate bioturbation moved the stones–no ichnofabric data or evidence of bioturbation in the form of biogenic structures in the loess. Thus, bioturbators moved the stones to a stone line below the paleosurface, and because the stones are so organized, they must have been moved by bioturbators–a perfectly circular argument. The fact is that plausible inorganic processes to organize the loessic stones in the sediment were published long ago (e. g., Shaler, 1891; Savage, 1915).

Cox's (1994, 1997, 1998) work was done in the context of understanding "biomantles" as stone lines overlain by sand and silt created by invertebrate burrowers (notably earthworms: Darwin, 1881) that moved the stones downward to their current stratigraphic levels (e.g., Johnson, 1990, 1993, 2002; Johnson and Balek, 1993; Johnson et al., 2005a, b; Johnson and Schaetzl, 2015). Most of these articles also endorse the pebbles in the loessic stone lines as avian gastroliths. However, a more insightful discussion by Van Nest (2002) recognized that only some of these exotic pebbles may actually be avian gastroliths, as there are many ways for such stones to arrive at and be buried in loesses and at archeological sites.

We also note that not a single bird bone was found in the loess anywhere near the pebbles studied by Cox (1994). Some loessic pebbles Cox studied are as much as 64 mm in diameter, so they are much larger than the pebbles that the largest birds, extinct and extant (moas, ostriches), are known to have swallowed. Thus, high polish = gastrolith needs to be abandoned in archeological and pedological studies. There needs to be a more rigorous appraisal to determine the origin of polished pebbles lacking an osteological association at archeological sites and in soil profiles (Lucas and Hunt, 2021).

Gastroliths as Trace Fossils

Bertling et al. (2006, p. 266), in their effort to standardize the study and terminology of trace fossils, defined a trace fossil as "a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organism) modifying the substrate." They regarded gastroliths as trace fossils, but they classified them as in a "gray zone" with coprolites, "regurgitaliths" (sic) and bite and gnaw structures that have not been considered trace fossils by some workers. Thus, gastroliths receive no mention in a very comprehensive book on ichnology by Buatois and Mángano (2011). Nevertheless, much earlier, Abel (1935), in a classic treatise on trace fossils, devoted 13 pages to reviewing the then published records of gastroliths. And, in their treatise on fossil behavior, Boucot and Poinor (2010; also see Boucot, 1990) regard gastroliths primarily as of use in digestion and assigned them as fossilized evidence of behavior to their highest category 1, or "frozen behavior."

As is currently the case in ichnology, Bertling et al. (2006) argued that all trace fossils need ichnotaxonomic nomenclature governed by the International Commission on Zoological Nomenclature. No ichnotaxonomy has been proposed for gastroliths. Bertling et al. (2006) state that gastroliths stand on the boundary between the work of (trace fossil) and the product of (not a trace fossil) an animal. They only list the etched sculpture of some gastroliths as a possible morphological character that could be of use in an ichnotaxobase.

However, we see gastroliths clearly as the work of an animal. Unlike eggs, for example, the sand/gravel that comprise gastroliths (our definition) is not made by animals–it is swallowed by, concentrated by, transported by and, in some cases, altered by animals. So, the trace-fossil status of gastroliths is unimpeachable by the Bertling et al. (2006) definition of a trace fossil.

We advocate development of an ichnotaxonomy for gastroliths. Ichnotaxonomic names, however, should not be assigned to individual grains/clasts of sand/gravel of fossil gastroliths. As the review above indicates, the numerous sand grains/gravel found in a fossil vertebrate digestive tract are often diverse in number, size, shape and composition. Naming single sand grains/gravel clasts would thus produce a bewildering plethora of names. Instead, we favor naming the entire gastrolith mass from a single abdominal cavity. Ichnotaxobases could be the number of gastroliths in the mass, their general petrographic composition, and their overall size, shape, surface texture and other shared morphological features. This likely would produce a workable ichnotaxonomy that recognizes ichnotaxa that are readily distinguished by morphological differences that are a direct reflection of varied behavior.

One problem little addressed is the taphonomy of gastroliths. Does a decomposing vertebrate carcass lose its gastroliths rapidly (cf. Everhart, 2005b), and could gastroliths be all that remain of a carcass otherwise disintegrated? To our knowledge the only taphonomic study of gastroliths is Wings (2003), whose actualistic studies suggest gastroliths are rapidly released from carcasses in water. Wings (2003) also noted that the integrity of a vertebrate animal's integument matters, as there are numerous crocodiles (strong integument) with gastroliths, and almost no birds (weak integument) with gastroliths at the Eocene Messel Lagerstätte in Germany. Further studies of gastrolith taphonomy are needed.

Gastroliths are a limited and somewhat perplexing part of the ichnological record of vertebrate consumption. Other than birds, relatively few vertebrate taxa utilize/utilized gastroliths in digestion to pulverize and disintegrate food (Fig. 19). Most of these non-avian vertebrates and the gastrolith-using birds are/were herbivores or omnivores. But, a compelling case has been made that plesiosaurs used gastroliths for digestion, yet they were predators.

We view gastroliths as a behavioral strategy primarily to grind food, mostly plant matter. Use for ballast in buoyancy control may have been the function of gastroliths in some animals, notably some crocodiles and marine mammals, but this is a little employed strategy for the use of gastroliths. Nevertheless, these strategies for gastrolith use have only been adopted idiosyncratically. Many taxa that could use a "gastric mill" lack it. Some members of taxonomic groups have gastroliths, whereas close relatives do not and, in populations of some vertebrate species that use gastroliths, not all individuals have gastroliths. These complexities of gastrolith distribution await further explanation, if an explanation is possible.

Gastroliths not only provide important information about feeding and buoyancy control, but the need for the animal to collect them provides insight into habitat. Thus, some plesiosaurs must have travelled hundreds of kilometers to acquire their gastroliths, whereas the gastroliths of moas are all of local origin, indicating little travel by these avian giants.

Thus, gastroliths are trace fossils in need of ichnotaxonomy. They provide important insights into various behaviors, notably diet, digestion, buoyancy control and habitat preferences.

COPROLITES

Introduction

There is an extensive literature on coprolites, fossilized feces, large portions of which we have reviewed elsewhere (Hunt et al., 2007, 2012d, 2013b, 2018; Hunt and Lucas, 2013, 2014a, 2016c, 2018c, 2021b). After footprints, they are the most studied vertebrate trace fossils, and coprolites are the subject of an extensive and rapidly growing literature.

History of Study

Several authors have reviewed the history of study of vertebrate coprolites (e.g., Reinhard and Bryant, 1992; Duffin, 2009, 2012a, b; Bryant and Reinhard, 2012; Hunt et al., 2012d; Pemberton, 2012; Shillito et al., 2020; Hunt and Lucas, 2021b), obviating the need for a lengthy review here. Bromalites, later identified as coprolites, have been known since the late seventeenth century (Duffin, 2012a). In the 1820s, Buckland identified aggregates of apatitic subspheroidal objects from a Pleistocene deposit in Kirkdale Cave in northern England as fossil hyena feces (Buckland, 1822, 1824). This was a relatively easy conclusion, as the cave contained many hyena bones, and Buckland could demonstrate that the new specimens were comparable to modern hyena feces.

Buckland made a much more important breakthrough in 1829, when he recognized spiral objects from the Early Jurassic of southern England as also representing what he then called coprolites (Buckland, 1829). This recognition, possibly aided by the famed fossil collector Mary Anning (Duffin, 2012a), led him to identify these types of fossil from many stratigraphic intervals from the Carboniferous to the Neogene (Buckland, 1829, 1835). Buckland realized that modern sharks and rays have spiral valves, and he filled modern shark intestines with Roman cement to demonstrate that they might produce spiral feces (Buckland, 1835). Despite this innovative study, he still referred some spiral coprolites to ichthyosaurs. In an impressive decade of early research on vertebrate trace fossils, Buckland also recognized dentalites (fossil bite marks) and fossil footprints, and was equally diligent in conducting actualistic studies – feeding cow bones to modern hyenas to examine the feces they produced and the bite marks they left on the bones, and making tortoises walk across wide sheets of pastry to compare their footprints to fossil tracks (Buckland, 1822, 1824, 1829, 1835, 1836; Pemberton et al., 2007).

Buckland's recognition of fossil feces sparked interest, and it inspired what Duffin (2012a) termed "copromania," particularly in Victorian England, but also in Europe and in the United States, that lasted till about the middle of the nineteenth century (e. g., DeKay, 1830a, b; Geinitz, 1842; Hitchcock, 1844; Dana, 1845; Henslow, 1845; Quadrat, 1845; Fischer, 1856; Reuss, 1856). But, during the subsequent 100 years, there was only intermittent interest in coprolites. Notable publications included the first study of human coprolites by Young (1910), descriptions of large coprofaunas from the Permian and Cretaceous (Bertrand, 1903; Neumayer, 1904) and the first paper by Eric Callen (1912-1970) on archaeological coprolites (Callen and Cameron, 1955).

There was increased study of coprolites between 1960 and 1990. Callen's discovery of a methodology to reconstitute desiccated coprolites using trisodium phosphate (Callen and Cameron, 1960) ushered in a three-decade-long "Golden Age of Coprolite Analysis" for human specimens (Bryant, 1994; Bryant and Reinhard, 2012). This work focused largely on North America, principally in the western (e.g., Fry, 1969; Hall, 1969; Heizer and Napton, 1969; Callen and Martin, 1969; Napton and Heizer, 1970) and southwestern (e.g., Williams-Dean and Bryant, 1975; Irwin-Williams and Shelley, 1980; Reinhard, 1988) United States, including Texas (e.g., Bryant, 1969, 1974; Williams-Dean, 1978; Sobolik, 1988, 1994). Other human coprolites were described from the southeastern United States (e.g., Watson and Yarnell, 1966; Bryant, 1974; Schoenwetter, 1974), Mexico (e.g., Callen, 1963, 1967a, 1967b, 1968; Bryant, 1975) and South America (e.g., Callen and Cameron, 1960; Callen, 1965). De Lumley (1969) and Trevor-Deutsch and Bryant (1978) studied coprolites of *Homo erectus,* Callen (1969) studied those of Neanderthals, all from France, and others worked on younger European latrinites (e.g., Callen, 1969). Earlier studies in Europe tended to focus on latrinites (cess pits, latrines) because these are prevalent, and isolated coprolites that characterize cave sites in the Americas, are rare (Shillito et al., 2020). Lipid biomarkers have been the focus of increased study of archaeological coprolites during the past 20 years around the world (e.g., Shillito et al., 2013; Zhang et al., 2019, 2020).

The decades of the 1960s through 1990s also saw an increased interest in paleontological coprolites. As the work of Callen had stimulated studies of human coprolites, Paul S. Martin (1928-2010) had a similar effect on the study of Pleistocene vertebrate coprolites. Martin and his students and collaborators, notably Jim I. Mead, became the driving force behind the study of the desiccated coprolites from caves in the American Southwest (Martin, 2005; Mead and Swift, 2012; Mead et al., 2020). Much of this work was focused on the palynology and paleobotany of coprolites and their ages and relationship to late Pleistocene extinctions (e.g., Martin et al., 1961, 1985; Hansen, 1978, 1980; Mead et al., 1984, 1986a, b, 1993, 2020; Agenbroad and Mead, 1987, 1989; Mead and Agenbroad, 1989, 1992). Outside of the Americas work has focused on hyena coprolites and their palynology, principally in caves in Europe, Africa and Asia (Hunt and Lucas, 2020a and references cited therein).

The development of the study of older coprolites was slower during this timeframe. The majority of this work was on the coprolites of the Paleozoic (e.g., Zangerl and Richardson, 1963; Williams, 1972; McAllister, 1985, 1988, 1996), Triassic (e.g., Ochev, 1974; Duffin, 1979; Jain, 1983) and Cretaceous fish (e.g., Stewart, 1978) and of Cenozoic mammals (e.g., Jepsen, 1963; Vogeltanz, 1965, 1967; Clark et al., 1967; Lemley, 1971; Edwards, 1973a, b; Edwards and Yatkola, 1974; Packard and Allison, 1980).

Karen Chin did much to popularize the study of coprolites within paleontology in the 1990s and 2000s as she and co-workers studied the coprolites of the most glamorous of fossil vertebrates, the dinosaurs (e.g., Chin, 1996; Chin and Gill, 1996; Chin et al., 1998, 2003, 2009; Chin and Kirkland, 1998; Chin, 2007). In a similar timeframe, we began to collect and analyze large samples of coprolites, especially of Triassic age (e.g., Lucas et al., 1985a; Hunt, 1992; Hunt et al., 1994a, 1998, 2007, 2018). This period also saw the first applications of DNA analysis to the study of ground sloth coprolites (Höss et al., 1996; Poinar et al., 1998, 2003). Ironically, as the study of human coprolites declined (Bryant and Reinhard, 2012), work on pre-Pleistocene coprolites intensified. Coprolite studies expanded in South America, notably due to the work of Souto and of Dentzien-Dias and their co-workers (e.g., Souto, 2001, 2007, 2008, 2010; Souto and Schwanke, 2010; Souto and Fernandes, 2015; Dentzien-Dias et al., 2012, 2013, 2017, 2021), and, in Europe, notably due to Qvarnström, Niedźwiedzki and Bajdek and their co-workers (Bajdek, 2013, 2014; Badjek et al., 2014, 2016, 2017, 2019; Niedźwiedzki et al., 2016b; Qvarnström et al. 2019a, b, c, 2021; Bajdek and Bienkowska-Wasiluk, 2020; Qvarnström, 2020b). Hunt et al. (1998) applied the first binomial ichotaxonomy to vertebrate coprolites, and several ichnotaxa have subsequently been named (Table 3). The study of parasites in coprolites has a long history in archeology (Bryant and Reinhard, 2012; Camacho and Reinhard, 2020; Blong and Shillito, 2021). There is a now an extensive and growing literature on parasites in paleontological coprolites (Dentzien-Dias et al., 2013, 2017; Cardia et al., 2019, 2021; Ferreira et al., 2019; Barrios-de Pedro et al., 2020b; Agustín et al., 2021; De Baets et al., 2021; Oyarzún-Ruiz et al., 2021).

Hunt et al. (2012d) edited the first academic volume on vertebrate coprolites, which included diverse contributions that discussed the history of study, terminology, distribution and importance of bromalites. The last decade has been characterized by the use of new methodologies of study and a focus on inclusions in coprolites of fossils of organisms in

TABLE 3. Named coprolite ichnotaxa.

Ichnotaxon	Morphology	Author	Producer	Holotype Age	Age Range	Type Unit	Type locality
Alococopros indicus	Arcuate, large, sub-rounded in cross section, regularly spaced longitudinal grooves	Hunt et al. (2007)	Crocodylomorph	Late Cretaceous (Maastrichtian)	Late Cretaceous	Lameta Formation	Kadubana, India
Alococopros triassicus	Arcuate, small, sub-rounded in cross section, regularly spaced longitudinal grooves	Hunt et al. (2007)	Archosauromorph	Upper Triassic (late Carnian)	Early Permian-Late Eocene	Tecovas Formation of Chinle Group	Crosby County, Texas, USA
Beechybromus wellschi	Elongate sub-cylindrical coprolite composed of discoidal segments	Hunt and Lucas (2018b)	Mosasaur	Late Cretaceous (late Campanian)	Late Cretaceous	Beechy Member of Bearpaw Formation	Wellsch Valley, Saskatchewan, Canada
Bibliocoprus beemanensis	Scroll, cylindrical, parallel-sided, coils in lateral view that constitute less than 20% of the length	Hunt et al. (2012g)	Chondrichthyan	Late Pennsylvanian (Missourian)	Late Pennsylvanian	Beeman Formation	Sacramento Mountains, New Mexico, USA
Borocopros wangi	Segmented cylindrical containing abundant large bone fragments	Hunt and Lucas (2021c)	*Borophagus* spp.	latest Miocene	Latest Miocene - latest Pliocene	Mehrten Formation	Turlock Lake, California, USA
Castrocopros martini	Sub-cylindrical comprised of anterior-posteriorly thick plates that are parallel-sided to wedge-shaped in cross section	Hunt and Lucas (2018c)	*Nothrotheriops shastensis*	Late Pleistocene	Late Pleistocene	Unnamed cave fill	Rampart Cave, Arizona, USA
Castrocopros hauthali	Sub-cylindrical composed of anterior-posteriorly thin plates that are parallel-sided to wedge-shaped in cross section	Hunt and Lucas (2018c)	*Mylodon darwinii*	Late Pleistocene	Late Pleistocene	Unnamed cave fill	Cueva de Milodón, Última Esperanza province, Chile
Costacoprus chinae	Cylindrical with closely spaced lateral ridges along its length that average 2-3 mm in width and that are at right angles to the long axis	Hunt et al. (2012c)	Fish	Early Cretaceous (Albian)	Early Cretaceous	"Cambridge Greensand"	Cambridge, England
Crassocoprus mcallisteri	Heteropolar macrospiral, approximately 10 tight, irregularly-spaced coils that constitute 75% of the length	Hunt et al. (2012i)	Chondrichthyan	Late Pennsylvanian (Missourian)	Late Pennsylvanian-Eocene	Tinajas Member of Atrasado Formation	Tinajas Lagerstätte, New Mexico, USA
Crustacoprus tinajaensis	Cylindrical, predominantly of conchostracan valves with abundant fine-grained phosphatic groundmass	Hunt et al. (2012i)	Acanthodian, platysomid	Late Pennsylvanian (Missourian)	Late Pennsylvanian	Tinajas Member of Atrasado Formation	Tinajas Lagerstätte, New Mexico, USA

TABLE 3. (continued)

Ichnotaxon	Morphology	Author	Producer	Holotype Age	Age Range	Type Unit	Type locality
Dakyronocopros arroyoensis	Teardrop-shaped in shape and laterally flattened, with no spiraling or inclusions	Hunt and Lucas (2005a)	Fish or tetrapod	Early Permian (Late Wolfcampian-Middle Leonardian)	Early Permian	Arroyo Formation	Taylor County, Texas, USA
Daniacopros hofstedtii	Microspiral heteropolar, posterior spire less than 50% length, irregular longitudinal striations	Milàn and Hunt (2016)	Fish less derived than teleosts or advanced actinopterygian	Early Paleocene	Early Paleocene	Stevns Klint Formation	Hammelev Quarry, Denmark
Dicynodontocopros maximus	Large, typically dark gray, up to 4 loose coils, containing large blebs of carbonaceous material, slightly arcuate, one end broadly rounded and the other acute	Hunt et al. (1998)	Dicynodont	Late Triassic (late Carnian)	Late Triassic	Tecovas Formation of Chinle Group	Crosby County, Texas, USA
Elacocoprus williamsi	Elongated amphipolar coprolite narrow, elongate, and tapering posteriorly	Hunt et al. (2012i)	Chondrichthyan or sarcopterygian	Late Pennsylvanian (Missourian)	Late Pennsylvanian	Tinajas Member of Atrasado Formation	Tinajas Lagerstätte, New Mexico, USA
Elongatocoprus amadoensis	Elongate gently coiled cylinder with a round cross section that is tightly spiraled in cross section	Hunt et al. (2012i)	Chondrichthyan or sarcopterygian	Late Pennsylvanian (Missourian)	Late Pennsylvanian	Tinajas Member of Atrasado Formation	Tinajas Lagerstätte, New Mexico, USA
Eucoprus cylindratus	Cylindrical with rounded ends and containing no osseous inclusions	Hunt and Lucas (2012b)	Fish, amphibians, tortoises, iguanas, crocodylians, theropods, birds, mammalian carnivores	Late Triassic (Rhaetian)	Early Triassic –late Eocene`	Redonda Formation of Chinle Group	Gregory Quarry, New Mexico, USA
Falcatocopros oxfordiensis	Long, narrow, tapering, cylindrical, curved	Hunt et al. (2007)	Vertebrate	Late Jurassic (Oxfordian)	Late Triassic-Late Jurassic	Oxford Clay	Peterborough, England
Heliocoprus clarki	Amphipolar with wide separation of the coils by deep sulci with a V-cross section	Hunt et al. (2015b)	Rajidae (skates)	Late Pliocene-Pleistocene	Late Pliocene-Pleistocene	Red Crag Formation	Ipswich, England.
Heteropolacopros texaniensis	Heteropolar, microspiral, three-four coils forming less than 50% of the length	Hunt et al. (1998)	Chondrichthyan	Upper Triassic (late Carnian)	Early Permian-Late Triassic	Tecovas Formation of Chinle Group	Crosby County, Texas, USA
Huberobromus ovatus	Large, flattened and sub-ovoid with groundmass and abundant fish debris	Hunt and Lucas (2021a)	Chondrichthyan	Late Pennsylvanian (Missourian)	Mississippian-Pennsylvanian	Tinajas Member of Atrasado Formation	Kinney Brick Quarry, New Mexico, USA

TABLE 3. (continued)

Ichnotaxon	Morphology	Author	Producer	Holotype Age	Age Range	Type Unit	Type locality
Hyaenacoprus bucklandi	A series of rounded segments, some of which are sub-spherical and are white in color with many small angular bone fragments	Hunt et al. (2012a)	Hyena	Late Pleistocene	Pliocene-Recent	Unnamed cave fill	Kirkdale Cave, England
Hyronocopros amphipola	Amphipolar, tight coils, no inclusions, typically six coils, small	Hunt et al. (2005b)	Sarcopterygian or chondrichthyan	Early Permian (Wolfcampian)	Late Pennsylvanian-Early Permian	El Cobre Canyon Formation	VanderHoof Quarry, New Mexico, USA
Hyronocopros hunti	Amphipolar, tight coils, elongate, large	Rummy et al. (2021)	Asipenceriformes	Early Cretaceous (Barremian)	Early Cretaceous	Tsagan-Tsab Formation	Tatal, Mongolia
Hyronocopros tsagantsabensis	Amphipolar, tight coils, elongate, tapered, inclusions	Rummy et al. (2021)	Asipenceriformes	Early Cretaceous (Barremian)	Early Cretaceous	Tsagan-Tsab Formation	Tatal, Mongolia
Ichthyosaurolites duffini	Wide, flattened rectangle with a rounded tip with abundant phosphatic groundmass and inclusions of multiple skeletal elements of juvenile ichthyosaurs	Hunt et al. (2012a)	Plesiosaur or ichthyosaur	Early Jurassic (Hettangian-Lower Pliensbachian)	Early Jurassic	Lias	Lyme Regis, England
Iuloeidocoprus mantelli	Amphipolar, cylindrical with multiple, closely spaced spirals	Hunt et al. (2012b)	Chondrichthyan or Osteicthyan	Late Cretaceous (Santonian-Maastrichtian)	Late Cretaceous	Selma Group	Huntsboro, Alabama, USA
Kalocoprus oteroensis	Dominantly amphipolar -spirals do not extend to the posterior end, small number of coils separated by deep sulci, unwound	Hunt et al. (2012g)	Chondrichthyan	Late Pennsylvanian (Missourian)	Late Pennsylvanian	Beeman Formation	Sacramento Mountains, New Mexico, USA
Kinneybromus jurgenai	Large, flat with elongate ovoid shape, scalloped margin and fine-grained matrix	Hunt and Lucas (2021a)	Chondrichthyan	Late Pennsylvanian (Missourian)	Late Pennsylvanian	Tinajas Member of Atrasado Formation	Kinney Brick Quarry, New Mexico, USA
Liassocopros hawkinsi	Heteropolar, macrospiral, maximum width at first spiral	Hunt et al. (2007)	Chondrichthyan	Early Jurassic (Hettangian-Lower Pliensbachian)	Late Pennsylvanian-Late Cretaceous	Lias	Lyme Regis, England
Maculacoprus ateri	Dense, dark flattened ovoid with macerated fish material and matrix	Hunt and Lucas (2021a)	Acanthodians, palaeonisciforms or platysomids	Late Pennsylvanian (Missourian)	Mississippian-Pennsylvanian	Tinajas Member of Atrasado Formation	Kinney Brick Quarry, New Mexico, USA
Malericopros matleyi	Heteropolar, microspiral, rounded ends, cylindrical	Hunt et al. (2007)	Chondrichthyan	(Late Triassic; late Carnian)	Permian-Late Triassic	Maleri Formation	Maleri, India
Megaheteropolacopros sidmacadami	Heteropolar, microspiral, four whorls forming less than 50% of the length, length greater than 5 cm	Hunt et al. (2005a)	Large chondrichthyan	Early Permian (middle Leonardian)	Early Permian (Wolfcampian-middle Leonardian)	Vale Formation	Sid McAdams locality, Texas, USA
Mammuthocopros allenorum	Flattened sphere shape, large size	Hunt and Lucas (2020)	*Mammuthus columbi*	Late Pleistocene	Late Pleistocene	Unnamed cave fill	Bechan Cave, Utah, USA

TABLE 3. (continued)

Ichnotaxon	Morphology	Author	Producer	Holotype Age	Age Range	Type Unit	Type locality
Megakalocoprus barremianensis	Amphipolar, coils separated by deep sulci, unwound, large	Rummy et al. (2021)	Asipenceriformes	Early Cretaceous (Barremian)	Early Cretaceous	Tsagan-Tsab formation	Tatal, Mongolia
Plektecoprus whitbyensis	Elongate, rounded in cross section with a loose spiral coil and having a conical posterior end and a broad, rounded anterior end	Hunt et al. (2012a)	Ichthyosaur or plesiosaur	Early Jurassic (Hettangian-Lower Pliensbachian)	Early Jurassic	Lias	Whitby, England
Rhynchocopros soutoi	Well rounded ovoid, wide, composed primarily of calcite, often occurring in masses of up to six	Hunt et al. (2013b)	Rhynchosaur	Middle Triassic (Ladinian)	Middle Triassic	Santa Maria Formation	Gal. Camara, Villa Melo, Brazil
Santamariacopros elongatus	Elongate, rounded cylinder, composed principally of calcite lacks inclusions, often occurs in masses of up to four	Hunt et al. (2013b)	Dicynodont	Middle Triassic (Ladinian)	Middle Triassic	Santa Maria Formation	Gal. Camara, Villa Melo, Brazil
Saurocopros bucklandi	Heteropolar, microspiral, small number of wide spirals	Hunt et al. (2007)	Chondrichthyan	Early Jurassic (Hettangian-Lower Pliensbachian)	Late Triassic-Early Jurassic	Lias	Lyme Regis, England
Scrollocoprus tatalensis	Scroll, small, anisopolar, cylindrical	Rummy et al. (2021)	Sarcopterygian	Early Cretaceous (Barremian)	Early Cretaceous	Tsagan-Tsab formation	Tatal, Mongolia
Speiracoprus socorroensis	Heteropolar, macrospiral, proportionally short and wide, three coils with deep sulci between them, a narrow, acutely tipped posterior end and a rounded, conical anterior termination	Hunt et al. (2012i)	Chondrichthyan or sarcopterygian	Late Pennsylvanian (Missourian)	Late Pennsylvanian	Tinajas Member of Atrasado Formation	Tinajas Lagerstätte, New Mexico, USA
Strabelocoprus pollardi	Heteropolar, microspiral, wide, small number of coils (<3) in lateral view, very wide spirals in posterior view	Hunt et al. (2012a)	Chondrichthyan or sarcopterygian	Late Triassic (Rhaetian)	Late Triassic-Early Jurassic	?Penarth Group	Watchet, England
Strophocopros valensis	Segmented, elongate, a surface texture with a fibrous, ropy texture, over 10 cm in length	Hunt and Lucas (2005b)	Chondrichthyan	Early Permian (middle Leonardian)	Early Permian	Vale Formation	Sid McAdams locality, Texas, USA
Tikicopros triassicus	Scroll, small, cylindrical, rounded anterior and tapering posterior ends, dense inclusions of bones and scales	Rakshit et al. (2019)	Hybodontid sharks - *Lonchidion* or *Pristrisodus*	Late Triassic (Carnian-Norian)	Late Triassic	Tiki Formation	Near the village of Tihki, Madhya Pradesh, India

TABLE 3. (continued)

Ichnotaxon	Morphology	Author	Producer	Holotype Age	Age Range	Type Unit	Type locality
Vinculostercus vermiformis	Amphipolar, small with narrow, flattened ribbons	Duffin and Ward (2020)	Chondrichthyans or actinopterygians	Early Carboniferous (Brigantian)	Early Carboniferous	Eyam Limestone Formation (Peak Limestone Group, Carboniferous Limestone Supergroup)	Once-A-Week Quarry, Derbyshire, England
Virgacoprus brevis	Flattened, small, narrow with rounded terminations, composed of macerated fish debris in fine-grained matrix	Hunt and Lucas (2021a)	Haplolepid, a small palaeonisciform or an acanthodian	Late Pennsylvanian (Missourian)	Late Pennsylvanian	Tinajas Member of Atrasado Formation	Kinney Brick Quarry, New Mexico, USA

coprolites such as bacteria and beetles, and structures such as hair that otherwise have a very limited and poor fossil record, as well as biochemicals (e.g., Dentzien-Dias et al., 2012, , 2021; Cosmidis et al., 2013; Beltrame et al., 2014; Khosla et al., 2015, 2016; Bajdek et al., 2016, 2017; Robin et al., 2016; Cin et al., 2017; Qvarnström et al. 2019a, b, c, 2021; Qvarnström, 2020b; Umamaheswaran et al., 2019; Runge et al., 2021; Tripp et al., 2021) culminated by the recognition by Qvarnström et al. (2016) of coprolites as Lagerstätten.

Terminology

Buckland (1829; see review in Hunt and Lucas, 2012a) introduced the term coprolite for preserved feces. The term coprolite has been consistently utilized for expelled feces, although there are a few examples of the term being utilized for consumulites (Hunt and Lucas, 2012a, 2020). Hunt and Lucas (2012a) reviewed all usage of terminology related to coprolites and introduced other terms including latrinite (accretionary and ethological) for accumulations of coprolites and guanolite (ornithoguanolite, pinnipedaguanolite, chiropteraguanolite) for fossil guano (Appendix B).

Neumayer (1904) first introduced a terminology for spiral coprolites from the early Permian of Texas. He recognized that some spiral coprolites have spirals that are distributed roughly evenly along the long axis in lateral view (amphipolar), whereas others have the spirals concentrated at one end (heteropolar) (Appendix B). Heteropolar coprolites are much more common throughout the fossil record than amphipolar forms. Scroll coprolites represent a third major morphology of spiral coprolites (Hunt and Lucas, 2012b). Hunt et al. (2007) recognized two forms of heteropolar morphology – microspiral, in which the posterior spire constitutes less than 50% of the length of the coprolite in lateral view, and macrospiral, in which it represents 50%-75% of the length of the coprolite (Appendix B). Several authors proposed different descriptive terminologies for spiral coprolites (e.g., Jain, 1983; McAllister, 1985; Laojumpon et al., 2012), and Hunt and Lucas (2012b) synthesized aspects of these schemes (coils, lip) and defined new terms (anterior coil, posterior spire) (Appendix B).

Non-spiral coprolites display a wide range of morphologies (e.g., Häntzschel et al., 1968, fig. 1). Thulborn (1991) noted that many coprolites have terminations of different shapes. He applied the term anisopolar to this type of coprolite and the term isopolar to forms in which the two ends are of the same shape (Appendix B). Typically, the posterior (distal) end of an anisopolar coprolite that emerges first from the anus/cloaca is broadly rounded, and the anterior (proximal) end is tapered to a point (mucro of Thulborn, 1991). The trailing end is pinched by the constriction of the cloaca/anal margins as it closes (Thulborn, 1991). Hunt and Lucas (2012b) proposed the term segments for the discrete longitudinal elements of a coprolite (pellets of Diedrich, 2012a; Appendix B).

Actualistic Studies

Buckland (1822, 1824) conducted the first actualistic studies of coprolites when he fed cow bones to a hyena and studied the resulting feces to assist in the identification of coprolites from a Pleistocene cave. Subsequently, Buckland recognized spiral coprolites, which he hypothesized were produced by chondrichthyans. Thus, he dissected extant rays and scyliorhinid sharks (dogfish) in order to study the spiral valves of their intestinal tracts, and subsequently he injected the intestines with Roman cement (Buckland, 1835; Duffin, 2009). The injection process produced "artificial coprolites that in form are exactly similar to many of our fossil specimens" (Buckland, 1835, p. 234). Zangerl and Richardson (1963) conducted analogous experiments.

Modern feces have been the subject of extensive study, but actualistic studies of coprolites have been mainly limited to anecdotal comments (e.g., Jain, 1983; McAllister, 1996), although there are a few notable exceptions (e.g., Esteban-Nadal et al., 2010; Milàn and Hedergaard, 2010; Milàn, 2012; Wings, 2012). However, many neontological studies provide important data for the study of coprolites such as the particle size of ingesta (Fritz, 2007; Fritz et al., 2009), fecal dimensions relative to body size (Platt et al., 2020) and fecal composition, diet and digestive physiology (Canfield and Fairburn, 1983; Doherty, 2009). There is clear potential for more actualistic studies related to coprolites.

Fossil Record

Introduction

We have previously reviewed the fossil record of coprolites (Hunt et al., 2012d) and some of the coprofaunas from the Carboniferous-Permian (Hunt and Lucas, 2013), Triassic (Hunt et al., 2007, 2013b, 2018), Jurassic (Hunt and Lucas, 2014a), Cretaceous-Paleogene (Hunt and Lucas, 2007a, 2016a; Hunt et al., 2015c), Cenozoic (Hunt and Lucas, 2007a) and Pleistocene (Hunt and Lucas, 2018c, 2020a).

Paleozoic

The oldest vertebrate body fossils are from the lower Cambrian of China (e.g., Shu et al., 1999, 2003; Shu, 2008). Cambrian coprolites occur at a number of localities, but all have been attributed to invertebrates (e.g., Peel, 2015; Shen et al., 2014; Kimmig and Strotz, 2017; Kimmig and Pratt, 2018). Some larger forms could have arguably been produced by vertebrates, such as round masses of fragmented skeletal material from the middle Cambrian Spence Shale of Utah. These were identified as coprolites by Conway Morris and Robison (1986), and attributed either to very large individuals of the arthropod predator *Anomalocaris* or to another unidentified large predator.

There are several occurrences of clusters of conodont elements from the Early Ordovician of Kazakhstan, Sweden and Australia that probably represent coprolites (Tolmacheva, 1996; Tolmacheva and Purnell, 2002; Stewart and Nicoll, 2003). These coprolites were most likely produced by conodont animals (Tolmacheva and Purnell, 2002).

The Middle Ordovician Winneshiek Lagerstätte of Iowa in the United States and the Late Ordovician Soom Shale Lagerstätte of South Africa both preserve diverse bromalites that probably include some of vertebrate origin (Aldridge et al., 2006; Hawkins et al., 2018). The Winneshiek Shale yields a variety of vermiform bromalites that are principally preserved three-dimensionally and composed of calcium phosphate with a minority preserved as carbonaceous compressions (Briggs et al. 2015; Liu et al. 2017; Hawkins et al., 2018). Hawkins et al. (2018) identified five morphotypes that may have been produced by eurypterids, agnathans and/or conodonts. Inclusions identified in thin sections are principally conodonts but also include phyllocarids, other small arthropods such as ostracods, and linguloids. Some Winneshiek bromalites preserve a concentrically layered internal structure, which is characteristic of the coprolites of animals with a valvular intestinal tract such as chordates (Hawkins et al., 2018). The abundance and diversity of the Winneshiek bromalites may provide independent evidence of predation in the fauna during the Great Ordovician Biodiversification Event (Hawkins et al., 2018).

Aldridge et al. (2006) described five principal morphotypes of Ordovician bromalites, including coprolites. Brachiopod-bearing coprolites could pertain to conodont animals or several groups of invertebrates. Some coprolites, or possibly regurgitalites, are composed of conodont elements more fragmented than those in the Early Ordovician specimens, and they were probably produced by conodont animals (Aldridge et al., 2006). Corrugated⁄spiral bromalites, coiled coprolites and wrinkled coprolites could all have been produced by vertebrates. The most likely vertebrate coprolites are those that are amphipolar spiral in morphology (Aldridge et al., 2006, pl. 1, figs. 9-10). This corresponds to the intestinal morphology of many early fish (McAllister, 1987). While eurypterids also possessed a partially spiraled gut, there is no evidence that they produced spiral coprolites. Caster and Kjellesvig Waering (1964) described a putative eurypterid coprolite containing fragments of the exoskeleton of the eurypterid *Megalograptus ohioensis* and a trilobite cephalon, in association with body fossils of *M. ohioensis* from the Ordovician of Ohio, as evidence of cannibalism. Unstructured masses containing disarticulated agnathan fragments are common in the Monks Water fish bed in the Silurian Hagshaw Hills inlier in Scotland, together with the eurypterid *Lanarkopterus dolichoschelus,* and these were interpreted by Selden (1979) as eurypterid coprolites. These examples suggest eurypterid coprolites consist of unstructured material. Thus, we consider the spiral morphology to be diagnostic of vertebrates.

There are few putative Early or Middle Silurian vertebrate coprolites. There are Early Silurian coprolites from Scotland and Nova Scotia of a size that they could have been produced by vertebrates, but they have been attributed to large predatory eurypterids such as *Lanarkopterus* (Gilpin, 1886; Rolfe, 1973; Selden, 1984; Turner, 1999). Late Silurian coprolites include two unusual morphologies. Gilmore (1992) described more than 150 scroll and non-spiral coprolites from western Ireland and southern Scotland. The coprolites are composed of argillaceous clastic material. These coprolites occur with body fossils of agnathans, to which they are attributed. Scroll coprolites are uncommon in the fossil record (e.g., Hunt et al., 2012b; Stringer and King, 2012), and the only other examples of non-phosphatic spiral coprolites are from the Permian of Antarctica (Retallack

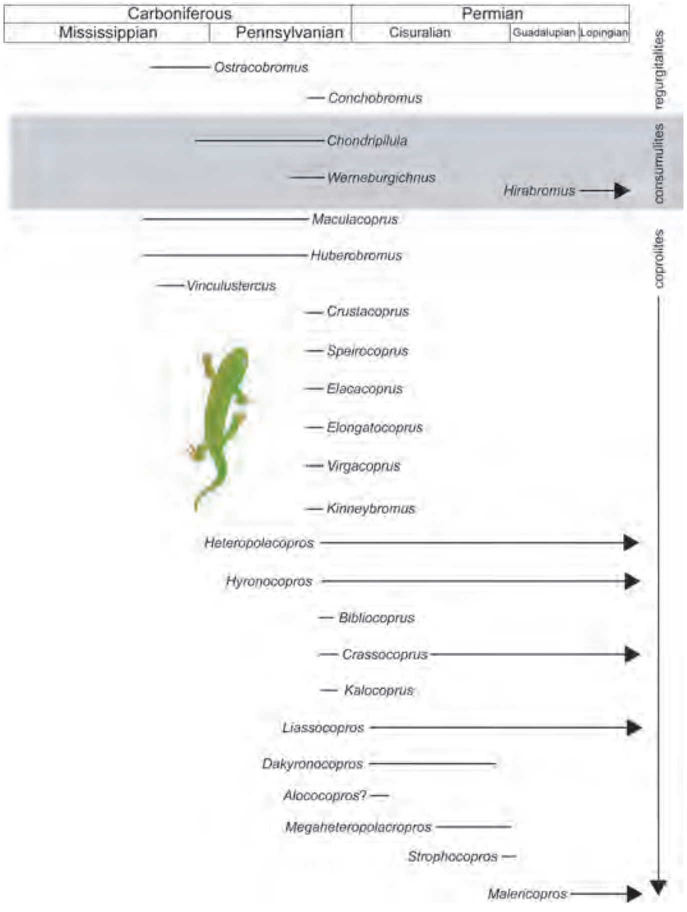


FIGURE 25. Stratigraphic distribution of Paleozoic bromalite ichnogenera.

and Krull, 1999).

The Telychian/Llandovery agnathan locality of Birk Knowes, Lanarkshire, Scotland, yields a large number of coprolites. They are composed principally of agnathan fragments with little matrix. Specimens at the Hunterian Museum in Glasgow preserve two principal morphologies. The majority of the bromalites are flattened ovoids averaging 30 mm in length and 40 mm in height. A small number of specimens are parallel-sided linear ribbons with a maximum length of 105 mm and a width of 24 mm. The lack of matrix may suggest that these bromalites represent regurgitalites. However, the abundance of specimens and the regular size of the pellets suggest they are coprolites, albeit unusual ones.

The Ludlow bone bed (Ludlow Bone Bed Member of Downton Castle Sandstone Formation) is a Late Silurian source of vertebrates in the area along the border between England and Wales. Coprolites have long been known to be locally common in the Ludlow bone bed (Strickland and Hooker, 1853; Murchison, 1867). They include spiral morphologies and are phosphatic, and are thus similar to many geologically younger coprolites (Murchison, 1839, p. 607, pl. 2, figs. 46-47, 54- 55).

Vertebrate coprolites become more common in the Devonian, with the most important assemblages derived from fossil-fish localities in Scotland, and Lagerstätten elsewhere. The most significant Early Devonian coprolites from Scotland derive from the Lochkovian Tillywhandland Quarry, Forfarshire (Trewin and Davidson, 1996). Many coprolites contain spines and scales of the acanthodian fish *Mesacanthus* and were probably produced by *Ischnacanthus* (Trewin and Davidson, 1996; Trewin, 2008; Newman and Davidson, 2010). The *Mesacanthus* spines are usually oriented anteriorly, which indicates head first ingestion of spiny acanthodians (Trewin, 2008). Most coprolites are flattened. A second important assemblage of coprolites occurs at Duntrune Quarry in Angus. Spiral coprolites are uncommon in the nonmarine assemblages of the Early Devonian of Scotland.

The Early Devonian Hunsrück Slate Lagerstätte of Germany yields pyritized coprolites of various morphologies and includes local concentrations (Bartels et al., 1998; Wagner and Boyce, 2006; Kühl et al., 2012). Small strings of feces that represent deposit feeders are widespread, but larger coprolites attributed to fish are only common in the northern Hunsrück where body fossils are rare (Bartels et al., 1998). These coprolites range from ovoids to spirals in morphology and locally are concentrated in thin layers (Bartels et al., 1998, fig. 220; Kûhl et al., 2012, fig. 119).

The Achanarras Quarry in the Upper Flagstone Group of the Middle Old Red Sandstone of Caithness (Eifelian–Givetian) yields a large sample of Middle Devonian coprolites (Rayner, 1963; Trewin, 1986; Hamilton and Trewin, 1988, 1994). Other Scottish Middle Devonian coprolites derive from Orkney and Moray. Most coprolites are preserved three dimensionally and include several examples of spiral coprolites, and one with a scroll morphology.

McAllister (1996) published a detailed study of more than 120 bromalites, principally coprolites, from the Upper Devonian Escuminac Formation of the Miguasha Lagerstätte, Quebec, Canada. These coprolites are typical of Devonian assemblages in that spiral forms are relatively uncommon (only 3-4 in the Escuminac) as are specimens over 4-5 cm in length, and larger forms are very rare. Small vertebrate coprolites occur in the Late Devonian of Poland, and one larger spiral specimen contains conodont elements (Zatoń and Rakociński, 2014; Zatoń et al., 2017). Devonian coprolites have been reported from other areas, including Brazil (Maisey and Melo, 2005), Latvia/Estonia (Hunt et al., 2012b) and the United States (e.g., Branson, 1914).

Carboniferous strata record the first large samples of vertebrate coprolites (Turner, 1999; Fig. 25). This is a strictly Laurussian record that increases in diversity and abundance from the Mississippian into the Pennsylvanian. Mansky et al. (2012) described coprolites from the Early Mississippian (Tournaisian) Horton Bluff Formation of Nova Scotia. In Scotland, there are Early Mississippian coprolites (e.g., Pollard, 1985) as well as large collections of coprolites from three Middle Mississippian (Viséan) localities: (1) East Kirkton, West Lothian; (2) Wardie, Midlothian; and (3) Anstruther, Fife (Buckland, 1836; Sumner 1991,1994). The Wardie and Anstruther localities yield the oldest coprofaunas dominated by spiral coprolites. These coprolites occur in concretions and average about 5 cm in length. Very large coprolites from East Kirkton measuring more than 17 cm in length have been attributed to eurypterids (Sumner, 1994). The Late Mississippian (Serpukhovian) of Bearsden, East Dunbartonshire, Scotland, yields a large sample of coprolites, as does the similar age Bear Gulch Lagerstätte of Montana, USA (Zidek, 1980; Clark, 1989; Hunt et al., 2012e). Other Mississippian coprolites occur in the USA (e.g., Fayetteville Shale of Arkansas and Oklahoma, Michigan Formation of Michigan, Buffalo Wallow Formation of Kentucky) and England (Hunt and Lucas, 2013; Greb et al., 2015).

The first abundant samples of vertebrate coprolites occur in the Pennsylvanian (Fig. 25). Coprolites are found in marine and lagoonal shales at many localities as well as in some nonmarine coal successions (Hunt and Lucas, 2013). Four bromalite faunas of Late Pennsylvanian (Missourian/Kasimovian) age in New Mexico, USA, represent an ecological transect from lacustrine to basinal marine: (1) Tinajas Lagerstätte – lacustrine; (2) Kinney Brick Quarry Lagerstätte – lagoonal; (3) Erickson site – nearshore marine; and (4) Sacramento Mountains (Fig. 26) – offshore marine (Hunt and Lucas, 2017a). There are clear trends through these ichnofaunas from lacustrine to offshore marine in terms of a trend of flattened preservation to three dimensional preservation, decreasing diversity of kinds of bromalites (regurgitalites, consumulites) and increasing proportions of spiral coprolites (Hunt and Lucas, 2017a).

There are several Pennsylvanian examples of stratigraphically narrow but geographically widespread zones rich in spiral coprolites in marine shales in Colorado (Weber Formation, lower Belden Formation) and West Virginia (Conemaugh Group) in the USA, and in Germany (Göttelborner Beds) (Price, 1927; Johnson, 1934; Guthörl, 1959; Kneuper and Schönenberg, 1962; Hunt et al., 2012b; Hunt and Lucas, 2013). A variety of Pennsylvanian Lagerstätten in the United States preserve coprolites, including Mazon Creek in Illinois, the Hamilton Quarry of Kansas and the Kinney Brick Quarry and Tinajas localities of New Mexico (McAllister, 1988; Shabica and Godfrey, 1997; Hunt et al., 2012h, i; Hunt and Lucas, 2017a, 2021b; Tripp et al., 2021). Marine invertebrates in coprolites from Hamilton aid in paleoenvironmental interpretation (Cunningham et al., 1993). Zangerl and Richardson (1963) conducted a classic and extensive study of the paleoecology of the Middle Pennsylvanian (Desmoinesian/Moscovian) Mecca Quarry Shale and Logan Quarry members of the Carbondale Formation in western Indiana, USA, and described multiple bromalites (coprolites and regurgitalites: Elder, 1985; Elder and Smith, 1988).

Dawson (1854, 1862) first noted common coprolites in the fossil-bearing tree stumps of the Early Pennsylvanian Joggins Formation of Nova Scotia, and they have been described from various localities in eastern Canada (Brown, R. and Lyell, C., 1845; Keighley and Pickerill, 1997; Falcon-Lang et al., 2006; Ó Gogáin et al., 2016; Chipman, 2017; Chipman et al., 2020; Bingham-Koslowski et al., 2021). Other coal-bearing Pennsylvanian strata in England, Scotland, Belgium, Germany and Poland yield coprolites (e.g., Buckland, 1836; Bayer, 1934; Anderson et al., 1997; Hunt et al., 2012b, c; Hunt and Lucas, 2013; Krzykawski et al., 2014, Lomax et al., 2016). Hodnett and Lucas (2018) described an unusual, large coprolite that

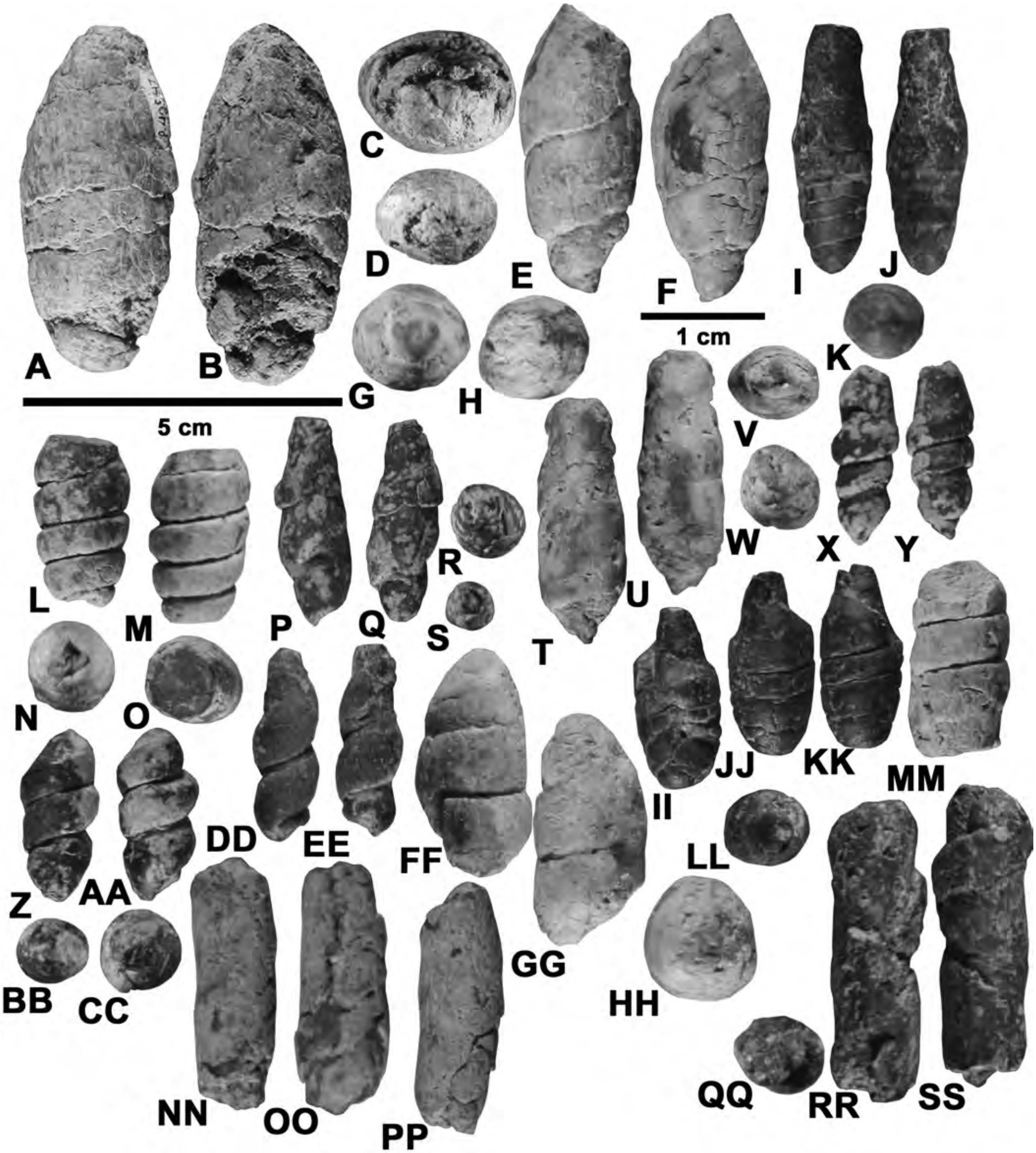


FIGURE 26. Selected spiral coprolites from the Late Pennsylvanian (Missourian) Beeman Formation, Otero County, New Mexico, USA. **A-D,** *Liassocoprus hawkinsi*, NMMNH P-42547, coprolite in A-B, axial and C-D, polar views. **E-H,** *Hyronocoprus* isp., NMMNH P-63521, coprolite in E-F, axial and G-H, polar views. **I-K,** *Heteropolacoprus texaniensis*, NMMNH P-63514, coprolite in I-J, axial and K, polar views. **L-O,** *Hyronocoprus amphipola*, NMMNH P63520, coprolite in L-M, axial and N-O, polar views. **P-S,** *Kalocoprus oteroensis*, NMMNH P-63511, coprolite in P-Q, axial and R-S, polar views. **T-W,** *Heteropolacoprus* isp., NMMNH P-63517, coprolite in T-U, axial and V-W, polar views. **X-CC,** *Kalocoprus oteroensis*. X-Y, NMMNH P-63527, coprolite in axial views. Z-CC, NMMNH P-63523, coprolite in Z-AA, axial and BB-CC, polar views. **DD-EE,** *Kalocoprus oteroensis*, NMMNH P-63513, coprolite (holotype) in axial views. **FF-HH,** *Hyronocoprus amphipola*, NMMNH P-63519, coprolite in FF-GG, axial and HH, polar views. **II-LL,** *Heteropolacoprus texaniensis*, NMMNH P-63524, coprolite in II-KK, axial and LL, polar views. **MM,** *Hyronocoprus amphipola*, NMMNH P-63518, coprolite in axial view. **NN-SS,** *Bibliocoprus beemanensis*. NN-PP, NMMNH P-63515, coprolite in axial views. QQ-SS, NMMNH P-63503, coprolite (holotype) in QQ, polar and RR-SS, axial views (from Hunt et al., 2012g, fig. 1).

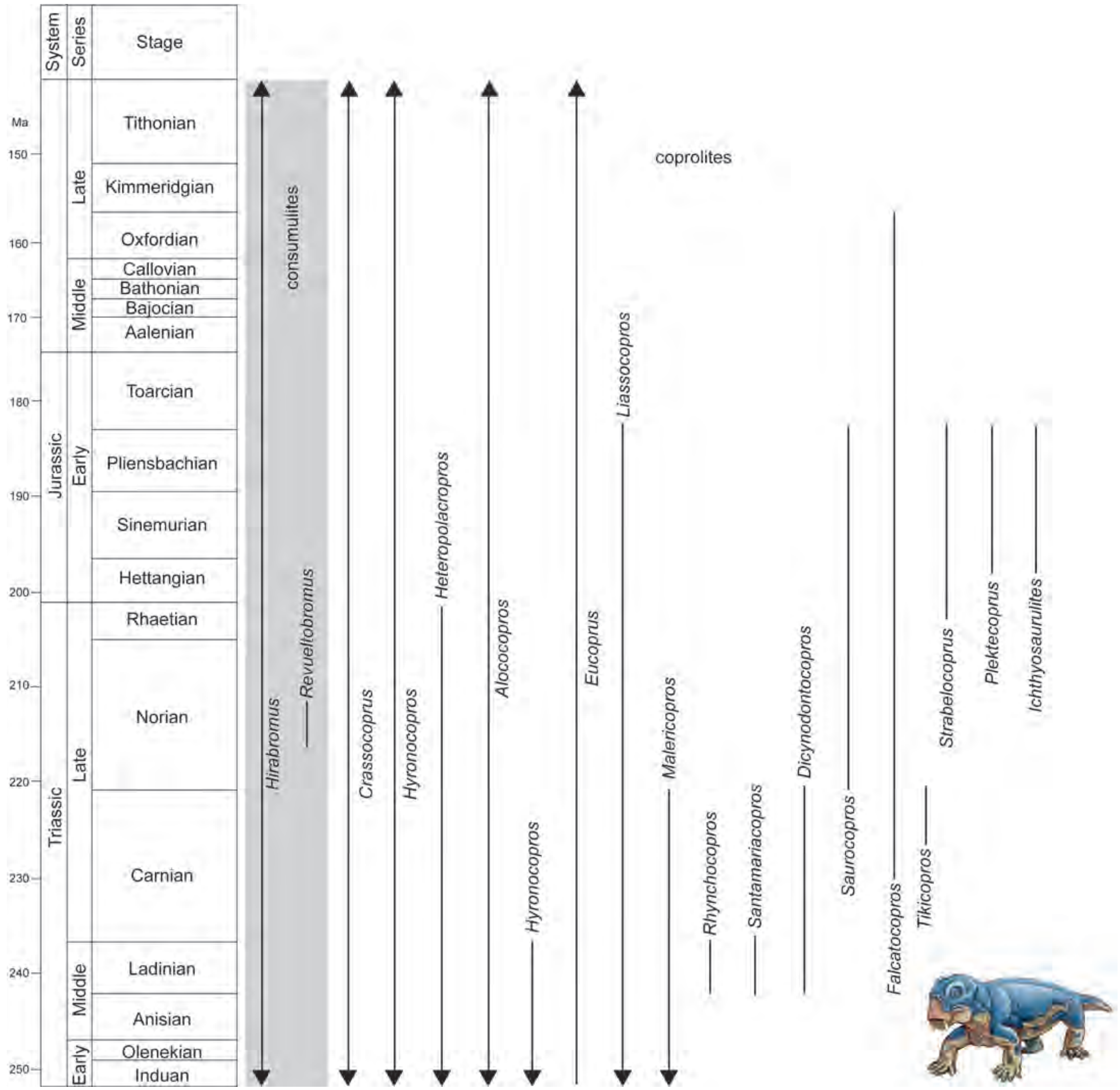


FIGURE 27. Stratigraphic distribution of Triassic and Jurassic bromalite ichnogenera.

contained body fossils of fishes and a tetrapod from the Upper Pennsylvanian of New Mexico that may represent a fecal cloud derived from a large shark.

Many Pennsylvanian coprolites have a spiral morphology, and most of these are heteropolar in form, including *Crassocoprus* and *Heteropolacopros* (Hunt et al., 2012a, b, c, 2013c; Hunt and Lucas, 2017a; Chipman et al., 2020; Figs. 25-26). Amphipolar morphologies, such as *Kalocoprus* and *Hyronocoprus,* are less common, and scroll coprolites (e.g., *Bibliocoprus*) are only locally present (Hunt et al., 2012g; Hunt and Lucas, 2017a; Chipman et al., 2020; Fig. 26). The Benxi Formation of Mississippian/Pennsylvanian (Serpukhovian to Bashkirian) age in northern China yields small coprolites that could have been produced by fish (Gong et al., 2010).

Whereas the Carboniferous coprolite record is strictly Laurussian, the Permian coprolite record globalizes to include records from Gondwana (Hunt and Lucas, 2013). A similar pattern is seen in the bone record, and this is due, at least in part, to the glaciations in Gondwana during parts of the Carboniferous-earliest Permian, which restricted the distribution of vertebrates in the southern continents (Lucas, 2006). Permian coprolites are even more abundant than those of the Pennsylvanian and are particularly common in redbeds.

Early Permian coprolites occur in redbeds of the American Southwest in New Mexico (Hunt et al., 2005b, 2013a; Cantrell et al., 2012), Texas (Neumayer, 1904; Olson, 1966; Olson and Mead, 1982; Sander, 1989; Hunt and Lucas, 2005a, b, Hunt et al., 2005a, 2012c) and Oklahoma (Olson, 1971, 1977; Hunt et al., 2012b), and in marine strata in Kansas (Williams, 1972; McAllister, 1985). These ichnofaunas principally yield spiral coprolites that are commonly heteropolar (*Heteropolacopros*, "*Megaheteropolacopros,*" *Liassocoprus*, *Malericoprus*, *Saurocoprus*), although amphipolar (*Hyronocoprus*) and nonspiral forms (*Alococopros, Dakyronocopros, Strophocoprus*) are also present (Neumayer, 1904; Hunt and Lucas, 2005a, b; Hunt et al., 2005a, 2012a, b, 2013a; Cantrell et al., 2012; Fig. 26). Similar age coprolites are present in the lower Permian Dunkard Group of West Virginia in the eastern United States (Bowen, 2013; Lucas, 2013; Hembree and Blair, 2016; Hembree and Bowen, 2017).

Coprolites are common in the Rotliegend strata of Western and Central Europe, including France (Gaudry, 1887), Germany (Lohmann and Sachs, 2001; Eichler and Werneburg, 2010) and the Czech Republic (Lemke and Weiler, 1942; Zajíc, 2014). Other early Permian coprolites are found in Brazil and Namibia and include specimens associated with skeletons of *Mesosaurus* (Ruedemann, 1929; Horsthemke et al., 1990; Warren et al., 2001; Silva et al., 2017). Middle Permian coprolites are less common, but they are present in Brazil (Dentzien-Dias et al., 2012, 2013, 2017), Russia (Ochev, 1974) and Antarctica (Retallack and Krull, 1999). The Antarctic specimens are of note because they are composed of arenaceous matrix (Retallack and Krull, 1999). Late Permian coprolites have been reported from England (Bell et al., 1979) and South Africa (Smith, 1993; Smith and Botha-Brink, 2011), but they are most common in Russia where one specimen contains possible pre-mammalian hair (Owocki et al., 2012; Sennikov and Golubev, 2012; Bajdek et al., 2016, 2017; Niedźwiedzki et al., 2016b).

Mesozoic

There is an abundant record of vertebrate coprolites in the Triassic that increases in abundance and diversity through the period (Hunt et al., 2018; Fig. 27). As in the Permian, Triassic, coprolites are particularly abundant in nonmarine redbeds. Early Triassic coprolites are geographically widely dispersed but relatively small in number. The largest sample is from the Arcadia Formation (Induan) in Queensland, northeastern Australia (Northwood, 1997, 2005). This ichnofauna includes *Hyronocopros amphipola*, *Alococopros triassicus*, *Eucoprus* sp. and indeterminate coprolites (Hunt et al., 2007). Other significant nonmarine coprofaunas occur in the Burgersdorp Formation (Olenekian) of South Africa (Bender and Hancox, 2004; Yates et al., 2012), the Vokhama Formation in Russia (Niedźwiedzki et al., 2016b) and the Bulgo Sandstone in Australia (Niedźwiedzki et al., 2016a). Other coprolites occur in units of the Buntsandstein in France (Gall, 1971; Gall and Grauvogel-Stamm, 1993) and Germany (e.g., Dachroth, 1985) and the Beaufort Group in South Africa (Smith and Botha-Brink, 2011). Early Triassic coprolites from marine strata of Japan and Poland have been utilized to address changing ecosystems after the PTB extinctions and in relation to the "Mesozoic Marine Revolution" (Nakajima and Izumi, 2014; Brachaniec et al., 2015). Similarly, Luo et al. (2017) utilized a diverse coprolite fauna from the Middle Triassic of Luoping, China to indicate the emergence of complex trophic ecosystems in the Anisian as evidence for biotic recovery after the Early Triassic extinctions.

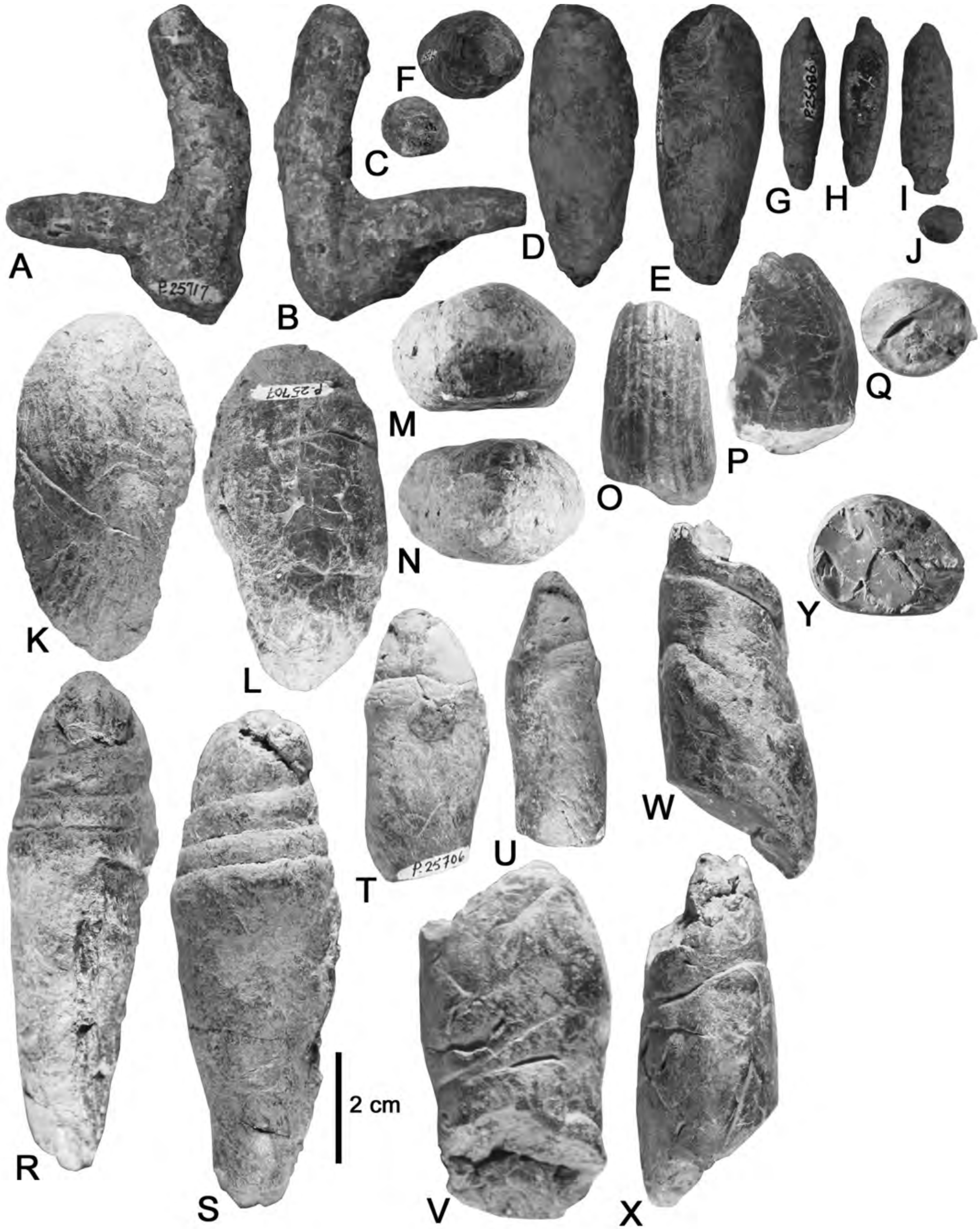
Middle Triassic nonmarine coprolite localities are widely dispersed in North (USA) and South America (Argentina, Brazil), Europe (England, France, Germany, Switzerland, Italy, Poland, Slovenia), Asia (Russia, Kazakhstan, India, China) and Africa (South Africa) (Hunt et al., 2013b). The best described Middle Triassic ichnofaunas are from Brazil (Santa Maria Formation: Souto, 2001; Hunt et al., 2013b; Francischini et al., 2018), Argentina (Potrerillos, Cacheuta, Río Blanco and Chañares formations: Rusconi, 1947, 1949; Mancuso et al., 2004; Fiorelli et al., 2013; Loinaze et al., 2018; Mancuso et al., 2018), the United States (Moenkopi Formation: Benz, 1980; Morales, 1987; Boy et al., 2001; Schoch et al., 2010), Russia (Karagachka, Donguz I and Bukobay localities: Ochev, 1974), Kazakhstan (Mollo-Khara-Bala-Kantemir locality: Ochev, 1974) and Poland (Muschelkalk: Chrzastek, 2008; Kowal-Linka and Bodzioch, 2012). The Santa Maria Formation of Brazil yields the earliest unambiguous vertebrate herbivore coprolites, *Rhynchocopros* and *Santamariacopros* (Hunt et al., 2013b; but see Francischini et al., 2018). The oldest latrinite is from the Chañares Formation of Argentina (Fiorelli et al., 2013).

The Late Triassic sample of coprolites is by far the largest from this period, and the majority of specimens are from nonmarine strata (Figs. 27-28). There are records in the USA (Lucas et al., 1985a; Wahl et al., 1998; Hunt et al., 1998, 2007, 2013b, 2018), Greenland (Milàn et al., 2012b, 2021; Hansen, 2014; Hansen et al., 2016), England (Duffin, 1979; Swift and Duffin, 1999; Hunt et al., 2013b), The Netherlands (Klompmaker et al., 2010), Switzerland (Fluckiger, 1861), Germany (Fraas, 1891; Schoch, 2012), Poland (Badjek et al., 2014, 2019; Zatoń et al., 2015; Qvarnström et al., 2019a, b, 2021), India (Matley, 1939a, b; Sohn and Chatterjee, 1979; Jain, 1983; Vijaya et al, 2009; Rakshit et al., 2019; Umamaheswaran et al., 2019), Thailand (Laojumpon et al., 2012), Argentina (Contreras, 1995; Hollocher et al., 2005), Brazil (Langer, 2005), Morocco (Hunt et al., 2013b), Madagascar (Burmeister et al., 2006) and South Africa (Anderson et al., 1998). The majority of specimens are from the nonmarine Chinle Group and Newark Supergroup of western and eastern North America, respectively, and the marine Rhaetic bonebeds in Europe (Duffin, 1979; Swift and Duffin, 1999; Hunt et al., 2013b).

The largest and most studied Late Triassic coprolite assemblages are from about 20 stratigraphic units of the Chinle Group of the western and southwestern United States (Arizona, New Mexico, Colorado, Texas, Utah, Wyoming: Hunt et al., 1998, 2007, 2013b, 2018; Fig. 28). Late Triassic nonmarine coprofaunas include a wide diversity of morphologies representing large herbivores (*Dicynodontocopros*) and carnivores with heterospiral (*Heteropolacopros*), scroll and non-spiral (*Alococoprus, Eucoprus*) coprolite morphologies (Hunt et al., 2013b, 2018; Badjek et al., 2014; Zatoń et al., 2015; Rakshit et al., 2018; Bajdek et al., 2019; Qvarnström et al., 2019a, 2021; Fig. 28). The most abundant marine coprolites are from Rhaetian bonebeds of western Europe, notably the United Kingdom, and morphotypes include spiral and nonspiral forms (Duffin, 1979; Swift and Duffin, 1999; Hunt et al., 2013b; Cueille et al., 2020). Coprolites also occur in the marine Carnian of Austria (Lukeneder et al., 2020; Lukeneder and Lukeneder, 2021).

Jurassic coprolites are much less common than those in the Triassic and understudied, with the notable exception of those from the Lias of England, which yields several ichnotaxa, including multiple spiral forms such as *Liassocoprus, Strabelocoprus* and *Saurocoprus* (Hunt et al., 2007, 2012a; Duffin, 2009, 2010, 2012a; Fig. 27). Other Early Jurassic marine units in Europe yield relatively few coprolites, for example the

FIGURE 28**.** (facing page) Late Triassic (Adamanian) coprolites from the Ciniza pond locality, Bluewater Creek Formation, New Mexico, USA (NMMNH locality 1864). **A-C**, NMMNH P-25717, two conjoined coprolites of *Eucoprus cylindricatus*, in A-B, axial and C, polar views. **D-F**, NMMNH P-25692, heterospiral coprolite in D-E, axial and F, polar views. **G-J**, NMMNH P-25686 from NMMNH locality 1864, cf. *Heteropolacopros* isp. in G-I, axial and J, polar views. **K-N**, NMMNH P-25707, *Eucoprus cylindricatus*, in **K-L**, axial and **M-N**, polar views. **O-Q**, NMMNH P-25706, *Alococopros triassicus* in O-P, axial and Q, polar views. **R-S**, NMMNH P-1864, large *Heteropolacopros texaniensis* in axial views. **T-U**, NMMNH P-25706, partial *Heteropolacopros texaniensis* in axial views. **V-Y**, NMMNH P25709, segment of *Heteropolacopros texaniensis* in V-X, axial and Y, polar views (from Hunt et al., 2013, fig. 6).


A
P.25717
B
C
F
D
E
G
P.25686
H
I
J
K
L
P.25707
M
N
O
P
Q
R
S
T
P.25706
U
V
W
X
Y
2 cm

Posidonienschiefer of Germany (e.g., Hauff, 1921). Garassino and Donovan (2000) describe possible coprolites of marine reptiles, some containing coleoid hooks, which are common in ichthyosaur consumulites, from the Early Jurassic of Italy.

The Early Jurassic portion of the nonmarine Newark Supergroup in eastern North America contains coprolites that are little studied (e.g., Hitchcock, 1844; Dana, 1845; Gilfillian and Olsen, 2000; Lanzirotti et al., 2000), and a smaller number occur in the Glen Canyon Group of the southwestern USA (Clark and Fastovsky, 1986). Górecki et al. (2019) described plant material from the coprolite of a large predatory dinosaur from the Early Jurassic of Poland.

Nomarine Middle Jurassic coprolites are rare (as are terrestrial vertebrate body fossils). Hill (1976) described a mass of small pellets containing the plant *Ptilophyllum* in England and tentatively assigned them to an ornithopod dinosaur or mammal, although the latter is highly improbable given their size (about 1 cm in diameter) and age. The Natural History Museum in London has coprolite collections from the marine Purbeck Limestone and Oxford Clay formations of England, which are largely unstudied (Hunt et al., 2007, 2012c). The Oxford Clay is notable for yielding many vertebrate coprolites (Martill, 1985a).

Several lithographic limestone Lagerstätten of Late Jurassic age in Germany contain coprolites. Schweigert and Dietl (2012) described specimens from the Nusplingen Lithographic Limestone, and specimens are also common in the Solnhofen and Ettling Lagerstätten (Barthel et al., 1990; Kemp and Trueman, 2003; Röper, 2005; Ebert et al., 2015). Hone et al. (2015) described rare pterosaur coprolites from Solnhofen, and Qvarnström et al. (2019b) described others from Poland. The Talbragar Fish Bed Lagerstätte in New South Wales, Australia, is of Kimmeridgian-Tithonian age and yields abundant coprolites (Beattie and Avery, 2012; Schwarzhans et al., 2018).

Despite the local abundance of dinosaur body fossils in the Late Jurassic, their coprolites are rare. Hunt and Lucas (2014a) reviewed the record of Late Jurassic coprolites from the United States. It includes probable theropod specimens and putative specimens produced by herbivorous dinosaurs from the Morrison Formation (Chin and Kirkland, 1998; Chin and Bishop, 2004, 2007).

Cretaceous coprolites are more numerous and more widespread than in any earlier time period (Fig. 29). Early Cretaceous coprolites are mainly known from nonmarine settings and are relatively poorly documented, although their occurrences are widespread (North and South America, Africa, Australasia and Europe) (Hunt and Lucas, 2016c). Bertrand (1903) authored the first monograph on vertebrate coprolites, based on specimens that had been found in strata that yielded multiple skeletons of *Iguanodon* from Belgium. He ascribed them to theropod dinosaurs (see also Casier, 1960, 1978), but they more likely pertain to crocodiles (Abel, 1935). Multiple coprolites also occur in an *Iguanodon* bonebed at Nehden in Germany (Norman, 1987). Other notable coprofaunas from Early Cretaceous nonmarine strata include the Maceió and São Sebastião formations of Brazil (Souto, 2008; Souto and Schwanke, 2010), the Wealden Group of England (Buckland, 1835; Martill and Naish, 2001; Goldring et al., 2005), the Escucha Formation (Alcalá et al., 2012; Vajda et al., 2016) and La Huérguina Formation (Las Hoyas Konservat-Lagerstätte: Barrios-de Pedro et al., 2018, 2020a,c) of Spain, the Angeac-Charente bonebed of France (Rozada et al., 2021) and the Jehol Lagerstätte of China (Burnham, 2008; Pan et al., 2011, 2013). Other nonmarine Early Cretaceous coprolites are present in the United States, Mexico, Denmark, Tunisia and Mongolia (Hunt and Lucas, 2016c).

Marine reptile coprolites are uncommon. Early Cretaceous ichthyosaur coprolites occur with a large concentration of skeletons in the Zapata Formation at Torres del Paine National Park in Chile (Stinnesbeck et al., 2014). The lagoonal Civita di Pietraroja Lagerstätte in Italy has yielded coprolites of a herbivorous fish, possibly *Notagogus* (Russo et al., 2015).

The record of Late Cretaceous coprolites is much more extensive and more widespread than for the earlier part of the period (Hunt and Lucas, 2016c). In addition, there are much larger samples from marine units, reflecting the great extent of continental flooding. And, Late Cretaceous-Paleogene phosphorites yield coprolites over a wide area from northwest Africa to the Middle East (Hunt and Lucas, 2016c).

Woodward (1729) was the first to describe Late Cretaceous specimens that were later recognized as coprolites, from the marine Grey Chalk Group (Cenomanian) in England (Duffin, 2009; Hunt et al., 2015b). Subsequently, Mantell (1822) described and illustrated similar specimens and others from the Turonian-Maastrichtian White Chalk Group (Turonian-Maastrichtian), which Buckland (1835) ultimately identified as coprolites. Subsequently, several coprolites, principally

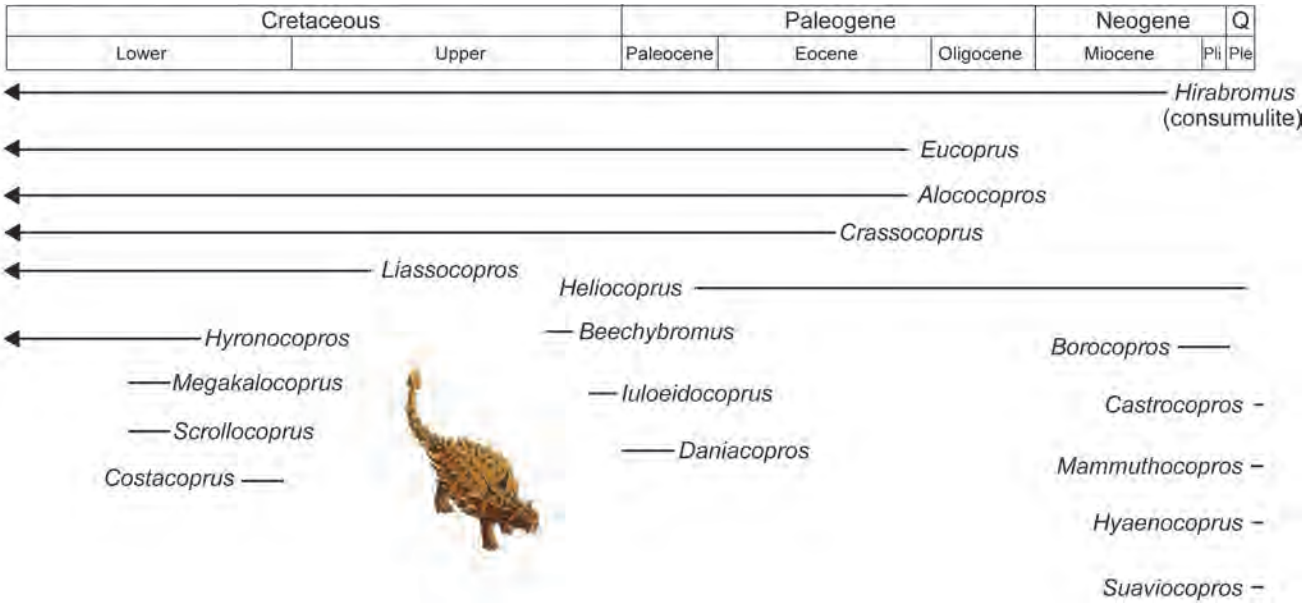


FIGURE 29. Stratigraphic distribution of Cretaceous-Quaternary bromalite ichnogenera.

heteropolar in form, were described from the Chalk of southern England (Longbottom and Patterson, 2002; Hunt et al., 2015b). Elsewhere, Late Cretaceous marine coprolites are widely distributed in three principal areas: (1) Europe; (2) Middle East/North Africa; and (3) North America. Many of the coprolites from Europe are spiral forms from chalk facies in the Netherlands, Belgium, Sweden, Germany, the Czech Republic, Austria and Poland (e.g., Hunt et al., 2015c; Milàn et al., 2015; Hunt and Lucas, 2016b). Non-spiral forms are locally common (Hunt and Lucas, 2018b). Large samples demonstrate a diversity of morphotypes (e.g., Eriksson et al., 2011; Anagnostakis, 2013), and coprolites from Austria and Poland are composed of *Inoceramus* shell fragments (Götzinger and Becker, 1932; Bajdek, 2013).

Phosphorites are nonrandomly distributed in space and time (e.g., Cook and McElhinny, 1979; Dornboss, 2011). The North Africa/Middle East phosphogenic province ranges in age from Late Cretaceous to Eocene and is part of the South Tethyan Phosphogenic Province (STPP) (e.g., Sheldon, 1964; Klemme, 1985). It yields reports of marine coprolites from Togo to Iraq, including Late Cretaceous specimens from Jordan, Israel, Syria, Egypt, Mauritania, Tunisia, Senegal, Morocco, Mali and Niger (Tapanila et al., 2008; Hunt and Lucas, 2016c). Many coprolites are correctly identified, but some of the putative coprolites are probably concretions (cf. Horton, 2012; Hunt and Lucas, 2016c). Capasso (2019b) described a coprolite of a pycnodont from the Cenomanian of Lebanon that is not associated with phosphorites and that appears to have been expelled just before fossilization.

The Western Interior Seaway in North America yields abundant marine coprolites. The first published record of a North American coprolite was a heteropolar specimen from the Upper Cretaceous of New Jersey (DeKay, 1830a, b; Buckland, 1835). Subsequently, coprolites have been described from elsewhere in the eastern United States, in New Jersey (Hunt and Lucas, 2016b, c), North Carolina (Hunt et al., 2012a), South Carolina (Hunt et al., 2012b; Schwimmer et al., 2015a, b), Georgia (Harrell and Schwimmer, 2010; Hunt et al., 2012b) and Alabama (Hunt et al., 2012a). The majority of the coprolites from the western United States derive from Kansas (e.g., Stewart, 1978; Hattin, 1996; Everhart, 2005e, 2017), but they also occur in Texas (Friedman, 2012), Colorado (Shimada et al., 2006; Hunt et al., 2012b) and Wyoming (Hunt and Lucas, 2016b). Mosasaur coprolites occur in southern Saskatchewan (Mahaney et al., 2013; Hunt and Lucas, 2018c), and other specimens occur in Cenomanian bonebeds in Saskatchewan and Manitoba (Schröder-Adams et al., 2001; Cumbaa et al., 2006; Phillips, 2008; Underwood and Cumbaa, 2010).

The majority of vertebrate coprolites from the nonmarine Late Cretaceous derive from North America, and there are also specimens from Europe, India and Africa. Many of the nonmarine units in the Western Interior of North America (Canada, United States, Mexico) that produce vertebrate body fossils, also yield coprolites, but there are relatively few published descriptions. The most extensive described samples in North America are from the San Juan Basin in New Mexico (Suazo et al., 2012; Sullivan and Jasinski, 2012; Hunt et al., 2012b), and the largest individual specimens are putative tyrannosaur coprolites from Saskatchewan and Alberta (Chin et al., 1988, 2003). Apart from putative coprolites of herbivorous dinosaurs from Montana (Chin and Gill, 1996; Hollocher et al., 2001; Chin, 2007; Chin et al., 2009) and possibly Coahuila, Mexico (Rodriguez de la Rosa et al., 1998) and Utah (Ridgewell et al., 2015), all other occurrences represent carnivores and include specimens from Texas, Utah, Wyoming, Montana and Alaska in the United States (Rowe et al., 1992; Baghai-Riding and DiBenedetto, 2001; Hollocher at al., 2010; Hunt et al., 2012b; Hunt and Lucas, 2016c), and Alberta in Canada (Waldman and Hopkins, 1970; Coy, 1995; Hunt and Lucas, 2016c). Other nonmarine Late Cretaceous coprolites occur in India (e.g., Matley, 1939a, b; Ghosh et al., 2003; Hunt et al., 2007; Khosla et al., 2016), France, (Robertson, 1834), Hungary (Segesdi et al., 2017), Austria (Ősi et al., 2021), Brazil (Souto, 2010; Souto and Fernandes, 2015; Ferreira et al., 2019; de Oliveira et al., 2021), Madagascar (Rogers et al., 2013) and Kazakhstan (Nesov, 1995, 1997; Averianov et al., 2015).

Paleogene

The majority of Paleogene coprolite localities are in nonmarine strata, although the largest sample sizes are from marine deposits (Hunt and Lucas, 2016c). North America has the best described record of Cenozoic vertebrate coprolites (Hunt and Lucas, 2007a, 2016b), with nonmarine specimens from every epoch and notably large samples from the Eocene Green River Formation (e.g., Edwards, 1976; Grande, 1980; 2013; Wilson, 1987; Wells et al., 1993; Hunt et al., 2012b) and Eocene/Oligocene White River Group, including a latrinite (e.g., Sinclair, 1921; Wanless, 1923; Abel, 1926, 1935; Stovall and Strain, 1936; Vogeltanz, 1965, 1967; Clark et al., 1967; Lemley, 1971; Edwards, 1973a, b; Edwards and Yatkola, 1974; Retallack, 1983; LaGarry, 1997; DiBenedetto, 2004; Hembree and Hasiotis, 2004, 2007; Meehan, 2007; Hunt and Lucas, 2007a; Hunt et al., 2012b, g).

Nonmarine Paleogene coprolites are present at several localities in South America, including the Paleocene of Brazil (Souto, 2007), Paleocene/Eocene of Argentina (Krause et al., 2007; Krause and Piña, 2012) and Oligocene of Brazil (Castro et al., 1988). Lucas et al. (2012) described a large coprofauna from the late Eocene of northeastern Kazakhstan, and other Asian localities are in the Paleocene of China (Young, 1964; Meng and Wyss, 1997) and the middle Eocene of Pakistan (Gingerich, 1977). Paleocene coprolites occur in the Menat Lagerstätte in France (Wedmann et al., 2018).

Coprolites, principally from crocodiles and fish, are known from both of the famous German Eocene Lagerstätten of Geiseltal (Voigt, 1934) and Messel (Fikentscher, 1933; Nürnberger, 1934; Schmitz, 1991; Richter and Baszio, 2001a, b; Richter and Wedmann, 2005). Baranov et al. (2021) described an unusual occurrence of fly larvae in a specimen of a mammalian coprolite within Eocene Baltic amber. Other nonmarine coprolites from Europe occur in the Eocene London Clay (Buckland, 1835; Cloutier et al., 2000; Rayner et al., 2009) and the Oligocene of France (Buckland, 1835; Duffin, 2009).

Paleogene phosphorites yield marine coprolites over a wide area of the South Tethyan Phosphogenic Province (STPP) from northwest Africa to the Middle East, including Iraq, Jordan, Egypt, Algeria, Senegal, Mali, Morocco, Algeria, Togo and Nigeria (Hunt and Lucas, 2016c). The marine Eocene is characterized by very large samples (> 1K specimens) of marine coprolites, notably the early Eocene Potapaco Member of the Nanjemoy Formation, Virginia (Dentzien-Dias et al., 2021) and the upper Eocene Yazoo Clay, Louisiana (Stringer and King, 2012), both in the United States, and from the middle Eocene Fürstenau Formation of Germany (Diedrich and Felker, 2012). The latter two coprofaunas consist principally of heteropolar spiral coprolites. Other marine coprolites occur in the Paleocene of Denmark (Milàn, 2010; Milàn et al., 2012b; Milàn and Hunt, 2016), the Oligocene of Germany (Weiler, 1922; Zotz, 1928; Martini, 1965), Oligocene of Denmark (Milàn et al., 2018), Oligocene of Poland (Bajdek and Bienkowska-Wasiluk, 2020) and the Paleocene and Eocene of France (Meillet, 1842) and Belgium (Buckland, 1835).

Neogene

The Neogene coprolite record is dominated by nonmarine assemblages with relatively few marine examples. Miocene coprolites have an almost worldwide distribution and occur in South, North and Central America, Europe, Asia, Africa and

Australasia. Virtually all examples are from nonmarine strata, and they include an increased number of coprolites attributed to herbivores relatively to older time intervals.

Some of the most significant Miocene coprofaunas from Europe are from Spain and yield the earliest hyena coprolites (Pesquero et al., 2011, 2013a, b), which were to become prevalent during the latest Neogene and Quaternary (Hunt and Lucas, 2020a). Abella et al. (2021) described two morphotypes of bone-consuming carnivores from Spain. Antunes et al. (2006a, b) reported the unusual occurrence of mammalian footprints in coprolites from Portugal. Miocene tetrapod coprolites occur in the Czech Republic (Fejfar et al., 2003; Mikuláš and Dvorák, 2010), and aquatic coprolites occur in Spain and Malta (Pedley, 1978; Peñalver and Gaudant, 2010).

One of the largest coprolite ichnofaunas from the Miocene of South America is from the Uranco Formation of Venezuela, and it includes specimens produced by herbivorous and carnivorous mammals and reptiles (Royo and Gomez, 1960; Dentzien-Dias et al., 2018). There are several localities yielding coprolites in Argentina (Tauber et al., 2007; Verzi et al., 2008; Tomassini and Montalvo, 2010; Aceñolaza, 2012; Montalvo et al., 2016, 2019; Tomassini et al., 2019), and specimens have been reported from Colombia (Carlini et al., 1997) and in northwestern Amazonia (Hoorn, 1994). In Central America, coprolites occur in Miocene strata in Panama (Whitmore and Stewart, 1965; Hastings et al., 2013).

Wang et al. (2018) described coprolites of the bone-cracking dog *Borophagus* from the Miocene of California in the western United States that Hunt and Lucas (2021d) subsequently named *Borocopros wangi*. Other borophagine coprolites occur in New Mexico and Texas (Hunt and Lucas, 2021a). Martin (1981) documented other carnivore coprolites to the north in Oregon. There are other undescribed Miocene coprolites from North America, including Miocene rhinoceros coprolites from Mexico (Hunt and Lucas, 2007a).

There are relatively few reports of Neogene coprolites from Africa and Asia, but they include specimens from terrestrial and lacustrine environments in Uganda and Kenya, respectively (Greenwood, 1951; Bishop, 1964), and crocodilian coprolites from India (Sharma and Patnaik, 2010). Australasian Miocene coprolites occur in a fluvial deposit in central Australia (Megirian et al., 1996) and a lacustrine maar Lagerstätte in New Zealand (Lindquist and Lee, 2009; Lee et al., 2016).

Miocene marine coprolites are uncommon, and most derive from the Calvert Cliffs of Maryland in the United States (e.g., Godfrey and Smith, 2010). Specimens of note include one yielding feather impressions and another that includes dentalites produced by a shark (Wetmore, 1943; Godfrey and Smith, 2010). Another dentalite-bearing coprolite derives from northern Italy (Collareta et al., 2019b).

The record of Pliocene coprolites is principally from nonmarine strata in Africa, Europe and South America. Most Pliocene African coprolites were discovered during studies of early hominins in the eastern and central parts of the continent, including Ethiopia (Jacobs, 1985), Tanzania (Harrison, 2011; Njau and Blumenschine, 2012) and Zaire (Harris et al., 1987). Other Pliocene coprolites occur in Namibia (Morales et al., 2011) and Libya (Muftah, 2020; Muftah et al., 2020). Pliocene or Villafranchian (late Pliocene-early Pleistocene) coprolites, principally derived from hyenas, are known from multiple localities in Europe, including Spain (Arribas et al., 2009; Madurell-Malapeira et al., 2010, 2011), France (Delson et al., 2006; Argant and Bonifay, 2011) and Italy (Girotti et al., 2004).

South American Pliocene coprolite records are principally from Argentina (Aceñolaza, 2012; Tomassini and Montalvo, 2013; Cenizo et al., 2016). The North American Pliocene has produced few coprolites. Hunt et al. (2019, 2021b) described a specimen of the borophagine coprolite *Borocopros* from southwestern New Mexico in the United States. There are possible Pliocene coprolites from China (Kao, 1962).

There are few records of Pliocene marine coprolites. Hunt et al. (2016b) named *Helicoprus clarki* for a spiral chondricthyan coprolite from the Red Crag Formation (upper Pliocene-lower Pleistocene) of England.

Quaternary

There are numerous Quaternary coprolites in paleontological and archeological sites worldwide, which include hominin specimens. The largest Quaternary coprolite fossil record is in North America, where the caves of the arid Southwest have yielded large accumulations of coprolites, including latrinites (e.g., Rampart Cave, Bechan Cave) of megaherbivore coprolites such as those of ground sloth and mammoth (*Castrocopros, Mammuthocopros*) as well as of smaller herbivores (Martin et al., 1961; Mead et al., 1984, 1986a, b, 1993, 2020; Glowiak, 2007; Mead and Swift, 2012; Hunt and Lucas, 2018c, 2020c; Figs. 29-30). The most extensive record is from small rodents such as *Neotoma* (Tweet et al., 2012). *Neotoma* coprolites also occur at the Rancho La Brea (tar pits) Lagerstätte (Rice et al., 2019; Mychajliw et al., 2020a).

There is a smaller but similar Quaternary coprolite record in South America (e.g., Spillmann, 1929; Verde and Ubilla, 2002; Kerber and Oliveira, 2008; Hunt and Lucas, 2018c). The Old World is characterized by caves with hyena coprolites and latrinites (Buckland, 1822, 1824, 1827; Chow, 1955; Kao, 1962; Musil, 1962; Mitzopoulos and Zapfe, 1963; Mohr, 1964; Scott, 1987; Fernandéz-Rodrìguez et al., 1995; Tournepiche and Couture, 1999; Diedrich, 2012a, c; Hunt and Lucas, 2020a). New Zealand and other Pacific islands yield locally abundant and important records of bird coprolites that are Quaternary and Holocene in age (James and Burney, 1997; Horrocks et al., 2004; Wood et al., 2008, 2012a, b). Human coprolites are present at a large number of archeological sites, but their study is generally in a separate literature from the paleontological literature, and there is little communication between the two sciences (e.g., Bryant and Reinhard, 2012; Shillito et al., 2020).

Davis (Davis et al., 1977; Davis, 1987; Davis and Shafer, 2006)) first recognized that spores of the dung fungus *Sporormiella* became abundant following the historic introduction of grazing herbivores in the western United States. During the Holocene this fungus is rare. However, *Sporormiella* spores are abundant before the extinction of Pleistocene megaherbivores, and they have been recovered from coprolites of *Mammuthocopros* from Bechan Cave in Arizona (Davis, 1987; Gill et al., 2013). So, *Sporormiella* spores are a proxy for an abundance of large terrestrial herbivores and can provide evidence for their extinction (Davis, 1987). Thus, *Sporormiella* spores have been widely utilized to study patterns of extinction or/and the immigration or introduction of moas in New Zealand (Wood et al., 2011), giant tortoises in the Galapagos Islands (Froyd et al., 2013), giant lemurs, elephant birds and the pygmy hippopotamus in Madagascar (Burney et al., 2003) and cattle in Brazil (Raczka et al., 2016).

Ichnotaxonomy

Bertling et al. (2006, p. 265) noted that "The need to name trace fossils…has unambiguously been accepted for decades." However, vertebrate ichnologists have been slow to name coprolites. Hunt et al. (1998) named the first valid ichnotaxa of vertebrate coprolites (*Dicynodontocopros maximus*, *Heteropolacopros texaniensis*). Indeed, the description and naming of vertebrate coprolites has allowed detailed analyses of distribution patterns, including a robust biostratigraphy and biochronology for the Triassic, utilizing 17 ichnogenera (Hunt et al., 2018, fig. 12.11; Fig. 27) and construction of paleoenvironmental transects in the Pennsylvanian using seven

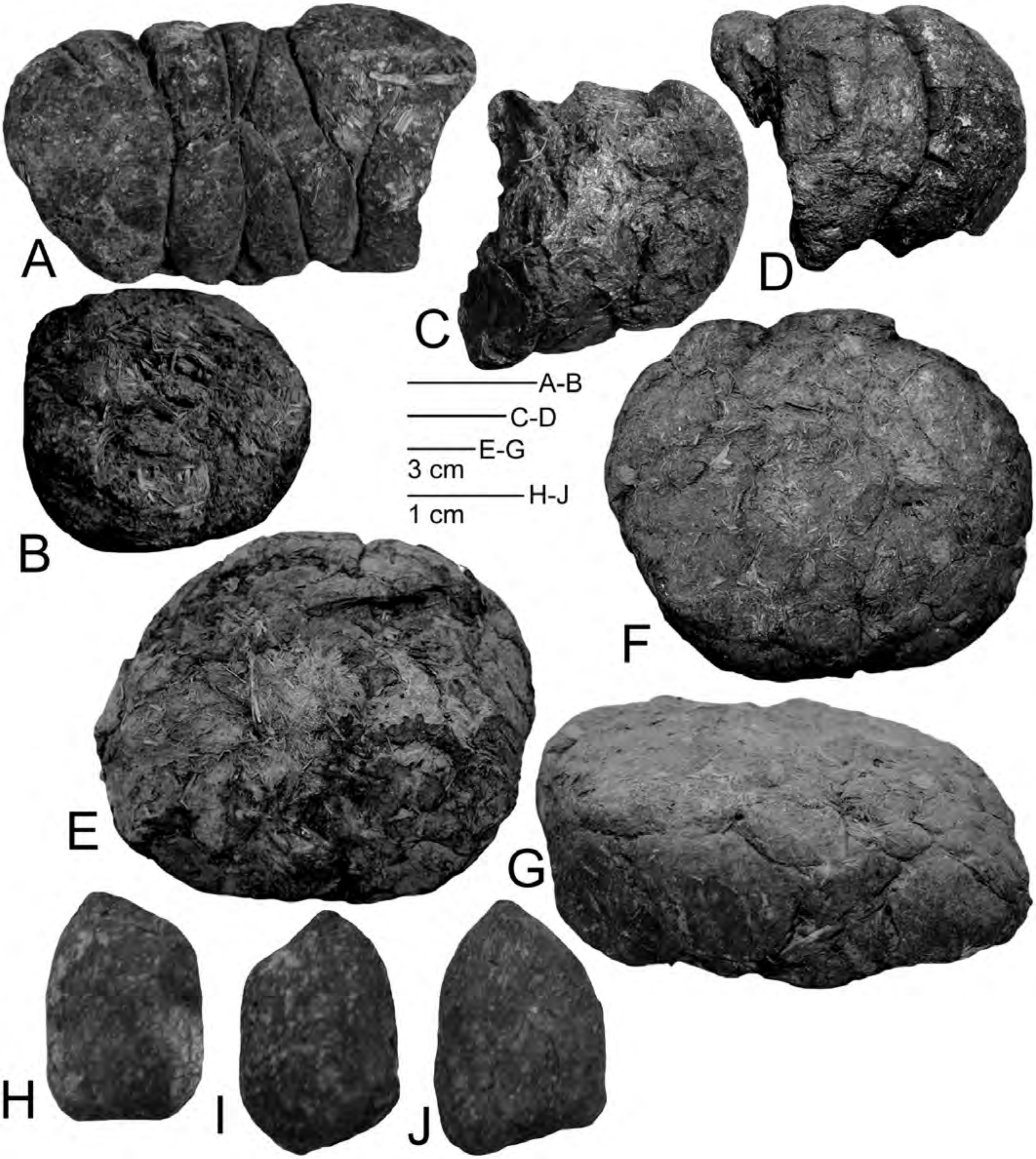


FIGURE 30. Late Pleistocene herbivore coprolites. **A–B**, USNM PAL 720155, *Castrocopros martini*, holotype coprolite from Rampart Cave, Arizona, USA, in lateral (A) and terminal (B) views. **C–D**, YPM 10574, *Castrocopros hauthali*, holotype coprolite from Cueva de Milodón, Ultima Esperanza Province, Chile in lateral views. **E–G**, GLCA 381, *Mammuthocopros allenorum,* holotype coprolite from Bechan Cave, Utah, USA, in terminal (E–F) and lateral (G) views. **H–J**, GLCA 2379, Three coprolites of *Suaviocopros harrisi* from Hooper's Hollow, Utah, USA, in lateral view (from Hunt and Lucas, 2020a, fig. 2).

ichnogenera (Hunt and Lucas, 2017a, fig. 1). Why, then, have relatively few other workers used a formal ichnotaxonomy for vertebrate coprolites, with a few notable exceptions (e.g., Duffin, 2010; Laojumpon et al., 2012; Milàn, 2018; Rakshit et al., 2019; Rummy et al., 2021; Table 3)?

Several authors have explicitly advocated the use of morphotypes rather than ichnotaxa for coprolites because: (1) different animals may produce similar fecal morphologies; (2) differing morphologies and contents of feces are driven by seasonal or ontogenetic factors; and (3) there is variation in preservation (Chin in Hunt et al., 1994a; Bajdek et al., 2014; Francischini et al., 2018). The first two arguments are based on the misconception that modern feces are not distinguishable because of variability, even though wildlife biologists routinely track and study the distribution of extant taxa based on the distinct morphologies of their feces (e.g., Murie, 1974; Jenkins and Burrows, 1980; Stuart and Stuart, 2000; Chame, 2003).

In large part, this reluctance to name coprolites stems from the fact that primates (such as ourselves) produce unusually variable morphologies of feces (Hunt et al., 2012d). However, the majority of vertebrates (carnivores and herbivores) produce a consistent morphology of feces, which, as just noted, is apparent from studies of Recent animal traces. Authors who decline to erect ichnotaxa discriminate morphotypes (e.g., Eriksson et al., 2011; Hansen et al., 2016; Francischini et al., 2018), which are ichnotaxa without names. A nomenclature that recognizes repetitive morphologies is essential for synthetic ichnology. Seilacher (1964, 1967) could not have recognized ichnofacies if all invertebrate ichnologists had described ichnofaunas in terms of ad hoc morphotypes. Thus, we strongly advocate the application of a rigorous ichnotaxonomy to vertebrate coprolites for both philosophical and practical reasons.

Ichnotaxobases

Vallon (2012) first explicitly discussed ichnotaxobases for coprolites. The most utilized ichnotaxobases for coprolites are:

1. External morphology – Coprolites and Recent feces display a range of morphotypes that are useful for definition (Häntzschel et al., 1968; Chame, 2003; Hunt and Lucas, 2012b).

2. Internal structure – Many coprolites have a spiral or scroll internal structure (Hunt and Lucas, 2012b). Spiral coprolites are either amphipolar or heteropolar (microspiral or macrospiral) in form (Appendix B). Many ichnotaxa are based on these structures (e.g., *Heteropolacopros:* Hunt et al., 1998; *Scrollocoprus*: Rummy et al., 2021).

3. Surface texture – Some coprolites such as *Strophocopros* have distinct surface textures (Hunt and Lucas, 2005b).

4. Size – Size by itself is not usually an ideal ichnotaxobase except in cases where there are very distinct size classes (e.g., *Megaheteropolacopros*: Hunt et al., 2005a).

5. Inclusions – Certain coprolites contain distinct and/or abundant inclusions, such as conchostracan valves in *Crustacoprus* (Hunt et al., 2012i).

6. Mineralogy – Most coprolites are phosphatic in composition, but others have different mineralogies, such as *Rhynchocopros soutoi* and *Santamariacopros elongatus,* which are calcareous (Hunt et al., 2013).

Producer

The majority of vertebrate coprolites represent those of carnivorous animals, because of two main factors: (1) herbivores defecate a large proportion of undigested vegetable material that is the basis of a diverse micro-ecosystem of bacterial and other scavengers that diminish and/or destroy the bolus, whereas carnivore feces are largely composed of unattractive waste products; and (2) the calcium phosphate in consumed bone facilitates the lithification of most carnivore feces (Hunt et al., 1994; Hollocher and Hollocher, 2012).

The main lines of evidence to identify the specific producer of a vertebrate coprolite type are:

1. Morphology - Some coprolites have a very distinctive morphology and structure. Notably, spiral coprolites that are

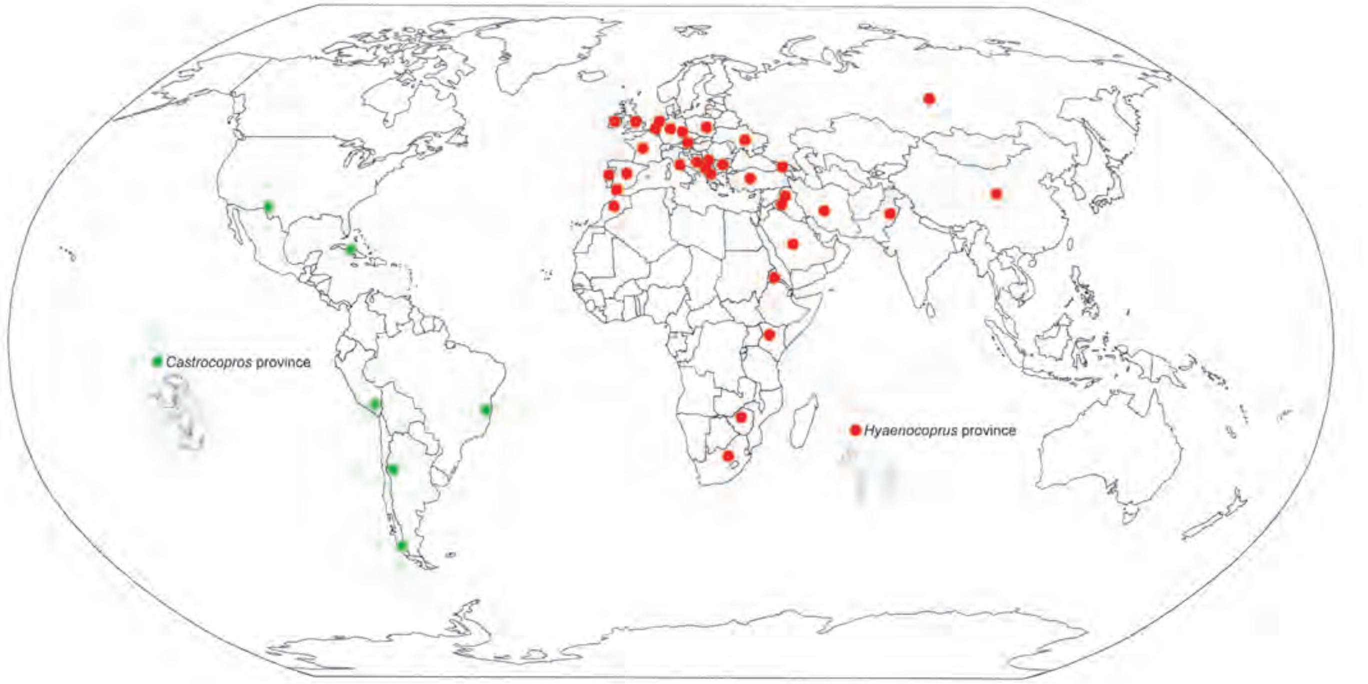


FIGURE 31. Late Pleistocene biogeographic provinces based on vertebrate coprolites. The *Castrocopros* province (green squares) characterized by *Castrocopros* ispp. produced by ground sloths and the *Hyaenacoprus* province (red circles) by *Hyaenacoprus bucklandi* produced by hyenas. Each symbol represents a single country. For details of localities see Hunt and Lucas (2020a, table 1 and Supplemental Data file) (from Hunt and Lucas, 2021b, fig. 9, adapted from Hunt and Lucas, 2020, fig. 1).

produced by sharks, rays or less advanced fish with spiral valves have been studied extensively to investigate their origins (Hunt and Lucas, 2012b).

2. Analogy – In the case of late Cenozoic animals, it is often possible to compare the morphology and content of coprolites with those of living animals. Thus, comparison of putative mammoth coprolites with elephant dung has been useful in identification of the producers (Mead et al., 1986a; Hunt and Lucas, 2020a).

3. Association in digestive tract – In a few rare instances, coprolites have been found within the body cavity of Paleozoic fish, Mesozoic dinosaurs and Cenozoic crocodilians, thus establishing their producers.

4. Association with skeletal remains (articulated carcass or bone bed) – Some coprolites are found in close association with skeletons but not within them, such as *Dicynodontocopros* at the Late Triassic *Placerias* quarry bone bed, which is dominated by the bones of dicynodonts (Hunt et al., 1998). The association thus suggests the producer.

5. Biochemistry – Pleistocene and Holocene coprolites are often identifiable to species level because of the preservation of complex organic molecules, including DNA (Poinar et al., 1998, 2003; Karpinksi et al., 2017).

6. Inclusions – Inclusions in coprolites can provide information about diet that may help identify the producer.

7. Size – Size can be of some use in the identification of the producer of coprolites, as small animals cannot produce large coprolites. In cases of very large dimensions, size may allow attribution. For example, very large Late Cretaceous coprolites have reasonably been attributed to tyrannosaurid dinosaurs, the only vertebrate taxon at that time large enough to produce such large coprolites (Chin et al., 1988, 2003).

Utility of Coprolites

Introduction

Coprolites can serve as proxies for biotaxa (the animals that produced them). The producer of individual vertebrate coprolites can usually only be identified at a high taxonomic level (order or higher) with very few exceptions before the Pleistocene, such as dicynodont therapsids from the Late Triassic of the United States and hyperodapedontid rhynchosaurs from the Middle Triassic of Brazil (Hunt et al., 2013b). Most Pleistocene vertebrate coprolites can be identified at the specific level on the basis of morphology and DNA (e.g., *Hyaenocoprus* derives from *Crocuta*: Bon et al., 2012). Regardless of the known taxonomic level of the producer, the distribution of a coprolite ichnotaxon is a proxy for a biological taxonomic unit. Vertebrate coprolites provide some biochronology in the Pennsylvanian to the Quaternary (Figs. 25, 27, 29), and invertebrate coprolites, although represented by far fewer ichnotaxa, provide a biochronology through the entire Phanerozoic (Knaust, 2020).

Vertebrate coprolites can delimit biogeographic regions. For example, there are two distinct biogeographic and taphonomic provinces for vertebrate coprolites in the Pleistocene (Fig. 31). The *Castrocopros* province of the New World characterized by a dominance of herbivore coprolites, which are preserved almost exclusively in caves, and the *Hyaenacoprus* province in the Old World, which is dominated by hyena coprolites that also occur mainly in caves (Hunt and Lucas, 2020a; Fig. 31).

All trace fossils, including coprolites, are facies fossils. Spiral vertebrate coprolites in shallow marine environments define the *Crassocoprus* ichnofacies that ranges from the Mississippian to the Eocene. On a finer scale, vertebrate coprolites allow the discrimination of three ichnocoenoses in the nonmarine Late Triassic and four in an ecological transect from lacustrine to shallow marine conditions in the Late Pennsylvanian (Hunt and Lucas, 2017a).

The first important inclusions to be recognized in coprolites were spores in arthropod coprolites and pollen in vertebrate herbivore coprolites. Subsequently, a wide range of organic materials, including soft tissues, have been identified in vertebrate coprolites, particularly muscle tissues, eggs, hair, parasites, bacteria, fungi and feathers. Thus, some coprolites represent Lagerstätten (Qvarnström et al., 2016).

Coprolites obviously represent the end point of digestion, so they can provide evidence about the evolution of feeding, diet and digestion. For example, vertebrate coprolites of the Silurian to Carboniferous demonstrate changing patterns of predation and food processing among carnivorous fishes as demonstrated by an increase in groundmass, increase in size and the diversification of spiral morphologies (Hunt and Lucas, 2016b).

Coprolites provide ecological information about their producers, and Niedźwiedzki and co-workers have utilized them to reconstruct ecosystems and analyze diversity (Niedźwiedzki et al., 2016a, b). Coprolites are also of utility in a number of other areas from the study of the evolution of human diseases to sedimentology to providing mineable resources (guanolite) (Hunt, 1992; Bryant and Reinhard, 2012; Hunt et al., 2012d).

Ichnofacies

Coprolites are trace fossils and thus facies fossils. Hunt and co-workers (Hunt et al., 1994, 1998, 2007, 2013a; Hunt and Lucas 2007b) first recognized discrete associations of vertebrate coprolites and sedimentary facies in the Late Triassic of western North America. Hunt and Lucas (2017a) recognized that four bromalite ichnofaunas of Missourian (Late Pennsylvanian) age in New Mexico represent an ecological transect from lacustrine to basinal marine: (1) Tinajas Lagerstätte – lacustrine; (2) Kinney Brick Quarry Lagerstätte – lagoonal; (3) Erickson site – nearshore marine; and (4) Sacramento Mountains – offshore marine. There are clear trends through these ichnofaunas (Tinajas-Kinney-Erickson-Sacramentos): (1) flattened preservation in matrix to isolated three dimensional; (2) diverse bromalites to only coprolites; and (3) increasing proportion of spiral coprolites, so that the most basinward ichnofauna is dominated by spiral coprolites. In addition, the Kinney ichnofauna is typical of lagoonal/estuarine ichnofaunas of the Paleozoic and Mesozoic. Hunt et al. (2015c) had identified the presence of abundant spiral coprolites as being characteristic of certain marine environments.

Buckland (1829, 1835) largely based his definition of coprolites on the recognition that heteropolar “bezoar stones” from the Early Jurassic of Lyme Regis in southwestern England represent fossil feces. Heteropolar coprolites occur in large numbers in shallow marine strata from the Mississippian to the Eocene (e.g., Hunt et al., 2015c). Hunt et al. (2018) defined the *Crassocoprus* ichnofacies to include marine trace fossil ichnocoenoses dominated by heteropolar coprolites and that include coprolites of low to moderate ichnodiversity. Shale substrates typify the *Crassocoprus* ichnofacies. The name is for *Crassocoprus*, a macrospiral heteropolar coprolite from the Pennsylvanian that is attributed to a chondrichthyan (Hunt et al., 2012i).

Heteropolar coprolites date back to the Devonian and first became abundant during the Pennsylvanian (Hunt and Lucas, 2013). The principal large samples of heteropolar coprolites (shallow marine setting unless indicated otherwise) occur in the: 1. Middle-Late Mississippian Wardie, Midlothian, Scotland (Middle Mississippian: Viséan) (Buckland, 1835; Sumner, 1991) Anstruther, Fife, Scotland (Middle Mississippian: Viséan) (Sumner, 1991). Bearsden, East Dunbartonshire, Scotland (Late Mississippian: Serpukhovian) (Clark, 1989). 2. Late Pennsylvanian of Park and Chaffee counties, Colorado, USA (Johnson, 1934), Bassam Park, Colorado, USA (Houck et al., 2004), Morgantown, West Virginia, USA (Price, 1927) and Sacramento Mountains, New Mexico, USA (Hunt et al., 2012g).

3. Early Permian Manhattan, Kansas, USA (Williams, 1972; McAllister, 1985). 4. Middle/late Permian southern Brazil – lacustrine (Dentzien-Dias et al., 2012). 5. Late Permian/Early Triassic European Russia – nonmarine (Niedźwiedzki et al., 2016b). 6. Early Jurassic Lyme Regis, England (Buckland, 1835; Hunt et al., 2012a). 7. Late Cretaceous southern England, Western Europe (Hunt et al., 2015c). 8. Middle-Late Eocene northern Germany (Diedrich and Felker, 2012) and Alabama, USA (Stringer and King, 2012).

Hunt et al. (2018) also named the *Gaspeichnus* Ichnofacies for traces developed on the substrate of a coprolite. Feces provide a source of food for some insects and vertebrates. Coprolites also undergo bioerosion and are the subject of accidental contact by vertebrates. Therefore, coprolites preserve a variety of traces including vertebrate dentalites, vertebrate footprints and invertebrate borings. The *Gaspeichnus* Ichnofacies was thus defined to include marine and nonmarine trace fossil ichnocoenoses of low diversity dominated by macroscopic borings and vertebrate dentalites and footprints that utilize coprolites as a substrate. The name is for *Gaspeichnus*, a sinuous coprolite boring from the Devonian (Hunt et al., 2018). Other examples of the *Gaspeichnus* Ichnofacies include: (1) flask-shaped borings in both bone and coprolites from the Cretaceous-Eocene of Mali that represent the putative bivalve boring named *Gastrochaenolites ornatus* (Tapanila et al., 2004); (2) an amphipolar coprolite with an invertebrate boring from the Rio do Rasto Formation (middle/upper Permian) in southern Brazil (Dentzien-Dias et al., 2012); (3) small holes in Late Triassic coprolites from Arizona, USA, produced by insects, such as dipteran larvae (Wahl et al., 1998); (4) putative examples of coprophagy traces of dung beetles in the Cretaceous and Paleogene of the USA (Bradley, 1946; Chin and Gill, 1996); (5) Miocene mammalian footprints preserved in coprolites from Portugal, including a tridactyl footprint that can be ascribed to a right foot of the rhinoceros *Hispanotherium matritensis*, a tridactyl, left foot impression of a perissodactyl, possibly an *Anchitherium*-like equid, and a didactyl track from a small-sized ruminant, most probably a cervid, genus *Procervulus* (Antunes et al., 2006b); and (6) coprolites containing dentalites (e.g., Godfrey and Smith, 2010; Godfrey and Palmer, 2015).

Biostratigraphy and Biochronology

Vertebrate coprolites can serve as proxies for biotaxa and thus are of biostratigraphic and biochronological utility (e.g., Hunt, 1992; Hunt et al., 1998, 2005a, 2007, 2013b, b, 2018; Figs. 25, 27, 29). However, vertebrate ichnotaxa almost always correspond to higher level taxonomic groups than do body fossils. Thus, footprint ichnogenera are often equivalent to the family (or higher) taxonomic level of body fossils (Lucas, 2007). Pre-Pleistocene coprolites probably represent, in most cases, even higher level taxonomic groups ("order" or above) (Hunt et al., 2007, 2013b). Examples of lower level identifications would be coprolites attributed to dicynodont therapsids from the Late Triassic of the United States (Hunt et al., 1998) and to tyrannosaurid theropods from the Late Cretaceous of Canada (Chin et al., 1988, 2003). Most Pleistocene vertebrate coprolites can be identified at the specific level on the basis of morphology (e.g., Mead and Swift, 2012) and more recently by DNA. For example, *Hyaenocoprus* derives from *Crocuta* (Bon et al., 2012), and *Mammuthocoprus* derives from *Mammuthus columbi* (Karpinski et al., 2017). However, all coprolite ichnotaxa do have defined stratigraphic ranges that parallel the stratigraphic ranges of the producing animals, so the coprolites have potential utility in biostratigraphy and biochronology (Hunt and Lucas, 2005c; Hunt et al., 2007, 2013a, b; Figs. 25, 27, 29). Indeed, coprolites have demonstrated biochronologic utility, particularly in the Late Triassic-Early Jurassic (Hunt et al., 2018, fig. 12.11: Figs. 25, 27, 29).

Biogeography

Vertebrate coprolites can delimit biogeographic regions as proxies for biotaxa. For example, there are two distinct biogeographic and taphonomic provinces for vertebrate coprolites in the Pleistocene (Hunt and Lucas, 2020a). The *Castrocopros* province of the New World is characterized by a dominance of herbivore coprolites, which are preserved almost exclusively in caves, and the *Hyaenacoprus* province in the Old World is dominated by hyena coprolites that occur mainly in caves (Hunt and Lucas, 2018c, 2019, 2020a; Fig. 31). Coprolites as proxy for biotaxa can record the presence of a taxon in the absence of bones (e.g., dicynodonts in the Late Triassic: Hunt et al., 2013b).

Lagerstätten

The first important inclusions to be recognized in vertebrate coprolites were pollen in herbivore coprolites (Martin et al., 1961; Hunt and Fiaconni, 2018). Subsequently, a wide range of organic materials, including soft tissues, have been identified in vertebrate coprolites, particularly muscle tissues, eggs, hair, parasites, bacteria, fungi and feathers (e.g., Chin et al., 1998, 2003). Recent studies have also highlighted that coprolites contain diverse body fossils of delicate and rare organisms (Dentzien-Dias et al., 2013, 2017; Bajdek et al., 2016; Chin et al., 2017; Qvarnström et al., 2016, 2017, 2019, 2021). Thus,

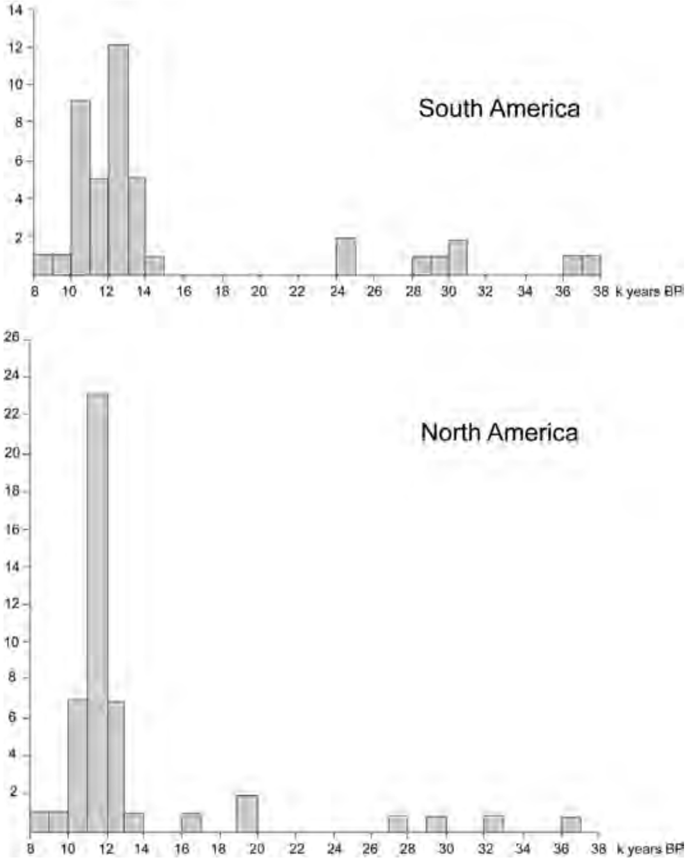


FIGURE 32. Age distribution of radioisotopic ages on ground sloth coprolites from caves in North and South America. These data demonstrate increased cave utilization during the latest Pleistocene, which is likely climate driven. There is virtually no evidence of humans hunting sloths, which would be another explanation for this behavioral shift. Thus, the giant sloth demise is more likely related to climatic factors than to human overkill, which are the two most prevalent hypotheses for their extinction. Age data from Hunt and Lucas (2018c, table 3) (from Hunt and Lucas, 2018c, fig. 8).

Qvarnström et al. (2016) concluded that the term Lagerstätte is applicable to some coprolites.

Paleoecology

Coprolites can provide diverse information about the diet and digestion of their producers (e.g., Hansen, 1978; McAllister, 1988; Qvarnström et al., 2019a, b). They can also inform analysis of ancient and modern human health (Bryant and Reinhard, 2012).

Faunal Evolution and Extinction

Coprolites can also be used as biotaxa proxies to analyze ecosystem evolution, extinction and diversity patterns (e.g., Nakajima and Izumi, 2014; Niedźwiedzki et al., 2016a, b; Fig. 32).

Conclusions

Coprolites have an extensive fossil record that has proven potential to address a broad range of paleontological issues. A challenge to their increased utility is the necessity for more comprehensive ichnotaxonomy.

1. Coprolites as proxy for biotaxa have utility in biochronology, biogeography and faunal turnover.
2. Coprolites as trace fossils can delimit a hierarchy of ichnocoensoes and ichnofacies.
3. Coprolites as end products of the gastrointestinal tract can provide evidence of digestive processes.
4. Internally, coprolites can be Lagerstätten that preserve a wide range of organisms with an otherwise poor fossil record.

OTHER BROMALITES

Digestilites

Food stuffs that pass through the digestive tract are subject to chemical and physical processes that result in characteristic damage that can be recognized in regurgitated or defecated material (e.g., Crandall and Stahl, 1995; Fernández-Jalvo et al. 2002, 2014, 2016; Esteban-Nadal et al., 2010; Cohen, 2003; Cohen and Kibii, 2015; Fernandez-Jalvo and Andrews, 2016; Meador, 2017; Montalvo and Fernández, 2019). For example, crocodilian-digested bones most closely resemble bones exposed to hydrochloric acid as opposed to the damage due to a mix of hydrochloric acid and digestive enzymes exhibited by bones consumed by mammalian and avian predators (Fernández-Jalvo et al., 2014; Meador, 2017). This exposure to digestive acid produces a number of unique and identifiable characteristics on bones and teeth, including: (1) surface etching; (2) corrosive pitting; (3) rounding; (4) enamel erosion; (5) foramen excavation; (6) reduction of cortical thickness; (7) corrosive holes; (8) undulations; (9) desquamation; (10) cupules; and (10) polishing (e. g., Lyman, 1994; Crandall and Stahl, 1995; Esteban-Nadal et al., 2010; Cohen, 2003; Cohen and Kibii, 2015; Brown et al., 2016; Meador, 2017; Montalvo and Fernández, 2019). Such specimens clearly represent morphologically recurrent structures resulting from the life activity of an individual organism modifying the substrate, and thus are trace fossils (Bertling et al., 2006). We propose the term digestilite, from the Latin *digestus* (digestion), for fossil specimens that preserve evidence of digestion.

FIGURE 33. Digestilite composed of etched skeletal elements of a hatchling turtle (FHSM VP-17572) from lower Santonian chalk, Kansas, USA. Scale bar in mm (Everhart, 2017, fig. 6.12 partim). Photograph courtesy of Michael Everhart.

The investigation of damage to ingested vertebrate hard tissue was initially stimulated by the study of the accumulation mechanisms of micromammal taphocoenoses (Dodson, 1973; Dodson and Wexlar, 1979; Korth, 1979; Fisher, 1981a,b; Andrews and Evans, 1983; Andrews, 1990). However, larger bones, such as a hominin bone from Zhoukoudian in China, also show clear evidence of digestion (Boaz et al., 2000). Thus, Zhoukoudian *Homo erectus* Femur V exhibits a breakage pattern characteristic of hyenas and also has rounded edges and pitting associated with ingestion and partial digestion (Weidenreich, 1941; Boaz et al., 2000).

Digestilites record evidence of mechanical and/or chemical digestion and may derive from regurgitation (e.g., Boaz et al., 2000) or defecation (e.g., Fisher, 1981a,b). The most well-known digestilite is probably the Denisova 11 hominid, which is the fragmentary limb bone of a Denisovan and Neantherdal hybrid from Denisova Cave, Siberia (Brown et al., 2016; Slon et al., 2018).

Ingested hard tissue constitutes an important contribution to the fossil record. It is widely recognized that many terrestrial microvertebrate fossil faunas are composed of digestilites, the majority from bird regurgitalites, but also from carnivore and crocodile coprolites (Dodson, 1973; Mellet, 1975; Dodson and Wexlar, 1979; Korth, 1979; Fisher, 1981a,b; Andrews and Evans, 1983; Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Williams, 2003; Denys, 2011; Fernández-Jalvo et al., 2016; Denys et al., 2018; Montalvo and Fernández, 2019). Thus, for example, Coco et al. (2020) described late Pleistocene bones of owls (*Tyto, Athene, Glaucidium*) that exhibit breakage and weathering, consistent with digestion by the giant strigiform *Asio ecuadoriensis.*

The other major importance of digestilites is in the processing of invertebrate hard parts into the sedimentological record. Thus, Oji et al. (2003) and Salamon et al. (2014) conducted actualistic studies that demonstrated that predation by fish on bivalves produces shell fragments with sharp, angular margins, in contrast to non-biogenic physical processes that produce abraded and rounded shell fragments. They thus utilized angular shell fragments as a proxy for the feeding of durophagous fish in the Paleozoic (and later). Digestilites composed of invertebrate material may encompass a significant portion of shell beds from the Mississippian to the Recent (Oji et al., 2003; Salamon et al., 2014). Vertebrate predation is also important in the production of Recent coral sands from reefs, notably by scarid parrotfish (Peyrot-Clausade et al., 2000).

Digestilites are also important in other taphonomic settings. Wilson (1987) suggested that fish bones in some Eocene lake deposits of British Columbia and Washington are partly dissolved due to possible ingestion, probably by birds.. Digestilites also occur in the Late Cretaceous marine strata of western North America, representing fish, turtles, mosasaurs and dinosaurs (Everhart, 2017, figs. 3.19, 4.3, 6.12, 12.2; Fig. 33).

Pabulites

Montalvo et al. (2016) introduced the term "leftover prey remains," which represent accumulations of uneaten prey remains discarded by a predator. These remains are identified on the basis of anatomical representation, degree of bone breakage and the presence of dentalites. They based the term on late Miocene microvertebrate accumulations from Argentina. It may have some utility in assessing microvertebrate accumulations to distinguish the genesis of the assemblage that result from concentrations produced by digestion (regurgitalites or coprolites).

Klug et al. (2021a) coined the formal term pabulite for fossilized food that never entered the digestive tract. They note that pabulites are normally incomplete animals that preserve traces of predation. They describe the example of the belemnite *Passaloteuthis laevigata* from the Toarcian Posidonienschiefer Lagerstätte. Most of the soft parts are missing, but the arm crown is one of the best preserved that is known. Klug et al. (2021a) suggest that the belemnite represents the remnant of the food of a predatory fish, possibly the shark *Hybodus huffianus*. Subsequently, Klug et al. (2021b) described another possible pabulite from the Cenomanian of Lebanon. A specimen of the cymatoceratid cephalopod *Syrionautilus libanoticus* preserves soft tissues but lacks the arms and the hood, and the plane of symmetry is perpendicular to bedding. This specimen may be a pabulite or represent incomplete scavenging (Klug et al., 2021b).

The development of the study of pabulites requires: (1) ichnotaxobases – see Montalvo et al. (2016); (2) actualistic studies; (3) documentation of new examples; and (4) review of their fossil record. Pabulites may be difficult to recognize in the absence of other traces. For example, a partial skeleton with some bite marks was likely scavenged, so it is probably a pabulite, whereas an incomplete carcass with no dentalites could have other causation. Many vertebrate specimens exposed on an oxygenated substrate are probably subject to scavenging and may represent pabulites (cf. Early Jurassic Holzmaden ichthyosaurs).

Micturalites

Micturalites are trace fossils produced by interaction between liquid urine and substrate (Hunt and Lucas, 2012). These ichnofossils are rare. McCarville and Bishop (2002) interpreted a sub-circular depression (scour?) at a Late Jurassic tracksite in Colorado, USA as eroded by liquid urine of a sauropod. There is no evidence that this trace fossil resulted from urine impacting the substrate. Fernandes, and Souto and co-authors, described a more convincing trace ichnofossil from the Early Cretaceous of Brazil (Fernandes et al., 2004; Souto and Fernandes, 2015). They compared this "urolite" to erosional depressions produced in the substrate by liquid waste of the Recent ratite *Struthio camelus* (ostrich).

OTHER TRACE FOSSIL EVIDENCE OF VERTEBRATE FEEDING

Introduction

Dentalites, gastroliths and bromalites are not the only trace fossils that provide evidence of vertebrate feeding. Footprints, some nests and other traces also can record evidence of vertebrate predation and consumption.

Footprints and Handprints

There are several examples of trackways that purport to capture an act of predation. The first specimen to be so recognized was from the Early Cretaceous of Texas and purports to show a theropod attacking a sauropod (Bird, 1954, 1985; Thomas and Farlow, 1997). The theropod repeatedly stepped in the prints made by the sauropod, and the trackways of both made a turn at the same point, which may suggest that the carnivore was following the herbivore (Farlow, 1987a, b; Thomas and Farlow, 1997). Bird (1954, 1985) believed that the theropod actually attacked the sauropod as indicated by a missing left carnivore footprint, which was interpreted to represent the animal being dragged off its feet by the forward motion of the much larger herbivore (Bird, 1985, p. 173; Thomas and Farlow, 1997). However, the subsequent footprint's location and morphology do not support that hypothesis (Lockley and Hunt, 1995; Hunt and Lucas, 1998; Farlow et al., 2012).

The Lark Quarry tracksite from the Early Cretaceous of Australia was originally interpreted to represent a large predatory theropod causing a stampede of small ornithopods and theropods (Thulborn and Wade, 1979, 1984). However, there is a lack of clarity about the taxonomy of the trace makers, the contemporaneity of the trackways and the speed of the smaller dinosaurs, so the predatory theropod hypothesis is problematic (Romilio and Salisbury, 2011; Romilio et al., 2013; Thulborn, 2013, 2017).

Weems (2018, 2020) described a theropod trackway of *Kayentapus minor* from the Late Triassic of the Culpeper Quarry in Virginia, USA, that is purported to be a possible record of predation. This trackway preserves changing locomotion of an individual – acceleration, running, slowing, slight skid, walking, stopping and slight shifting of position. This is interpreted as the behavior associated with the capture of prey, but it is not a convincing interpretation.

There are five examples from the Permian of trackway terminations of vertebrates and invertebrates that have been interpreted as evidence of predation (Lockley and Madsen, 1993; Kramer et al., 1995; Hunt and Lucas, 1998; Santi and Stoppini, 2005; Citton et al., 2012). In each case, one trackway appears to terminate at another with no change of pace. Nevertheless, none of these examples satisfy more than one of the five criteria established by Hunt and Lucas (1998) to evaluate trackway evidence of predation in such cases: (1) in the case of intersecting trackways, one trackway should terminate at the other; (2) in the case of parallel pursuit trackways, one trackway should end; (3) there should be evidence of a pursuer adjusting length of stride to sync with prey stride length; (4) one or both trackways should demonstrate change in direction or/and speed -evasion and compensation; and (5) the trackway of the prey should show evidence of a struggle – slowing, terminating or lateral movement. In addition, it is not clear in the cases of supposed Permian trackway documentation of predation that the trackways are synchronous or even on the same bedding plane.

Theropod tracks and inferred trampling have been found associated with large bone accumulations, and this could be evidence of scavenging (e.g., Lockley et al., 1998; Jennings and Hasiotis, 2006; Augustin et al., 2020a). An absence of tracks but a presence of broken bones that could have been impacted by trampling together with shed teeth has also been considered as evidence of scavenging (Eberth and Getty, 2005; Snyder et al., 2020). Simpson et al. (2010) described putative digging traces produced by a maniraptoran theropod dinosaur in association with mammalian den complexes from the Late Cretaceous of Utah, which they interpreted as evidence of predation.

Nests

Lucas and Hunt (2006) defined a nest as the structure made by, or the place chosen by, an animal for spawning, breeding and/or laying eggs and sheltering young. Carnivore nests, notably dens of Pleistocene hyenas in caves of the Old World, preserve abundant evidence of predation in terms of trace fossils such as dentalites and coprolites, but also body fossils that demonstrate aspects of prey selection, processing and utilization (e.g., Boaz et al., 2000; Marra et al., 2004; Stiner, 2004; Sala et al., 2012). The most abundant nests in the fossil record are of rodents, notably pack rats (*Neotoma*), which are widely distributed in the Late Pleistocene-Holocene of North America and other areas (e.g., Betancourt et al., 2010; Tweet et al., 2012). Discarded food items can also commonly be found below raptor nests, as may be the case for the South African Taung Child mentioned above (Berger and Clarke, 1995).

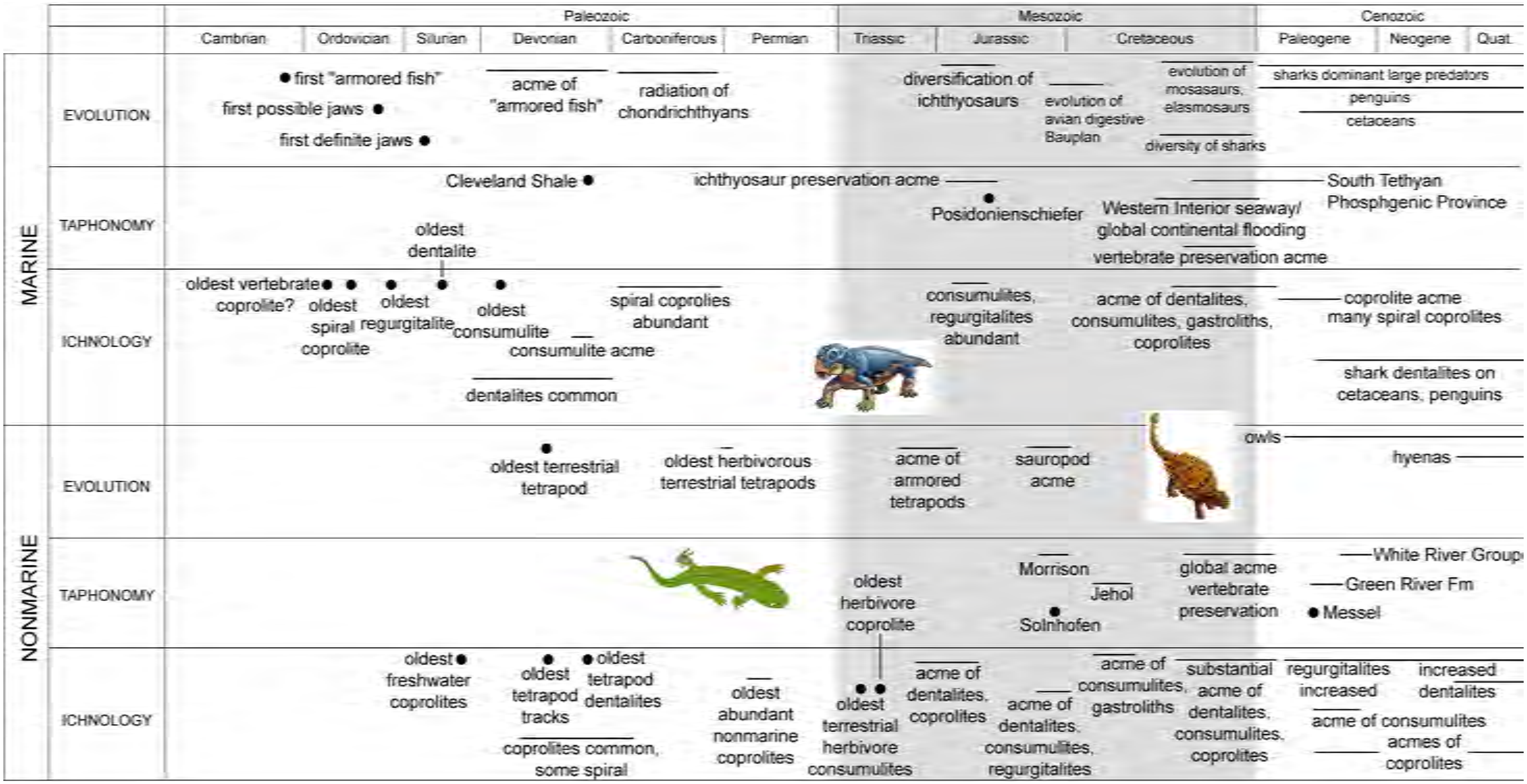


FIGURE 34. Major events in the evolution of vertebrate feeding, selected taphonomic episodes and significant highlights of the fossil record of related ichnofossils.

Tooth Wear

Fossil teeth preserve wear that has long been recognized as evidence of the nature of the food that is being processed. The study of tooth wear as it relates to diet became a robust tool with the examination of mammalian microwear (particularly with the SEM) in the late 1970s and early 1980s (e.g., Walker et al., 1978; Covert and Kay, 1981; Kay and Covert, 1983; Teaford and Walker, 1984). The majority of wear studies have been on the teeth of terrestrial mammals, but the same methodology has been subsequently applied to other groups such as marine mammals (e.g., Lambert and Bianucci, 2019) and reptiles (e.g., Fiorillo, 1998, 2011). Tooth wear is a type of trace fossil because it falls within "bite and gnaw structures" and reflects the interaction of an organism and a substrate (Bertling et al., 2006, table 1). Thus, we propose the term mololite from the Latin *molo* (to grind) for wear features, both mesowear and microwear (Fortelius and Solounias, 2000; Green and Croft, 2018), on fossil teeth. The study of microwear is now widespread, particularly with regard to hominins and other mammals (e.g., Merceron et al., 2005; Scott et al, 2005; Williams and Patterson, 2010; DeSantis, 2016; Ungar et al., 2016; Pappa et al., 2019) but also of fish (e.g., McLennan and Purcell, 2021) and of reptiles (e.g., Bestwick et al., 2019, 2020a-b; Winkler et al., 2019).

Association

The most famous association of vertebrates that has been interpreted as signs of predation (or at least of combat) are the "fighting dinosaurs" from the Upper Cretaceous Djadokhta Formation of Mongolia. Kielan-Jaworowska and Barsbold (1972) first described the entwined skeletons of *Velociraptor mongoliensis* and *Protoceratops andrewsi,* which have generally (e.g., Carpenter, 1998) but not exclusively (Osmólska, 1993) been interpreted as two animals that died while in the midst of a struggle.

Wilson et al. (2010) described multiple associations between the snake *Sanajeh indicus* and sauropod eggs from the Late Cretaceous of India. They interpreted this pattern as an "ethofossil" that preserves feeding behavior. Other associations interpreted as evidence of predation or scavenging are shed theropod or shark teeth in the absence of dentalites (e.g., Repenning and Packard, 1990; Schwimmer et al., 1997; Jennings and Hasiotis, 2006; Konuki, 2008; Meso et al., 2021).

Trace Elements

Feeding produces chemical signatures that provide evidence of diet (e.g., Toots and Voorhies, 1965; Boaz and Hampel, 1978; Sillen et al., 1995; Bourgon et al., 2020; Mychajliw et al., 2020b). However, a trace fossil is defined as a "morphologically recurrent structure" (Bertling et al., 2006, p. 266), so these chemicals are not trace fossils, though they may serve as proxies for traces and the behaviors they indicate.

THE ICHNOLOGICAL RECORD OF VERTEBRATE CONSUMPTION

Introduction

The fossil record of trace fossils provides substantial information about the evolution of vertebrate feeding. In addition, vertebrate (e. g., Lucas, 2019) and invertebrate (e. g., Buatois and Mángano, 2016a, b; Mángano and Buatois, 2006b, c) ichnofossils provide significant insight into major evolutionary events (Fig. 34).

Cambrian Explosion

The oldest record of predation on macroscopic organisms is ichnological. Thus, there are putative borings in *Cloudina* shells that coincide with the beginning of the radiation of skeletonized animals during the terminal Neoproterozoic (Bengtson and Zhao, 1992; Hua et al., 2003; Buatois and Mángano, 2016a; Mángano and Buatois, 2006a, 2021). However, these traces have also been interpreted as the result of the dissolution of microcrystals of dolomite (Debrenne and Zhuravlev, 1997), in which case the earliest ichnological evidence of predation may be early Cambrian ichnofossils from Mexico that have been interpreted to show a *Planolites* tracemaker consuming the producer of *Rusophycus multilineatus* (McMenamin, 2001, 2003).

Subsequently, during the Cambrian Explosion, there was a rapid diversification of macroscopic and anatomically complex predators that may have accelerated evolutionary diversification (Bengtson, 2002; Marshall, 2006; Leighton, 2011, but see Zhang et al., 2014; López-Villalta, 2016). These predators included conodonts and agnathan vertebrates, although there are some disagreements about phylogenetic relationships (Briggs, 1992; Donoghue and Purnell, 2009; Sansom et al., 2010; Turner et al., 2010). Coprolites are the only putative vertebrate feeding traces in the Cambrian, but they are diverse and reflect the Cambrian explosion of carnivores. Microscopic coprolites first are found in the lowest Cambrian strata (e.g., Chen and Chen, 1980), and macroscopic forms are present in several early Cambrian Lagerstätten, principally Burgess Shale-type (BST) deposits, of China (Vannier and Chen, 2005), the United States (Kimmig and Strotz, 2017) and the Czech Republic (Mikuláš, 1995). Macroscopic coprolites are also widespread in the middle Cambrian of Canada (Kimmig and Strotz, 2017; Kimmig and Pratt, 2018), the United States (Conway Morris and Robison, 1988; Kimmig and Strotz, 2017), China (Lin et al., 2010) and Sweden (Eriksson and Terfelt, 2007). Kimmig and Pratt (2018) demonstrate the earliest examples of coprophagy and the importance of fecal matter as an important source of nutrition in the Cambrian food web. However, no Cambrian coprolites have been attributed to vertebrates despite the fact that such organisms were present, and some larger coprolites could have arguably been produced by vertebrates (e.g., Conway Morris and Robison, 1988, fig. 10.2).

Great Ordovician Biodiversification Event

The only putative ichnofossils from the Ordovician possibly related to vertebrates are coprolites, principally from Lagerstätten. Clusters of conodont elements from the Early Ordovician of Kazakhstan, Sweden and Australia may represent coprolites of conodont animals, which are chordates and considered by some to be vertebrates (Tolmacheva 1996; Tolmacheva and Purnell 2002; Stewart and Nicoll 2003; Fig. 34). Middle Ordovician coprolites from the Winneshiek Lagerstätte have a concentrically layered internal structure, formed by animals with a valvular intestinal tract, such as some vertebrates (Hawkins et al., 2018). Spiral coprolites from the Late Ordovician Soom Shale Lagerstätte of South Africa are the first undoubted vertebrate coprolites (Aldridge et al., 2006; Fig. 34). This approximately correlates with the oldest record of jawed vertebrate body fossils and is a component of the Great Ordovician Biodiversification Event.

Ordovician vertebrate macrofossils are rare, and most complete body fossils represent arandaspid agnathans and allied genera and are from the second half of the period (Gagnier et al., 1986; Friedman and Sallan, 2012). Isolated vertebrate bone fragments and ichthyoliths from the later Ordovician lack definitive morphological characteristics, and have been erroneously assigned to more derived taxa such as heterostracan- and placoderm-grade taxa and even to gnathostomes such as chondrichthyans or acanthodians (Friedman and Sallan, 2012). The earliest putative regurgitalites are from the Late Ordovician and are tentatively assigned to conodont animals (Aldridge et al., 2006; Fig. 34).

Silurian

The Silurian record of vertebrate trace fossils related to feeding is still dominated by coprolites, but it includes more definitive examples as well as the oldest dentalite. There are a few putative Early or Middle Silurian coprolites that have been generally assigned to eurypterids, but may have been made by vertebrates, and they deserve more study (Gilpin, 1886; Rolfe, 1973; Selden, 1979, 1984; Turner, 1999). The oldest dentalite is on an unidentified cyathaspid element from the Middle Silurian Wenlock (Randle and Sansom, 2019a, b; Fig. 34), which indicates the presence of jawed fish at this time, preceding the unambiguous oldest occurrence of their body fossils. The Late Silurian first preserves a diversity of vertebrate coprolite morphotypes, including: (1) arenaeous scroll and non-spiral forms from Ireland and Scotland; (2) accumulations of agnathan fragments with little matrix from Scotland; and (3) phosphatic spiral and non-spiral coprolites from England that are characteristic of post-Silurian ichnofaunas (Murchison, 1839, 1867; Strickland and Hooker, 1853; Gilmore, 1992).

The impact of the end-Ordovician (Hirnantian) extinctions on fishes, except for conodonts, is difficult to assess because of a paucity of articulated specimens, particularly in the Lower Silurian (Friedman and Sallan, 2012). Sallan and Galimberti (2015) postulated a large reduction in body size in vertebrates following the end-Ordovician extinctions, but this is not currently testable in the coprolite record. Later in the period, the first well-preserved body fossils of gnathostomes appear in the latest Ludlow (Zhu et al., 1999, 2009; Zhang et al., 2010). The diversification of jawed fish in the later Silurian to Early Devonian is both taxonomic and ecological, with a major shift from benthic to nektonic lifestyles (Anderson et al., 2011; Klug et al., 2011; Friedman and Sallan, 2012). The diversification of vertebrate coprolite morphotypes in the Late Silurian presumably reflects the diversification of gnathostomes (and agnathans).

Devonian

The Devonian yields the first large samples of vertebrate feeding traces, both in terms of numerous specimens (e.g., dentalites, coprolites) and all of the different kinds of feeding traces (dentalites, regurgitalites, consumulites, gastroliths, coprolites), as well as the first nonmarine occurrences. This reflects: (1) increased abundance of fish in the fossil record; (2) large numbers of articulated skeletons, notably in the Upper Devonian Cleveland Shale (Fig. 34) – required for recognition of consumulites and gastroliths; (3) rise of the biting gnathostomes; (4) a succession of substantial body faunas through the span of the period, with many from Scotland; and (5) increased vertebrate exploitation of freshwater and ultimately terrestrial environments. This latter feature is part of the "terrestrialization" of the nonmarine biota that took place during the Devonian (e.g., Isozaki and Servais, 2017; Lucas, 2019).

Fish assemblages of macrofossils are dominated by jawless forms until the end of the Early Devonian, after which jawed gnathostomes dominate (Boucot and Janis, 1983; Anderson et al., 2011). However, dentalites increase at the onset of the Devonian and peak in the Givetian (Lebedev et al., 2009; Randle and Sansom, 2019a). Early Devonian coprolites from Scotland yield common acanthodian elements, although jawless fish dominate the associated body-fossil faunas. The orientation of acanthodian spines in Early Devonian coprolites, and a Middle Devonian consumulite, both provide the oldest evidence of head-first swallowing, which has been prevalent in fish predation until the Recent (Ahlberg, 1992; Trewin, 2008). Tail-first swallowing of invertebrates with tentacles is first recorded in the Late Devonian Cleveland Shale (Williams, 1990). Marine and nonmarine Devonian fish coprolites are mainly fusiform, with only a minority displaying a spiral morphology. There is no major change in mean size or morphology of coprolites during the Devonian. The Devonian yields some of the earliest regurgitalites in the Lower Devonian of Scotland and the Upper Devonian of Morocco, indicating that early gnathostomes undertook regurgitation (Burrow and Turner, 2010; Klug and Vallon, 2018).

The first terrestrial(?) dentalites occur on a tetrapod bone, a humerus, from the Famennian of the Canadian Arctic (Shubin et al., 2004; Fig. 34). Given the underived dentitions and jaw musculature of early tetrapods, it is unlikely that they manipulated their prey effectively, so Devonian dentalites would be predicted to be infrequent.

Devonian Extinctions and the Middle Paleozoic Marine Revolution

Early paleontologists, such as Agassiz (1833–1845a,b) and Marsh (1877), recognized that there were significant changes in vertebrate faunas between the "Age of Fishes" (Devonian) and the "Age of Amphibians" (Carboniferous). Newell (1952, 1962) and Schindewolf (1953) later first identified a Late Devonian mass extinction. This mass extinction is actually a series of events. The Kellwesser Crisis of the Frasnian-Fammenian boundary was previously considered the most significant for vertebrates (Long, 1995), but more recently the Hangenberg Crisis of the end Fammenian (end of the Devonian) is recognized to have had a more major impact on vertebrate (fish) extinctions, except for tetrapods (Sallan and Coates, 2010; Kaiser et al., 2016; Lucas, 2021).

Signor and Brett (1984) analyzed changes in predation patterns in the marine Devonian-Carboniferous, and they are widely credited with having introduced the term "Mid-Palaeozoic Revolution" (MPR) (e.g., Borszcz and Zatoń, 2013) or "Middle Paleozoic Marine Revolution" (MPMR) (e.g., Salamon et al., 2014), though they did not explicitly use either of these terms. Brett et al. (2002, p. 98) apparently first utilized the term Middle Paleozoic Revolution (MPR), and Baumiller and Gahn (2004) introduced the term Middle Paleozoic Marine Revolution (MPMR). We prefer the latter term, as it is more precise. The marked increase in durophagous fish during the later Devonian and Carboniferous (Signor and Brett, 1984, fig. 1) that resulted is documented by an increase in angular digestilites of invertebrates in the Missisippian (Salamon et al., 2014).

The first large ichnofaunas of coprolites are found in the Carboniferous, and they are significantly different from those of the Devonian, and thus document both the extinction and subsequent fish diversification and the MPMR. Other traces such as dentalites, evisceralites and consumulites are much less common in the Carboniferous relative to the Devonian.

The Carboniferous is characterized by shallow marine coprofaunas dominated by spiral forms, and, in several examples, the spiral forms are present to the near exclusion of other morphologies. Notable among the latter are the Mississippian Wardie Shale of Scotland, first reported by Buckland (1835), and the Pennsylvanian Weber Formation and Conemaugh Group of the United States (Price, 1927; Johnson, 1934). Hunt et al. (2017) named this recurrent association of spiral coprolites in shallow marine environments, which ranges from the Carboniferous to at least the Eocene, the *Crasssocoprus* Ichnofacies.

The heterospiral coprolites clearly pertain to chondrichthyans (e.g., McAllister, 1985; Williams, 1872; Diedrich, 2012b). Most or all of the pre-Carboniferous spiral coprolites, such as in the Ordovician, presumably derived from other fish that had spiral valves (McAllister, 1987). Chondrichthyan feces must have elevated preservational potential relative to those of other fish, because many coprofaunas dominated by spiral coprolites of the *Crassocoprus* Ichnofacies are often associated with body fossil faunas dominated by other fish. There is clearly a disparity between the high taxonomic diversity of some fish faunas, notably in the Pennsylvanian, Late Cretaceous and Eocene, and the low diversity of associated chondrichthyan-dominated coprolite ichnofaunas, and Hunt et al. (2015c) termed this the "Shark Surplus Paradox."

There is a marked reduction in dentalites in marine environments from the Devonian to the Carboniferous, which presumably is largely due to the Devonian extinctions of the armored fishes, whose extensive skeletons preferentially preserved such traces. Most nonmarine trace fossils derive from Lagerstätten, which in the Carboniferous notably yield several consumulites from sharks and amphibians. Among Carboniferous amphibians, consumulites have been analyzed to distinguish dietary changes during ontogeny in branchiosaurs (e.g., Werneburg et al., 2007).

Permian

Whereas most vertebrate feeding traces in the Carboniferous are marine rather than nonmarine, the reverse is true in the Permian. The earliest example of dentalites documenting extensive scavenging of a terrestrial tetrapod is from the early Permian of the United States (Reisz and Tsuji, 2006). Consumulites from the Permian of the United States and Germany provide direct evidence of insectivory and herbivory in tetrapods (Munk and Sues, 1993; Modesto et al., 2009; Reisz et al., 2014).

Nonmarine coprolites are abundant for the first time in Permian redbeds in the southwestern United States and have a wide distribution throughout the nonmarine strata of Permian Pangea (Hunt and Lucas, 2013). The majority of specimens represent aquatic organisms, and many have a heterospiral or scroll morphology. The first common evisceralites occur in the nonmarine Permian of China (Seilacher et al., 1991).

End-Permian Extinctions

It is not clear that the end-Permian extinction (PTME: Permian-Triassic Mass Extinction) had a significant impact on marine (Friedman and Sallan, 2012) or nonmarine (Lucas, 2009, 2017) vertebrates. However, Niedźwiedzki et al. (2016) studied the distribution of vertebrate coprolites across the nonmarine Permo-Triassic boundary in Russia and interpreted the results to demonstrate an extinction. Nevertheless, given the tenuous attribution of coprolite morphotypes to body-fossil taxa, the magnitude of the turnover supposedly demonstrated by coprolites is unclear.

"Mesozoic Marine Revolution"

Marine bromalites are well known from the Triassic, and they have the potential to provide information about the evolution of diet at the beginning of the Mesozoic Marine Revolution (MMR). Vermeij (1977) introduced the term MMR for macroecological and macroevolutionary predation-driven changes in marine ecosystems, predominantly during the later Mesozoic. "This term might seem to imply that a dramatic development of marine predators was initiated at the Triassic; a continuous intensification of predator-prey relationships has been envisaged. In actuality, the Mesozoic and Cenozoic evolution of predators involved a series of episodes" (Walker and Brett, 2002, p. 119). Nevertheless, this was probably too protracted an event (it lasted from the Triassic through much of the Cretaceous) to deserve the term "revolution" (Lucas and Tanner, 2018).

Early Triassic coprolites have been used to suggest that the MMR began early in the Triassic (Nakajima and Izumi, 2014; Brachaniec et al., 2015; Antczak et al., 2020), as is also suggested by evidence from body fossils (e.g., Hu et al., 2011; Stubbs and Benton, 2016). There is evidence from ichnology for increased vertebrate predation on invertebrates (Tables A.1-2, 5, 8-9) in the Jurassic and Cretaceous, including regurgitalites (e.g., Zatoń et al., 2007; Borszcz and Zatoń, 2013), consumulites (e.g., Pollard, 1968; Přikryl et al., 2012) and digestilites (e.g., Oji et al., 2003). Consumulites of ichthyosaurs demonstrate some feeding changes, as Early and Middle Triassic specimens yield only cephalopod hooklets, whereas Late Triassic examples include both vertebrate remains and mollusk-shell fragments (Rieber, 1970; Camp, 1980; Brinkmann, 2004; Buchy et al., 2004; Cheng et al., 2006; Druckenmiller et al., 2014). This corresponds to an ecomorphological diversification documented by hard parts (Stubbs and Benton, 2016). Marine coprolites occur throughout the Triassic, but are most abundant in the Rhaetic bonebeds in England and elsewhere in Europe (Cueille et al., 2020).

Triassic Terrestrial Radiations

Coprolites occur throughout the Triassic but are most numerous and widely dispersed in redbeds of Late Triassic age. The oldest vertebrate herbivore coprolites are from the Middle Triassic of Brazil (Hunt et al., 2013b: Fig. 34). Nonmarine dentalites are abundant in the Late Triassic, but rarer earlier in the period. The Late Triassic is also a time interval characterized by the presence of extensive osteoderms in a wide range of carnivorous (phytosaurs, paracrocodylomorphs, crocodylomorphs) and herbivorous (non-archosaurian archosauriforms, pseudosuchians, aetosaurs, turtles, *Doswellia*) reptiles, suggesting a substantial amount of evolutionary escalation. More armor and more dentalites are characteristic of both the aquatic Devonian and the terrestrial Late Triassic.

Terminal Triassic Extinction

Contrary to a large volume of literature, there is no single mass extinction at the end of the Triassic that affects either fish (e. g., McCune and Schaeffer, 1986; Bambach et al., 2004) or tetrapods (Lucas and Tanner, 2015, 2018). The record of vertebrate coprolites similarly shows no significant turnover across the Triassic/Jurassic boundary (Hunt and Lucas, 2018a; Hunt et al., 2018).

Jurassic

The majority of marine trace fossils of vertebrate consumption in the Jurassic are dentalites and consumulites related to the development of ecosystems with diverse marine reptiles of large body size, a trend that started in the Early Jurassic. Large bones aid in the recognition of dentalites, and consumulites are more easily identified in relatively large, articulated skeletons. While the majority of Jurassic consumulites pertain to ichthyosaurs that ingested coleoids or belemnites, many dentalites were produced by predatory pliosaurs, plesiosaurs and marine crocodylomorphs. Jurassic marine coprolites are not abundant, except in the Lias of England where multiple large spiral forms such as *Liassocoprus, Strabelocoprus* and *Saurocoprus* indicate that chondrichthyans were important predators during the Early Jurassic.

Nonmarine coprolites in the redbeds of the Lower Jurassic of western and eastern North America are little different from those of the Upper Triassic, supporting the absence of a mass extinction of vertebrates on land across the Triassic-Jurassic boundary. The most significant Jurassic vertebrate trace fossils occur in the Upper Jurassic. The Solnhofen and related Lagerstätten of Germany (Fig. 34) produce over 100 fish consumultites as well as specimens preserved in pterosaurs and a theropod that facilitate the construction of food webs (Wellnofer, 1970; Ostrom, 1978; Viohl, 1990; Ebert et al., 2015). The first large samples of terrestrial dentalites occur in Late Jurassic dinosaurs. These demonstrate that dinosaur communities yield significantly fewer dentalites than mammal communities, because non-avian dinosaurs lacked the dentition or jaw mechanics to adeptly manipulate and modify bones (Fiorillo, 1991a). Jurassic and Cretaceous dentalites demonstrate that crocodylomorphs only preyed on smaller bodied animals, such as other crocodylomorphs or turtles, and that only theropods attacked large dinosaurs.

Origin of the Avian Digestive Bauplan

One of the most important aspects of the record of vertebrate trace fossils is the documentation of the development of the avian digestion system (crop, two-part stomach – proventriculus and ventriculus) as demonstrated by gastroliths, consumulites, regurgitalites and coprolites from small, derived theropods and birds, principally from the Early Cretaceous Jehol Lagerstätte but also from the Late Jurassic Yanliao Biota (O'Connor and Zhou, 2015, 2020; O'Connor et al., 2019; Fig. 34, Table A.9). This documents a trophic shift from carnivory to herbivory (fruit, seed, and/or nut eater) with the origin of birds (Wu, 2021). Among the conclusions based on examination of the ichnofossils record are (O'Connor, 2019): (1) the two-part stomach evolved outside Aves; (2) evolution of the crop and use of the esophagus to store food is only documented in Aves among the Theropoda; (3) *Jeholornis* (the only long, bony-tailed bird other than *Archaeopteryx*) and *Sapeornis* both ate seeds, and, like living granivores, utilized a gastric mill, although only the more derived *Sapeornis* possessed a crop for food storage; (4) a modern alimentary canal was present in the earliest members of Ornithuromorpha, but the Enantiornithes were characterized by a primitive alimentary canal – no grinding gizzard, crop or bidirectional peristalsis; (5) the two-part stomach is inferred to have evolved outside Aves, but the evolution of the crop and use of the esophagus to store food occurred later and is thus far only documented in Aves among the Theropoda; (6) the role of the gizzard in the loss of teeth in Aves is more complex than in non-avian theropod lineages and may not be entirely indicative of herbivory, although this diet does appear to correlate with complete tooth loss in this clade; and (7) whole fish and clusters of macerated fish remains in specimens of *Yanornis* suggests that food items that were difficult to digest could be moved between parts of the digestive tract through peristalsis-antiperistalsis and regurgitated, increasing digestive efficiency; and (8) advanced digestive abilities like those observed in living birds are probably unique to the Ornithuromorpha and may represent a major factor in the current success of this clade.

Cretaceous Acme of Feeding Traces and the Cretaceous Terrestrial Revolution

The Cretaceous yields the largest record of vertebrate trace fossils prior to the Quaternary (Fig. 34). With the exception of gastroliths, the majority of specimens of vertebrate ichnofossils derive from the Late Cretaceous. This is in large part a taphonomic artifact associated with the abundance of fossils preserved within continental floodings with related tectonic sediment sourcing. It also partly reflects the Taxophile Effect, particularly with regard to dinosaur dentalites. An apparent expansion of dinosaur diversity occurred in the mid-Cretaceous, with the emergence of new groups (e.g. neoceratopsians, ankylosaurid ankylosaurs, hadrosaurids and pachycephalosaurs), but this is a sampling artifact not related to the Cretaceous Terrestrial Revolution (KTR) (Lloyd et al., 2008). However, the KTR undoubtedly affected food webs and vertebrate feeding with potential for documentation from ichnofossils. For example, Prasad et al. (2005) document the inclusion of grasses in dinosaur diet based on Late Cretaceous coprolites from India.

Ichnofossils from the nonmarine Late Cretaceous provide diverse evidence of feeding and other behavior in dinosaur communities, including the digestion of tyrannosaurs (e.g., Chin et al., 1998), scavenging of dinosaurs by mammals (e.g., Longrich and Ryan, 2010), the disparity between the density of dentalites on ceratopsians and hadrosaurs (Jacobsen, 1998) and intraspecific head biting among large theropods (e.g., Brown et al., 2020a). Many smaller Late Cretaceous coprolites probably pertain to crocodylomorphs, so there is a scant record of small theropod coprolites (Hunt and Lucas, 2017b).

Ichnofossils of marine ecosystems of the Late Cretaceous document disproportionate evidence of predation by two groups, sharks and mosasaurs. The earliest known shark dentalites were produced by a cretoxyrhinid on a specimen of *Kronosaurus* from the Early Cretaceous of Australia (Holland, 2018). Subsequently, dentalites produced by sharks, notably *Squalicorax* and *Cretoxyrhina*, are abundant in the Late Cretaceous and demonstrate widespread predation on marine tetrapods that continued into the Cenozoic. Large chondrichthyans and teleosts, the latter undergoing a substantial radiation during this time (Underwood, 2006; Cavin and Forey, 2007; Cavin et al., 2007; Guinot et al., 2012), also exhibit dentalites predominantly produced by large sharks. Sharks dominate the record of both marine coprolites and dentalites from the Late Cretaceous onwards.

A large number of mosasaur dentalites and consumulites in the Late Cretaceous demonstrate the diversification and importance of this group as predators in Late Cretaceous marine environments. Marine coprolites are very abundant, particularly in the South Tethyan Phosphogenic Province, and in chalk facies (Hunt et al., 2015; Hunt and Lucas, 2016c).

K-Pg Extinctions

The change in mean body size and taxonomic composition of terrestrial vertebrates across the K/Pg boundary resulted in large changes in the ichnofaunas. The rare but very visible and much studied dentalites of dinosaurs are replaced by more common but much less studied and recognized dentalites on small mammal bones in the Paleocene.

There is a limited change in coprolite morphotypes across the K-Pg boundary in nonmarine environments (Suazo et al., 2012; Hunt and Lucas, 2016c). Thus, for example, *Alococopros* and *Eucoprus* extend across the boundary, and there is no significant change in the overall median size of coprolites (except for the loss of the rare putative tyrannosaurid coprolites). This suggests that ornithischian and non-avian theropod coprolites are not commonly preserved in the Cretaceous. Most small carnivore coprolites probably represent crocodylomorphs, which do not demonstrate significant changes across the boundary (Sullivan, 1987; Mardwick, 1998; Vasse and Hua, 1998; but also see Puertolas-Pascual et al., 2016). Similarly, there is also no significant change in coprolite morphologies across the K/Pg boundary in marine environments (Hunt and Lucas, 2016c). This is consistent with the hypothesis that many marine coprolites represent chondrichthyans (Hunt et al., 2015b), which exhibit limited extinction across the boundary (Adolfssen and Ward, 2014; Bazzi et al., 2021).

Cenozoic

There is a significant reduction in marine vertebrate ichnofossils in the Paleogene. This is probably largely due to the extinction at the K-Pg boundary of the large-bodied marine reptiles, whose body fossils preferentially preserve such traces, but also to the significant retreat of the epicontinental seas that preserved them. The largest number of reports of marine dentalites from the Cenozoic are related to large, non-delphin cetaceans from the Neogene that were bitten by large sharks (Fig. 34). Spiral shark coprolites of the *Crassocoprus* Ichnofacies dominate many shallow marine ichnofaunas, particularly those of large size from the Eocene (Diedrich and Felker, 2012; Stringer and King, 2012). There is a small but widespread record of dentalites on fossil penguins, whose robust bones give them both an enhanced preservational potential over those of other birds and a better chance of preserving bite marks.

There are well known ichnofaunas of coprolites from the nonmarine Paleocene that show little change from those of the Late Cretaceous except for the absence of the extremely rare, large specimens attributed to tyrannosaurs (Suazo et al., 2012). This is probably due to the fact that the most common carnivorous coprolites of Late Cretaceous and Paleogene are small in size and represent crocodylomorphs rather than small theropods or mammals (e.g., *Alococoprus*).

Digestilites of marine invertebrates composed of angular fragments increase dramatically from the Paleogene to Neogene in Japan (Oji et al., 2003). This suggests increased durophagy by teleosts during the Cenozoic.

Dentalites remain common but relatively understudied throughout the Cenozoic. Paleogene Lagerstätten, notably Messel and the Green River, produce abundant ichnofossils, in particular consumulites, regurgitalites and even gastroliths. Messel yields the oldest evidence of owl predation by strigilites, which become increasingly common later in the Neogene.

Quaternary Acme

Pleistocene vertebrate ichnofossils are abundant. Buckland first found coprolites and dentalites in a Pleistocene cave, and this environment is disproportionately important in the preservation of vertebrate trace fossils in the Quaternary (e.g., Brain, 1981; Andrews, 1990; Hunt and Lucas, 2018c, 2020a).

Terminal Pleistocene Extinctions

One of the primary motivations for the study of the extensive Pleistocene coprolites of the Western United States was to better understand extinctions of the megafauna (Martin et al., 1985; Mead and Agenbroad, 1992; Martin, 2005; Hunt and Lucas, 2018c, 2020a). Paul Martin and his co-workers conducted the majority of this work, and they are proponents of the human overkill hypothesis of terminal Pleistocene extinction (e.g., Martin et al., 1985; Martin, 2015). However, Hunt and Lucas (2018c; Fig. 33) concluded that the pattern of preservation of sloth coprolites suggests that climate rather than overkill was most significant in the extinction of ground sloths. S*porormiella,* serving as a proxy for coprolites, has widespread utility in analyzing the timing of extinctions (Davis, 1987; Perotti, 2018).

PROSPECTUS

Introduction

There is a large fossil record of diverse ichnofossils that relate to the feeding of vertebrates. This database provides an opportunity to investigate a number of significant issues in paleobiology.

Data Set

There is a substantial and growing literature on vertebrate coprolites that documents an extensive fossil record (e.g., Dentzien-Dias et al., 2012, 2021; Hunt et al., 2012a, b, c, 2018; Qvarnström et al., 2016, 2017, 2019a-d). Here, we have documented that there is also a substantial record of other ichnofossils related to feeding that include dentalites, consumulites, gastroliths and, to a lesser extent, regurgitalites (see Tables A.1-11), There are still notable areas of understudy such as dentalites in Paleogene mammals, and coprolites in many Lägerstatten. The trace-fossil record of vertebrate feeding also has systematic biases, mostly documents vertebrate-on-vertebrate interactions and suffers from a paucity of herbivore traces. Overall, however, the large datasets encompassed by dentalites, consumulites, gastroliths and regurgitalites provide diverse opportunities for further research.

Methodologies

Significant methodological innovations have been introduced into the study of coprolites in the last decade (e.g., micro CT scans, biogeochemical analyses, SEM, etc: Milàn et al., 2012a; Wang et al., 2018; Qvarnström et al., 2019a, b; Umamaheswaran et al., 2019; Cueille et al., 2020; Qvarnström, 2020b). These techniques have only been utilized to a very limited extent in other bromalites (e.g., Gordon et al., 2020) and have great potential to further the study of other trace fossils, notably consumulites.

Taphonomy

The nature and pattern of the fossil record of vertebrate ichnology has received relatively little attention (e.g., Hunt et al., 2018). There are clearly both biological and physical factors that influence the nature of the fossil record of traces related to vertebrate feeding (and other ichnofossils) that can be investigated. For example, how much is the Late Cretaceous acme of all types of traces related to tectonics and sea-level changes and how much to the diversification of sharks, mosasaurs and the large theropods that produce a seemingly disproportionate amount of the fossil record of coprolites and dentalites?

Ichnotaxonomy

Vertebrate ichnology, with the exception of the study of tracks and more recently dentalites, has been hindered by a reluctance to utilize a formal ichnotaxonomy. This is particularly notable with regard to bromalites (coprolites, consumulites and regurgitalites) and gastroliths. Synthetic studies require a common framework of ichnotaxonomy that is generally lacking with regard to the ichnofossils related to vertebrate feeding.

Evolution of Ecosystems

Vertebrate feeding traces provide direct and indirect information on trophic levels and food webs in ancient communities and can aid in the study of ecosystem evolution. Notably, digestilites composed of invertebrate debris provide a particularly important insight into the evolution of durophagous fish and also constitute a significant sediment source, particularly in the Cenozoic. This large topic is deserving of substantial study.

Predation and Evolution

Predation has had a significant impact on macroevolution (e.g., Huntley and Kowalewski, 2007; Stanley, 2008; Sallan et al., 2011). However, predator–prey interactions are thought to be "notoriously difficult to define in the fossil record" (Sallan et al., 2011, p. 8335). Previously, there was recognition of a significant volume of data on the ichnology of invertebrate predation (e.g., Huntley and Kowalewski, 2007), and herein we review an extensive trace fossil record of vertebrate predation. The ichnological record of vertebrate feeding is clearly significant in its extent and can be utilized in modeling evolutionary scenarios.

Predation and Environment

Predation is known to vary among Recent environments (e.g., Harper and Peck, 2016; Sanford, 1999; Sperling et al., 2013; Klompmaker et al., 2019). Environmental factors related to predation include water depth, substrate, oxygenation, temperature and ocean acidification (Klompmaker et al., 2019). Large ichnological data sets, such as from the Late Cretaceous of North America, allow the investigation of environmental factors related to vertebrate feeding traces.

Lagerstätten Without

Lagerstätten yield a disproportionate number of consumulites. However, with a few notable exceptions (e.g., Hunt, 1992; Schweigert and Dietl, 2012; Barrios-de Pedro et al., 2018, 2020a, b), there has been relatively little study of the numerous coprolites and other bromalites from Lagerstätten.

Lagerstätten Within

Bromalites are loci for exceptional preservation and thus constitute Lagerstätten (Wilby and Martill, 1992; Qvarnström et al., 2016; Gordon et al., 2020). Coprolites preserve muscle tissues, eggs, hair, parasites, bacteria, fungi and feathers (Qvarnström et al., 2016), consumulites preserve lepidopteran wings, hair and embryos (Wilby and Martill, 1992) and regurgitalites preserve muscle tissue (Gordon et al., 2020). There is clearly great potential to examine the plethora of bromalites discussed above for the preservation of organic materials that have an otherwise under-represented fossil record.

Vertebrate Predation on Invertebrates

Vertebrate predation is often cited as an important influence on invertebrate evolution (e.g., Vermeij, 1977; Walker and Brett, 2002; Baumiller and Gahn, 2004; Klompmaker et al., 2019). However, the ichnological record of predation of invertebrates by vertebrates is extremely limited. This record needs to be further developed and requires much more research.

Defense

A significant portion of the literature on predation on invertebrate fossils relates to the development of protective measures preserved in hard tissues of organisms, such as thickened shells and the evolution of spines (e.g., Vermeij, 1977; Brett and Walker, 2002). An equivalent arms race occurred during vertebrate evolution, and this invites varied research questions. For example, what is the significance of the relative prevalence of dentalites among unarmored nonmarine herbivores (dicynodonts) in the Late Triassic relative to armored herbivores (aetosaurs).

Conclusions

1. There is a long tradition of inferring feeding in fossil and Recent animals indirectly from functional morphology. Ichnology provides direct evidence of feeding.
2. The bromalite and dentalite records are highly skewed towards carnivores and also have distinct size and facies biases.
3. There is an almost 200 year-long history of naming vertebrate tracks, but there is reluctance to apply a binomial ichotaxonomy to traces relating to feeding that impedes the development of their study.
4. There is a large fossil record of vertebrate dentalites, principally on bony substrates but also on invertebrate hard parts, coprolites, lithic substrates and others. The record requires more synthetic study, an ichnotaxonomy and the development of criteria for establishing inferences about behavior.
5. Regurgitalites are the least studied bromalites and the most difficult to identify. Their record is strongly controlled by taxonomic and taphonomic factors. Avian (notably owl) regurgitalites are a significant source of microvertebrate faunas.
6. There are many descriptions of consumulites, but they are often hidden within publications with a different focus. Consumulites provide the most unambiguous attribution of the tracemaker of any bromalites and provide direct evidence of the nature of digestion and the structure of the digestive tract. They are particularly important in comprehending the evolution of the avian digestive system.
7. Most records of gastroliths are from plesiosaurs, birds and some dinosaurs that provide important insights into varied behaviors, including diet, digestion, buoyancy control and habitat preferences. None are highly polished. Gastroliths are in need of an ichnotaxonomy.
8. Coprolites serve as proxies for biotaxa with demonstrated utility in biochronology, biogeography and the understanding of extinction dynamics.
9. Diverse other ichnofossils provide some information on feeding, including tracks, nests, pabulites and mololites
10. Digestilites are an important source of microvertebrate assemblages, provide insight into the evolution of durophagous fish and constitute an important sediment source in the Cenozoic.
11. The first large sample of vertebrate ichnofossils related to feeding is from the Devonian, but the largest acme is in the Late Cretaceous, which results from taphonomy (continental flooding), the evolution of predators and the Taxophile Effect.
12. Vertebrate feeding traces provide important evidence for major evolutionary events.
13. Bromalites are Lagerstätten that provide important preservational environments.

ACKNOWLEDGMENTS

Numerous colleagues have graciously allowed us access to collections, and many others have collaborated in prior research or/and have provided insightful discussions, including Lewis Binford, Michael Brett-Surman, Brooks Britt, Bret Buskirk, Ken Carpenter, Sarah Chapman, Karen Chin, Neil Clark, Sebastian Dalman, Paula Dentzien-Dias, Chris Duffin, Mike Everhart, Nick Fraser, John Foster, Janet and David Gillette, Stephen Godfrey, Paul Jeffery, Jim Jensen, Martin Lockley, Greg McDonald, Jim Mead, Christian Meyer, Jesper Milàn, Angela Milner, Gary Morgan, Vince Santucci, Alan Tennyson and Justin Tweet. Mike Everhart, Stephen Godfrey, Vincent Santucci, Günter Schweigert and Ralf Werneburg kindly supplied images, and Jesper Milàn and Mike Everhart provided insightful reviews.

REFERENCES

Aas, T.S., Sixten, H.J., Hillestad, M., Sveier, H., Ytrestøyl, T., Hatlen, B. and Åsgård, T., 2017, Measurement of gastrointestinal passage rate in Atlantic salmon (*Salmo salar*) fed dry or soaked feed: Aquaculture Reports, v. 8, p. 49-57.

Abel, O., 1922a, Die Schnauzenverletzungen der Parasuchier und ihre Biologische Bedeutung: Päleontologische Zeitschrift, v. 5, p. 25–57.

Abel, O., 1922b, [Discussion of Krausel, 1922]: Paläontologische Zeitschrift, v. 4, p. 87.

Abel, O., 1926, Amerikafahrt: Beobachtungen und Studeien eines Naturforschers auf einer Reise nach Nordamerika und Westindien. Jena, G. Fischer, 462 p.

Abel, O., 1935, Vorzeitliche Lebensspuren. Jena, Verlag von Gustav Fischer, 644 p.

Abella, J., Martín-Perea, D. M., Valenciano, A., Hontecillas, D., Montoya, P. and Morales, J. 2021, Coprolites in natural traps: Direct evidence of bone-eating carnivorans from the Late Miocene Batallones-3 site, Madrid, Spain: Lethaia, doi: org/10. 1111/let.12438.

Abrahams, P.W., 2003, Human geophagy: A review of its distribution, causes, and implications; *in* Skinner, H.C. and Berger, A.R., eds., Geology and health: Closing the gap. Oxford, Oxford University Press, p. 31-36.

Abrahams, P. W., and Parsons, J. A., 1996, Geophagy in the tropics–a literature review: Geographical Journal, v. 162, p. 63-72.

Aceñolaza, F.G., 2012, Neogene coprolites (Upper Miocene-Lower Pliocene) of Entre Ríos province, northeastern Argentina. Universidad Autónoma de Entre Ríos: Secretaría de Ciencia y Técnica, Scientia Interfluvius, v. 3, p. 41-53.

Adolfssen, J.S. and Ward, D.J., 2014, Crossing the boundary: An elasmobranch fauna from Stevns Klint, Denmark: Palaeontology, v. 57, p. 591–629.

Agassiz, L., 1833, Letter to Prof. Bronn of Nov. 8, 1833: Neues Jahrbuch für Mineralogie, Geologie und Petrefaktendkunde, p. 675-677.

Agassiz, L., 1833-1845a, Recherches sur les Poissons Fossiles. Tome 2. Neuchatel, Imprimerie de Petitpierre et Prince, 288 p.

Agassiz, L., 1833-1845b, Recherches sur les Poissons Fossiles. Tome 4. Neuchatel, Imprimerie de Petitpierre et Prince, 188 p.

Agenbroad, L.D. and Mead, J. I., 1987, Late Pleistocene alluvium and megafauna dung deposits of the central Colorado Plateau; *in* Davis, G. H. and Van den Dolder, E. M., eds., Geologic diversity of Arizona and its margins: Excursions to choice areas: Arizona Bureau of Geology and Mineral Technology, Geological Survey Branch Special Paper, v. 5, p. 68–84.

Agenbroad, L.D. and J.I. Mead, 1989, Quaternary geochronology and distribution of *Mammuthus* on the Colorado Plateau: Geology, v. 17, p. 861-864.

AGI (American Geological Institute), 1960, Glossary of geology and related science with supplement (Second edition). Washington, D. C., National Academy of Science, 325 p. and 72 p. (supplement).

AGI (American Geological Institute), 1974, Dictionary of geological terms. Garden City, New York, Anchor Press/Doubleday, 545 p.

Aguilera, O. and Rodrigues de Aguilera, D.R., 2004, Giant-toothed white sharks and wide-toothed mako (Lamnidae) from the Venezuela Neogene: their role in the Caribbean, shallow-water fish assemblage: Caribbean Journal of Science, v. 40, p. 368-382.

Aguilera, O.A., García, L. and Cozzuol, M.A., 2008, Giant-toothed white sharks and cetacean trophic interaction from the Pliocene Caribbean Paraguaná Formation: Paläontologische Zeitschrift, v. 82, p. 204-208.

Agustín, B., Julián, F.F. and Ornela, B.M., 2021, Carnivore coprolites from "Gruta del Indio" site as source of paleoparasitological and paleoecological evidences (late Pleistocene-Holocene, Mendoza, Argentina): Archaeological and Anthropological Sciences, v. 13, p. 1-14.

Ahlberg, A., Herman, A.B., Ratkevitch, M., Rees, A. and Spicer, R.A., 2002, Enigmatic Late Cretaceous high palaeo-latitude lonestones in Chukotka, northeastern Asia: GFF, v. 124, p. 197-199.

Ahlberg P.E., 1992, The palaeoecology and evolutionary history of the porolepiform sarcopterygians; *in* Mark-Kurik, E., ed., Fossil fishes as living animals. Volume 1. Tallinn, Estonian Akademia, p. 71–90.

Akersten, W.A., 1985, Canine function in *Smilodon* (Mammalia; Felidae; Machairodontinae): Contributions in Science, Natural History Museum Los Angeles County, v. 356, p. 1-22.

Albersdörfer, R. and Häckel, W. 2015, Die Kieselplattenkalke von Painteni; *in* Arratia, G., Schultze, H.P., Tischlinger, H. and Viohl, G., eds., Solnhofen – ein Fenster in die Jurazeit. München, Verlag Dr. F. Pfeil, p. 126–133.

Albright, L.B., 1994, Lower vertebrates from an Arikareean (earliest Miocene) fauna near the Toledo Bend Dam, Newton County, Texas: Journal of Paleontology, v. 68, p. 1131-1145.

Alcalá, L., Espílez, E., Mampel, L., Kirkland, J.I., Ortiga, M., Rubio, D., González, A., Ayala, D., Cobos, A., Royo-Torres, R., Gascó, F. and Pesquero, M.D., 2012, A new Lower Cretaceous vertebrate bonebed near Ariño (Teruel, Aragón, Spain); found and managed in a joint collaboration between a mining company and a palaeontological park: Geoheritage, doi:10.1007/s12371-012-0068-y.

Aldridge, R.J., Gabbott, S.E., Siveter, L.J. and Theron, J.N., 2006, Bromalites from the Soom Shale Lagerstätte (Upper Ordovician) of South Africa: palaeoecological and palaeobiological implications: Palaeontology, v. 49, p. 857–871.

Alexander, J., 1992, Alas, poor *Notharctus*: Natural History, v. 101, p. 54-59.

Alexander, J. P. and Burger, B. J., 2001, Stratigraphy and taphonomy of Grizzly Buttes, Bridger Formation, and the middle Eocene of Wyoming; *in* Gunnell, G. F., ed., Eocene biodiversity: Unusual occurrences and rarely sampled habitats. New York, Kluwer Academic/Plenum Publishers, p. 165-196.

Alexander, R.R., 1981, Predation scars preserved in Chesterian brachiopods: probable culprits and evolutionary consequences for the articulates: Journal of Paleontology, v. 55, p. 192-203.

Allaby, A. and Allaby, M., 1991, The concise Oxford dictionary of earth sciences. Oxford, Oxford University Press, 410 p.

Allain, R., 2005, The postcranial anatomy of the megalosaur *Dubreuillosaurus valesdunensis* (Dinosauria, Theropoda) from the Middle Jurassic of Normandy, France: Journal of Vertebrate Paleontology, v. 25, p. 850-858.

Allen, J.R.L. and Tarlo, L.B., 1963, The Downtonian and Dittonian facies of the Welsh borderland: Journal of the Geological Society of London, v. 138, p. 375-405.

Alonso, A., Canudo, J.I., Fernández-Baldor, F.T. and Huerta, P., 2017, Isolated theropod teeth associated with sauropod remains from El Oterillo II (Early Cretaceous) site of Salas de los Infantes (Burgos, Spain): Journal of Iberian Geology, v. 43, p.193-215.

Álvarez-Parra, S., Albesa, J., Gouiric-Cavalli, S., Montoya, P., Peñalver, E., Sanjuan, J., and Crespo, V.D., 2021, The early Miocene lake of Foieta la Sarra-A in eastern Iberian Peninsula and its relevance for the reconstruction of the Ribesalbes– Alcora Basin palaeoecology: Acta Palaeontologica Polonica, v. 66 (supplement), doi: https://doi.org/10.4202/app.00842.2020.

Amalfitano, J., Dalla Vecchia, F.M., Giusberti, L., Fornaciari, E., Luciani, V. and Roghi, G., 2017, Direct evidence of trophic interaction between a large lamniform shark, *Cretodus* sp., and a marine turtle from the Cretaceous of northeastern Italy: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 469, p.104-121.

Amalfitano, J., Giusberti, L., Fornaciari, E., Dalla Vecchia, F.M., Luciani, V., Kriwet, J. and Carnevale, G., 2019, Large deadfalls of the 'ginsu' shark *Cretoxyrhina mantelli* (Agassiz, 1835) (Neoselachii, Lamniformes) from the Upper Cretaceous of northeastern Italy: Cretaceous Research, v. 98, p.250-275.

Amstutz, G., 1958, Coprolites: A review of the literature and a study of specimens from southern Washington: Journal of Sedimentary Petrology, v. 28, p. 498-508.

Anagnostakis, S., 2013, Upper Cretaceous coprolites from the Münster Basin (northwestern Germany) – a glimpse into the diet of extinct animals [M.S. thesis]: Lund, Lund University, 28 p.

Anderson, A., 1989, Prodigious birds: Moas and moa hunting in Prehistoric New Zealand. Cambridge, Cambridge University Press, 238 p.

Anderson, J.M., Anderson, H.M. and Cruickshank, A.R.I., 1998, Late Triassic ecosystems of the Molteno lower Elliot biome of southern Africa: Palaeontology, v. 41, p. 387-421.

Anderson, L.I., Dunlop, J.A., Horrocks, C.A., Winkelmann, H.M. and Eagar, R.M.C., 1997, Exceptionally preserved fossils from Bickershaw, Lancashire UK (upper Carboniferous, Westphalian A (Langsettian): Geological Journal, v. 3, p. 197-210.

Anderson, P.S.L., Friedman, M., Brazeau, M.D. and Rayfield, E.J., 2011, Initial radiation of jaws demonstrated stability despite faunal and environmental change: Nature, v. 476, p. 206–209.

Andersson, K. and Kaakinen, A., 2004, Floodplain processes in the shaping of fossil bone assemblages: an example from the Late Miocene, Bahe Formation, Lantian, China: GFF, v. 126, p. 279-287.

Andrade, M.B., Edmonds, R., Benton, M.J. and Schouten, R., 2011, A new Berriasian species of *Goniopholis* (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus: Zoological Journal of the Linnean Society, v.163, p. 66–108, doi: 10.1111/j.1096-3642.2011.00709.x 66e108.

Andrew, C., Howe, P. and Paul, C., 2015, Fatally bitten ammonites from septarian concretions of the 'Marston Marble' (Lower Jurassic, Sinemurian), Somerset, UK, and their taphonomy: Proceedings of the Geologists' Association, v. 126, p.119-129.

Andrew, C., Howe, P., Paul, C.R. and Donovan, S.K., 2010, Fatally bitten ammonites from the lower Lias Group (Lower Jurassic) of Lyme Regis, Dorset: Proceedings of the Yorkshire Geological Society, v. 58, p. 81-94.

Andrews, C.W., 1910, A descriptive catalogue of the marine reptiles of the Oxford Clay. Part I. London, British Museum (Natural History), 205 p.

Andrews, P., 1990, Owls, caves and fossils: predation, preservation and accumulation of small mammal bones in caves, with an analysis of the Pleistocene cave faunas from Westbury-sub-Mendip, Somerset, UK. Chicago, University of Chicago Press, 239 p.

Andrews, P. and Evans, E.N., 1983, Small mammal bone accumulations produced by mammalian carnivores: Paleobiology, v. 9, p. 289-307.

Andrews, P.L.R., Sims, D.W. and Young, J.Z., 1998, Induction of emesis by the sodium channel activator veratrine in the lesser spotted dogfish, *Scyliorhinus canicula* (Chondrichthyes: Elasmobranchii): Journal of the Marine Biological Association of the United

Kingdom, v. 78, p. 1269-1279.

Andrews, P.L.R., Axelsson, M., Franklin, C. and Holmgren, S., 2000, The emetic reflex in a reptile (*Crocodylus porosus*): Journal of Experimental Biology, v. 203, p. 1625–1632.

Angielczyk, K.D. and Gingerich, P.D., 1998, New specimen of cf. *Asiatosuchus* (Crocodyloidea) from the middle Eocene Drazinda Formation of the Sulaiman Range, Punjab (Pakistan): Contributions from the Museum of Paleontology, University of Michigan, v. 30, p. 163-189.

Antczak, M., Ruciński, M.R., Stachacz, M., Matysik, M. and Król, J.J., 2020, Diversity of vertebrate remains from the Lower Gogolin Beds (Anisian) of southern Poland: Annales Societatis Geologorum Poloniae, v. 90, p. 419-433.

Antunes, M.T., Balbino, A.C. and Ginsburg, L., 2006a, Ichnological evidence of a Miocene rhinoceros bitten by a bear-dog (*Amphicyon giganteus*): Annales de Paléontologie, v. 92, p. 31–39.

Antunes, M.T., Balbino, A.C. and Ginsburg, L., 2006b, Miocene mammalian footprints in coprolites from Lisbon, Portugal: Annales de Paléontologie, v. 92, p. 13-30.

Appel, T.A., 1987, The Cuvier–Geoffrey debate: French biology in the decades before Darwin. Oxford, Oxford University Press, 306 p.

Arambourg, C., 1954, Les poisons Crétaces de Jebel Tselfat (Maroc): Éditions du Service géologique du Maroc Mémoire, v. 118, 188 p.

Araújo, R., Polcyn, M.J., Lindgren, J., Jacobs, L.L., Schulp, A.S., Mateus, O., Gonçalves, A.O. and Morais, M.L., 2015, New aristonectine elasmosaurid plesiosaur specimens from the early Maastrichtian of Angola and comments on paedomorphism in plesiosaurs: Netherlands Journal of Geosciences, v. 94, p. 93-108.

Argant, J. and Bonifay, M.F., 2011, Hyaena coprolites (*Pachycrocuta brevirostris*) from the Ceyssaguet Villafranchian site (Lavoûte-sur-Loire, Haute-Loire, France): Pollen analyses and palaeoenvironmental indications: Quaternaire, v. 22, p. 3-11.

Argyriou, T., Clauss, M., Maxwell, E.E., Furrer, H. and Sánchez-Villagra, M.R., 2016, Exceptional preservation reveals gastrointestinal anatomy and evolution in early actinopterygian fishes: Scientific Reports, v. 6, 18758, doi: 10.1038/srep18758 (2016).

Armitage, I.A. and Gingras, M.K., 2003, Sedimentologic and environmental implications of Atlantic sturgeon (*Acipenser oxyrhynchus*) feeding traces, Bay of Fundy, New Brunswick, Canada: Geological Society of America, Abstracts with Programs, v. 35(6), p. 578.

Arratia, G., 1987, *Anaethaleon* and similar teleosts (Actinopterygii, Pisces) from the Late Jurassic (Tithonian) of southern Germany and their relationships: Palaeontographica, Abtheilung A, v. 200, p. 1-44.

Arriaza, M. C., Aramendi, J., Maté-González, M. A., Yravedra, J. and Stratford, D., 2021, Characterising leopard as taphonomic agent through the use of micro-photogrammetric reconstruction of tooth marks and pit to score ratio: Historical Biology, v. 33, p. 176-185.

Arribas, A., Garrido, G., Viseras, C., Soria, J.M., Pla, S., Solano, J.G., Garcés, M., Beamud, E. and Carrión, J. S., 2009, A mammalian lost world in southwest Europe during the late Pliocene: PLoS ONE, v. 4(9): e7127, doi: org/10.1371/journal.pone.0007127.

Arsenault, M., 1982, *Eusthenopteron foordi*, a predator on *Homalacanthus concinnus* from the Escuminac Formation, Miguasha, Quebec: Canadian Journal of Earth Sciences, v. 19, p. 2214-2217.

Arsenault M. and Janvier P., 1991, The anaspid like craniates of the Escuminac Formation (Upper Devonian) from Miguasha (Quebec, Canada) with remarks on anaspid-petromyzontid relationships; *in* Chang M. M., Liu Y. H. and Zhang G. R., eds., Early vertebrates and related problems of evolutionary biology. Beijing, Science Press, p. 19-44.

Ashley-Ross, M.A. and Gillis, G.B., 2002, A brief history of vertebrate functional morphology: Integrative and Comparative Biology, v. 42, p. 183-189.

Auffenberg, W., 1981, The behavioral ecology of the Komodo Monitor. Gainesville, University Presses of Florida, 406 p.

Augustin, F.J., Matzke, A.T., Csiki-Sava, Z. and Pfretzschner, H.U., 2019, Bioerosion on vertebrate remains from the Upper Cretaceous of the Haţeg Basin, Romania and its taphonomic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 534, doi: org/10.1016/j.palaeo.2019.109318.

Augustin, F. J., Matzke, A. T., Maisch, M. W. and Pfretzschner, H.-U., 2020a, A theropod dinosaur feeding site from the Upper Jurassic of the Junggar Basin, NW China: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 560, doi: org/10.1016/j.palaeo.2020.109999.

Augustin, F.J., Matzke, A.T., Maisch, M.W., Hinz, J.K. and Pfretzschner, H.U., 2020b. The smallest eating the largest: The oldest mammalian feeding traces on dinosaur bone from the Late Jurassic of the Junggar Basin (northwestern China): The Science of Nature, v. 107, p. 1-5.

Averianov, A., Dyke, G., Danilov, I. and Skutschas, P., 2015, The paleoenvironments of azhdarchid pterosaurs localities in the Late Cretaceous of Kazakhstan: ZooKeys, v. 483, p. 59-80.

Avilla, L.S., Fernandes, R. and Ramos, D.F., 2004, Bite marks on a crocodylomorph from the Upper Cretaceous of Brazil: Evidence of social behavior?: Journal of Vertebrate Paleontology, v. 24, p. 971-973.

Avilla, L.S., Machado, H., de Araújo-Júnior, H.I., Mothé, D., Rotti, A., De Oliveira, K., Maldonado, V., Figueiredo, A.M.G., Kinoshita, A. and Baffa, O., 2018, Pleistocene *Equus* (Equidae: Mammalia) from northern Brazil: Evidence of scavenger behavior by ursids on South American horses: Ameghiniana, v. 55, p. 517-530.

Backus, G.J., 1964, The effects of fish-grazing on invertebrate evolution in shallow tropical waters: Occasional Papers of the Allan Hancock Foundation, v. 27, p. 1-34.

Bader, K.S., Hasiotis, S.T. and Martin, L.D., 2009, Application of forensic science techniques to trace fossils on dinosaur bones from a quarry in the Upper Jurassic Morrison Formation, northeastern Wyoming: Palaios, v. 24, p. 140-158.

Baghai-Riding, N.L. and DiBenedetto, J.N., 2001, An unusual dinosaur coprolite from the Campanian Aguja Formation, Texas: Transactions of the Gulf Coast Association of Geological Societies, v. 51, p. 9-20.

Bai, B., Wang, Y., Meng, J., Jin, X., Li, Q. and Li, P., 2011, Taphonomic analyses of an early Eocene *Litolophus* (Perissodactyla, Chalicotherioidea) assemblage from the Erlian Basin, Inner Mongolia, China: Palaios, v. 26, p. 187-196.

Bajdek, P., 2013, Coprolite of a durophagous carnivore from the Upper Cretaceous Godula Beds, Outer Western Carpathians, Poland: Geological Quarterly, v. 57, p. 361-364.

Bajdek, P. and Bienkowska-Wasiluk, M., 2020, Deep-sea ecosystem revealed by teleost fish coprolites from the Oligocene of Poland: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 540, doi: org/10.1016/j.palaeo.2019.109546.

Bajdek, P., Owocki, K. and Niedźwiedzki, G., 2014, Putative dicynodont coprolites from the Upper Triassic of Poland: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 411, p. 1-17.

Bajdek, P., Szczygielski, T., Kapuścińska, A. and Sulej, T., 2019, Bromalites from a turtle-dominated fossil assemblage from the Triassic of Poland: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 520, p. 214-228.

Bajdek, P., Owocki, K., Sennikov, A.G., Golubev, V.K. and Niedźwiedzki, G., 2017, Residues from the upper Permian carnivore coprolites from Vyazniki in Russia-key questions in reconstruction of feeding habits: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 482, p. 70-82.

Bajdek, P., Qvarnström, M., Owocki, K., Sulej, T., Sennikov, A.G., Golubev, V.K. and Niedźwiedzki, G., 2016, Microbiota and food residues including possible evidence of pre-mammalian hair in upper Permian coprolites from Russia: Lethaia, v. 49, p. 455-477.

Baker, A., 1956, The swallowing of stones by animals: Victorian Naturalist, v. 73, p. 2-95.

Bakker, R.T., 1971, Ecology of the brontosaurs: Nature, v. 229, p. 172.

Bakker, R.T., 1980, Dinosaur heresy-dinosaur renaissance why we need endothermic archosaurs for a comprehensive theory of bioenergetic evolution; *in* Thomas, R.D.K. and Olson, E.C., eds., A cold look at the warm-blooded dinosaurs. Boulder, Westview Press, p. 351-462.

Bakker, R.T., 1986, The dinosaur heresies. New York, William Morrow and Company, 481 p.

Bakker, R.T. and Bir, G., 2004, Dinosaur crime scene investigations: Theropod behaviour at Como Bluff, Wyoming, and the evolution of birdness; *in* Currie, P. J., Koppelhus, E.B., Shugar, M.A. and Wright, J.L., eds., Feathered dragons: Studies on the transition from dinosaurs to birds. Indianapolis, Indiana University Press, p. 301–342.

Balch, C. C. and Campling, R. C., 1965, Rate of passage of digesta through the ruminant digestive tract; *in* Dougherty, R.W., Allen, R.S., Burroughs, W., Jacobson, N.L. and McGillard, A.D., eds., Physiology of digestion in the ruminant. London, Butterworth, p. 108-123.

Baldanza, A., Bizzarri, R., Famiani, F., Monaco, P., Pellegrino, R. and Sassi, P., 2013, Enigmatic, biogenically induced structures in Pleistocene marine deposits: A first record of fossil ambergris: Geology, v. 41, p. 1075-1078.

Bambach, R.K., Knoll, A.H. and Wang, S.C., 2004, Origination, extinction, and mass depletions of marine diversity: Paleobiology, v. 30, p. 522-542.

Baranov, V.A., Engel, M.S., Hammel, J., Hörnig, M.K., van de Kamp, T., Zuber, M., and Haug, J.T., 2021, Synchrotron-radiation computed tomography uncovers ecosystem functions of fly larvae in an Eocene forest: Palaeontologia Electronica, v. 24(1): a07 doi: org/10.26879/1129.

Bardack, D., 1965, Anatomy and evolution of chirocentrid fishes: Paleontological Contributions of the University of Kansas, Vertebrata, v. 10, p. 1-88.

Bardet, N., Jagt, J.W.M., Kuypers, M.M.M. & Dorttmgs, R.W., 1998, Shark tooth marks on a vertebra of the mosasaur *Plioplatecarpus marshi* from the late Maastrichtian of Belgium: Publicaties van het Natuurhistorisch Genootschap in Limburg, v. 41, p. 52-55.

Barnes, K.M. and Hiller, N., 2010, The taphonomic attributes of a Late Cretaceous plesiosaur skeleton from New Zealand: Alcheringa, v. 34, p. 333-344.

Barnes, L.G., 1976, Outline of eastern North Pacific fossil cetacean assemblages: Systematic Zoology, v. 25, p. 321-343.

Barnes, L.G. and McLeod, S.A., 1984, The fossil record and phyletic relationships of grey whales; *in* Jones, M. L. and Swartz, S. L., eds., The Gray Whale *Enschrichtius robustus*. New York, Academic Press, p. 3-32.

Barrios-de Pedro, S., Chin, K. and Buscalioni, Á.D., 2020a, The late Barremian ecosystem of Las Hoyas sustained by fishes and shrimps as inferred from coprofabrics: Cretaceous Research, v. 110, p.104409, doi.org/10.1016/j.cretres.2020.104409.

Barrios-de Pedro, S., Osuna, A. and Buscalioni, Á.D., 2020b, Helminth eggs from Early Cretaceous faeces: Scientific Reports, v. 10(1), 18747, doi.org/10.1038/s41598-020-75757-4.

Barrios-de Pedro, S., Poyato-Ariza, F.J., Moratalla, J.J. and Buscalioni, Á.D., 2018, Exceptional coprolite association from the Early Cretaceous continental Lagerstätte of Las Hoyas, Cuenca, Spain: PLoS ONE, v. 13(5): e0196982, doi.org/10.1371/journal.pone.0196982.

Barrios-de Pedro, S., Rogers, K.M., Alcorlo, P. and Buscalioni, Á.D., 2020c, Food web reconstruction through isotopic compositions of fossil faeces: Insights into the ecology of a late Barremian freshwater ecosystem (Las Hoyas, Cuenca, Spain): Cretaceous Research, v. 108, doi: org/10.1016/j.cretres.2019.104343.

Bartels, C., Briggs, D.E.G. and Brassel, G., 1998, The fossils of the Hunsrück Slate: Marine life in the Devonian. Cambridge, Cambridge University Press, 309 p.

Barthel, K.W., 1978, Solnhofen: Ein Blick in der Erdgeschichte. Thun, Ott Verlag, 393 p.

Barthel, K.W. and Janicke, V., 1970, Aptychen als Verdauungsrückstand – Ein Fund aus den Solnhofener Plattenkalken, unteres Untertithon, Bayern: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 1970, p. 65-68.

Barthel, K.W., Swinburne, N.H.M., and Conway Morris, S., 1990, Solnhofen. A study in Mesozoic palaeontology. Cambridge, Cambridge University Press, 236 p.

Bartholommäus, W. A., Reich, M., Krüger, F. J., Ansorje, J., Wings, O., 2004, Das Liefergebeit der Magensteine von Baddeckenstedt: Bochumer Geowissenschaftliche Arbeiten, v. 4, p. 103-131.

Bartley, K.J., 2005, A taphonomic study of Clarendonian (Miocene) *Teleoceras* (Perissodactyla, Rhinocerotoidea) from the Ogallala Formation, northwestern Kansas [M.S. thesis]: Buffalo, State University of New York at Buffalo, 117 p.

Baumiller, T.K. and Gahn, F.J., 2004, Testing predator-driven evolution with Paleozoic crinoid arm regeneration: Science, v. 305, p.1453-1455.

Baumiller, T.K., Salamon, M.A., Gorzelak, P., Mooi, R., Messing, C.G. and Gahn, F.J., 2010, Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution: Proceedings of the National Academy of Sciences, v. 107, p. 5893-5896.

Bayer, B., 1934, Koprolity z kounovských vrestev na Plzensku: Príroda Brno, v. 27, p. 21-22.

Bazzi, M., Campione, N.E., Ahlberg, P.E., Blom, H. and Kear, B.P., 2021, Tooth morphology elucidates shark evolution across the end-Cretaceous mass extinction: PLoS Biol, v. 19(8): e3001108, doi.org/10.1371/journal.pbio.3001108.

Beattie, R.G. and Avery, S., 2012, Palaeoecology and palaeoenvironment of the Jurassic Talbragar Fossil Fish Bed, Gulgong, New South Wales, Australia: Alcheringa, v. 36, p. 453-468.

Becker, M.A., Chamberlain, J.A. and Goldstein, L., 2006, Evidence for a shark-bitten turtle costal from the lowermost Navesink Formation (Campanian-Maastrichtian), Monmouth County, New Jersey: Northeastern Geology and Environmental Sciences, v. 28, p. 174-181.

Behrensmeyer, A. K. and Hill, A. P. eds., 1980, Fossils in the making: Vertebrate taphonomy and paleoecology. Chicago, University of Chicago Press, 338 p.

Behrensmeyer, A. K., Kidwell, S. M. and Gastaldo, R. A., 2000, Taphonomy and paleobiology: Paleobiology, v. 26, p. 103–147.

Beintema, A.J., 1991, Penguins shed stomach linings: Nature, v. 352, p.480-481.

Bell, G. L. Jr. and Barnes, K.R., 2007, First record of stomach contents in *Tylosaurus nepaeolicus* and comments on predation among Mosasauridae: Second Mosasaur Meeting Abstract Booklet and Field Guide. Hays, Kansas, Sternberg Museum of Natural History, p. 9-10.

Bell, G.L. Jr. and Martin, J.E., 1995, Direct evidence of aggressive intraspecific competition in *Mosasaurus conodon* (Mosasauridae: Squamata): Journal of Vertebrate Paleontology, v. 15 (supplement to no.3), p. 18A.

Bell, G.L., Barnes, K.R. and Polcyn, M.J., 2013, Late Cretaceous mosasauroids (Reptilia, Squamata) of the Big Bend region in Texas, USA: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 103, p. 571-581.

Bell, J., Holden, J., Pettigrew, T.H. and Sedman, K.W., 1979, The Marl Slate and basal Permian breccia at Middridge, Co. Durham: Proceedings of the Yorkshire Geological Society, v. 42, p. 439-460.

Bell, P.R., 2010, Palaeopathological changes in a population of *Albertosaurus sarcophagus* from the Upper Cretaceous Horseshoe Canyon Formation of Alberta, Canada: Canadian Journal of Earth Sciences, v. 47, p. 1263-1268.

Bell, P.R. and Campione, N.E., 2014, Taphonomy of the Danek Bonebed: A monodominant *Edmontosaurus* (Hadrosauridae) bonebed from the Horseshoe Canyon Formation, Alberta: Canadian Journal of

Earth Sciences, v. 51, p. 992-1006.

Bell, P.R. and Currie, P.J., 2010, A tyrannosaur jaw bitten by a confamilial: Scavenging or fatal agonism?: Lethaia, v. 43, p. 278-281.

Bell, P.R., Currie, P.J. and Lee, Y.N., 2012, Tyrannosaur feeding traces on *Deinocheirus* (Theropoda:?Ornithomimosauria) remains from the Nemegt Formation (Late Cretaceous), Mongolia: Cretaceous Research, v. 37, p. 186-190.

Beltan, L., 1977, La parturition d'un Actinopterygian de l'Eotrias du nord-ouest de Madagascar: Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris, Série D, v. 284, p. 2223-2225.

Beltrame, M.O., Fugassa, M.H., Sauthier, D.U. and Sardella, N.H., 2014, Paleoparasitological study of rodent coprolites from "Los Altares" paleontological site, Patagonia, Argentina: Quaternary International, v. 352, p. 59-63.

Beltrame, M.O., Sardella, N.H., Fugassa, M.H. and Barberena, R., 2012, Palaeoparasitological analysis of rodent coprolites from the Cueva Huenul 1 archaeological site in Patagonia (Argentina): Memorias do Instituto Oswaldo Cruz, v. 107, p. 604-608.

Belvedere, M., Franceschi, M., Morsilli, M., Zoccarato, P.L. and Mietto, P., 2011, Fish feeding traces from middle Eocene limestones (Gargano Promontory, Apulia, southern Italy): Palaios, v. 26, p. 693-699.

Bender, P.A. and Hancox, P.J., 2004. Newly discovered fish faunas from the Early Triassic, Karoo Basin, South Africa, and their correlative implications: Gondwana Research, v. 7, p. 185-192.

Bengtson, S., 2002, Origins and early evolution of predation: Paleontological Society Papers, v. 8, p. 289-318.

Bengtson, S. and Zhao, Y., 1992, Predatorial borings in late Precambrian mineralized exoskeletons: Science, v. 257, p. 367-369.

Bennett, M.R., Doyle, P., and Mather, A.E., 1996, Dropstones: Their origin and significance: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 121, p. 331-339.

Bennett, S.C. 2001, The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*: Palaeontographica, Abteilung A, v. 260, p. 1-153.

Bennett, S.C., 2014, A new specimen of the pterosaur *Scaphognathus crassirostris*, with comments on constraint of cervical vertebrae number in pterosaurs: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 271, p. 327-348.

Benton, M.J., Minter, N.J. and Posmosanu, E., 2006, Dwarfing in ornithopod dinosaurs from the Early Cretaceous of Romania; *in* Csiiki, Z., ed., Mesozoic and Cenozoic vertebrates and paleoenvironments; tributes to the career of Prof. Dan Grigorescu. Bucharest, Ars Docendi, p. 79-87.

Benton, R.C., Terry Jr, D.O., Evanoff, E. and McDonald, H.G., 2015, The White River badlands: Geology and paleontology. Bloomington, Indiana University Press, 223 p.

Benz, S., 1980, The stratigraphy and paleoenvironment of the Triassic Moenkopi Formation at Radar Mesa, Arizona [M.S. thesis]: Flagstaff, Northern Arizona University, 43 p.

Berckheimer, F., 1928, Magensteine bei Mystriosaurien aus dem Oberlias Deutstchland: Paläontologische Zeitschrift, v. 10, p. 63-68.

Berger, L.R. and Clarke, R.J., 1995, Eagle involvement in accumulation of the Taung child fauna: Journal of Human Evolution, v. 29, p. 275-299.

Bermúdez-Rochas, D.D., Delvene, G. and Ruiz-Omeñaca, J.I., 2013, Evidence of predation in Early Cretaceous unionoid bivalves from freshwater sediments in the Cameros Basin, Spain: Lethaia, v. 46, p. 57-70.

Bertling, M., Braddy, S. J., Bromley, R. G., Demathieu, G. R., Genise, J., Mikuláš, R., Nielsen, J. K., Nielsen, K. S. S., Rindsberg, A. K., Schlirf, M., Uchman, A., 2006, Names for trace fossils: A uniform approach: Lethaia, v. 39, p. 265-286.

Bertrand, C.E., 1903, Les coprolithes de Bernissart. I. Partie: Les coprolithes qui ont ete attribues aux *Iguanodons*: Mémoire du Musée Royal d'Histoire Naturelle de Belgique, Brussels, v. 1, p. 1-154.

Bestwick, J., Unwin, D. M. and Purnell, M. A., 2019, Dietary differences in archosaur and lepidosaur reptiles revealed by dental microwear textural analysis: Scientific Reports, v. 9(1), p.1-11: 9:11691, doi: org/10.1038/s41598-019-48154-9.

Bestwick, J., Jones, A. S., Purnell, M. A. and Butler, R. J., 2020a. Dietary constraints of phytosaurian reptiles revealed by dental microwear textural analysis: Palaeontology, v. 64, p. 119–136.

Bestwick, J., Unwin, D.M., Butler, R.J. and Purnell, M. A., 2020b*,* Dietary diversity and evolution of the earliest flying vertebrates revealed by dental microwear texture analysis: Nature Communications, v. 11**,** 5293, doi: org/10.1038/s41467-020-19022-2.

Betancourt, J.L., Van Devender, T.R. and Martin, P.S., eds., 2010, Packrat middens: The last 40,000 years of biotic change. Tucson, The University of Arizona Press, 467 p.

Bi, D.-C., 1986, Ecological explanation of some abnormal phenomena in fossil conchostracan shells: Selected papers from the 13th and 14th Annual Conventions of the Paleontological Society of China. Hefei, Anhui Science and Technology Publishing House, p. 229-235.

Bianucci, G. and Gingerich, P.D., 2011, *Aegyptocetus tarfa*, n. gen. et sp. (Mammalia, Cetacea), from the middle Eocene of Egypt: clinorhynchy, olfaction, and hearing in a protocetid whale: Journal of Vertebrate Paleontology, v. 31, p. 1173–1188.

Bianucci, G., Sorce, B., Storai, T., Landini, W., 2010, Killing in the Pliocene: Shark attack on a dolphin from Italy: Palaeontology, v. 53, p. 457–470.

Bianucci, G., Bisconti, M., Landini, W., Storai, T., Zuffa, M., Giuliani, S. and Mojetta, A., 2002, Trophic interaction between white shark (*Carcharodon carcharias*) and cetaceans: A comparison between Pliocene and recent data from central Mediterranean Sea; *in* Vacchi, M., La Mesa, G., Serena, F. and Séret, B., eds., Proceedings of the IV European Elasmobranch Association Meeting, Livono Italy. Abbeville, Imprimerie F. Paillart, p. 33-48.

Bianucci, G., Collareta, A., Bosio, G., Landini, W., Gariboldi, K., Gioncada, A., Lambert, O., Malinverno, E., de Muizon, C., Varas-Malca, R. and Villa, I.M., 2018, Taphonomy and palaeoecology of the lower Miocene marine vertebrate assemblage of Ullujaya (Chilcatay Formation, East Pisco Basin, southern Peru): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 511, p. 256-279.

Bigelow, P.K., 1994, Occurrence of a squaloid shark (Chondrichthyes: Squaliformes) with the pinniped *Allodesmus* from the upper Miocene of Washington: Journal of Paleontology, v. 68, p. 680-684.

Binford, L.R., 1981, Bones: Ancient men and modern myths. New York, Academic Press, 320 p.

Bingham-Koslowski, N., Grey, M., Ehrman, J.M. and Pufahl, P., 2021, Investigating the relationship between the elemental composition of coprolites and trophic level: A brief digest of late Carboniferous coprolites from the Joggins Formation, Nova Scotia, Canada: Atlantic Geology, v. 57, p. 107-108.

Bird, R.T., 1954, We captured a "live" brontosaur: National Geographic, v. 105, p. 707-722.

Bird, R.T., 1985, Bones for Barnum Brown. Fort Worth, Texas Christian University Press, 225 p.

Bisconti, M., 2010, New description of '*Megaptera*' *hubachi* Dathe, 1983 based on the holotype skeleton held in the Museum für Naturkunde, Berlin: Quaderni del Museo di Storia Naturale di Livorno, v. 23, p. 37-68.

Bisconti, M. and Bosselaers, M., 2016, *Fragilicetus velponi*: A new mysticete genus and species and its implications for the origin of Balaenopteridae (Mammalia, Cetacea, Mysticeti): Zoological Journal of the Linnean Society, v. 177, p. 450-474.

Bishop, G. A., 1972, Crab bitten by a fish from the Upper Cretaceous Pierre Shale of South Dakota: Geological Society of America

Bulletin, v. 83, p. 3823-3826.

Bishop, G.A., 1975, Traces of predation; *in* Frey, R. W., ed., The study of trace fossils. New York, Springer, p. 261-287.

Bishop, W.W., 1964, More fossil primates and other Miocene mammals from north-east Uganda: Nature, v. 203, p.1327-1331.

Bjork, P.R. 1981, Food habits of mosasaurs from the Pierre Shale of South Dakota: Geological Society of America, Abstracts with Programs, v. 13(4), p. 191.

Blieck, A., 2017, Heterostracan vertebrates and the Great Eodevonian Biodiversification Event–an essay: Palaeobiodiversity and Palaeoenvironments, v. 97, p. 375–390.

Bloch, J. I. and Boyer, D.M., 2001, Taphonomy of small mammals in freshwater limestones from the Paleocene of the Clarks Fork Basin: University of Michigan Museum of Paleontology Papers, v. 33, p.185-198.

Blumenschine, R. J., 1986, Carcass consumption sequences and the archaeological distinction of scavenging and hunting: Journal of Human Evolution, v. 15, p. 639-659.

Blumenschine, R. J., 1988, An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages: Journal of Archaeological Science, v. 15, p. 483-502.

Boaz, N. T. and Hampel, J., 1978, Strontium content of fossil tooth enamel and diet of early hominids: Journal of Paleontology, v. 52, p. 928–933.

Boaz, N.T., Ciochon, R.L., Xu, Q. and Liu, J., 2000, Large mammalian carnivores as a taphonomic factor in the bone accumulation at Zhoukoudian: Acta Anthropologica Sinica, v. 19 (supplement), p. 224-234.

Boaz, N.T., Ciochon, R.L., Xu, Q. and Liu, J., 2004, Mapping and taphonomic analysis of the *Homo erectus* loci at Locality 1 Zhoukoudian, China: Journal of Human Evolution, v. 46, p. 519-549.

Bochenski, Z.M., Tomek, T., Boev, Z. and Mitev, I., 1993, Patterns of birdbone fragmentation in pellets of the tawny owl (*Strix aluco*) and the eagle bowl (*Bubo bubo*) and their taphonomic implications: Acta Zoologica Cracoviensia, v. 36, p. 313–328.

Bochenski, Z.M., Huhtala, K., Jussila, P., Pulliainen, E., Tornberg, R. and Tunkkari, P.S., 1998, Damage to bird bones in pellets of Gyrfalcon *Falco rusticolus*: Journal of Archaeological Science, v. 25, p. 425–433.

Boeskorov, G.G., Potapova, O.R., Mashchenko, E.N., Protopopov, A.V., Kuznetsova, T.V., Agenbroad, L. and Tikhonov, A.N., 2014, Preliminary analyses of the frozen mummies of mammoth (*Mammuthus primigenius*), bison (*Bison priscus*) and horse (*Equus* sp.) from the Yana-Indigirka Lowland, Yakutia, Russia: Integrative Zoology v. 9, p. 471-480.

Boeskorov, G.G., Lazarev, P.A., Sher, A.V., Davydov, S.P., Bakulina, N.T., Shchelchkova, M.V., Binladen, J., Willerslev, E., Buigues, B. and Tikhonov, A.N., 2011, Woolly rhino discovery in the lower Kolyma River: Quaternary Science Reviews, v. 30, p. 2262-2272.

Boeskorov, G.G., Potapova, O.R., Protopopov, A.V., Plotnikov, V.V., Agenbroad, L.D., Kirikov, K.S., Pavlov, I.S., Shchelchkova, M.V., Belolyubskii, I.N., Tomshin, M.D. and Kowalczyk, R., 2016, The Yukagir Bison: The exterior morphology of a complete frozen mummy of the extinct steppe bison, *Bison priscus* from the early Holocene of northern Yakutia, Russia: Quaternary International, v. 406, p.94-110.

Boessenecker, R.W. and Perry, F.A., 2011, Mammalian bite marks on juvenile fur seal bones from the late Neogene Purisima Formation of central California: Palaios, v. 26, p. 115–120.

Boessenecker, R.W., Ahmed, E. and Geisler, J.H., 2017, New records of the dolphin *Albertocetus meffordorum* (Odontoceti: Xenorophidae) from the lower Oligocene of South Carolina: Encephalization, sensory anatomy, postcranial morphology, and ontogeny of early odontocetes: PLoS ONE, v. 12(11): e0186476, doi: org/10.1371/journal.pone.0186476.

Bohatý, J., 2008, Classification of pre- and postmortem ossicular modifications of the cupressocrinitid skeletons (Crinoidea) ; in Kroh, A. and Schmid, B., eds., Devonian 4, Arbeitstreffen deutschsprachiger Echinodermenforscher, 4th Workshop of German and Austrian Echinoderm Research Abstracts, Naturhistorisches Museum, Wien, p. 3-13.

Bohatý, J., 2009, Pre-and postmortem skeletal modifications of the Cupressocrinitidae (Crinoidea, Cladida): Journal of Paleontology, v. 83, p. 45-62.

Böhme, M., Prieto, J., Schneider, S., Hung, N. V. and Tran, D. N., 2011, The Cenozoic on-shore basins of Northern Vietnam: Biostratigraphy, vertebrate and invertebrate faunas: Journal of Asian Earth Sciences, v. 40, p. 672-687.

Boles, Z.M., 2016, Vertebrate taphonomy and paleoecology of a Cretaceous-Paleogene marine bonebed [Ph.D. dissertation]: Philadelphia, Drexel University, 263 p.

Boles, Z. and Lacovara, K., 2013, Evidence of extensive scavenging/predation by Late Cretaceous marine organisms from the basal Hornerstown Formation, New Jersey, USA: Journal of Vertebrate Paleontology (supplement to no. 3), p. 89A.

Bon, C., Berthonaud, V., Maksud, F., Labadie, K., Poulain, J., Artiguenave, F., Wincker, P., Aury, J. M. and Elalouf, J. M., 2012, Coprolites as a source of information on the genome and diet of the Cave Hyena: Proceedings of the Royal Society B: Biological Sciences, v. 279, p. 2825-2830.

Bonaparte, J. F. and Mateus, O., 1999, A new diplodocid, *Dinheirosaurus lourinhanensis* gen. et. sp. nov., from the Late Jurassic beds of Portugal: Revista del Museo Argentino de Ciencias Naturales, v. 5, p. 13-29.

Bond, G., 1955, A note on dinosaur remains from the Forest Sandstone: Occasional Papers of the National Museum of Rhodesia, v. 2, p. 797.

Bond, P. N. and Saunders, W. B., 1989, Sublethal injury and shell repair in Upper Mississippian ammonoids: Paleobiology, v. 15, p. 414-428.

Bonde, N., 1987, Moler: Its origin and its fossils especially fishes. Skamol, Nykøbing Mors, 53 p.

Boreske, J. R. Jr., 1974, A review of North American amiid fishes: Museum of Comparative Zoology, Bulletin, v. 146, p. 1-87.

Borsuk-Bialynicka, M., 1977, A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n., sp. n. from the Upper Cretaceous of Mongolia: Palaeontologia Polonica, v. 37, p. 5-64.

Borszcz, T. and Zatoń, M., 2013, The oldest record of predation on echinoids: Evidence from the Middle Jurassic of Poland: Lethaia, v. 46, p.141-145.

Botfalvai, G., Prondvai, E. and Ősi, A., 2014, Inferred bite marks on a Late Cretaceous (Santonian) bothremydid turtle and a hylaeochampsid crocodilian from Hungary: Cretaceous Research, v. 50, p. 304-317.

Böttcher, R., 1989, Über die Nahrung eines *Leptopterygius* (Ichthyosauria, Reptilia) aus dem süddeutschen Posidonienschiefer (Unterer Jura) mit Bemerkungen über den Magen der Ichthyosaurier: Stuttgarter Beiträge zur Naturkunde, Serie B, v. 155, p. 1-19.

Böttcher, R., 1990, Neue Erkenntnisse über die Fortpflanzungsbiologie der Ichthyosaurier (Reptilia): Stuttgarter Beiträge zur Naturkunde, Serie B, v. 164, p. 1-51.

Bottema, S., 1975. The use of gastroliths in archaeology; *in* Clasen, A.T., ed., Archaeological studies. Amsterdam, North Holland, p. 397-406.

Boucot, A.J., 1990, Evolutionary paleobiology of behavior and coevolution. Amsterdam, Elsevier, 735 p.

Boucot, A. J. and Janis, C., 1983, Environment of the early Paleozoic vertebrates: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 41, p. 251-287.

Boucot, A. J. and Poinor, G. O., Jr., 2010, Fossil behavior compendium. Boca Raton, CRC Press, 391 p.

Bourgon, N., Jaouen, K., Bacon, A.-M., Jochum, K.P., Dufour, E., Duringer, P., Ponche, J.-L., Joannes-Boyau, R., Boesch, Q., Antoine, P.-O., Hullot, M., Weis, U., Schulz-Kornas, E., Trost, M., Fiorillo, D., Demeter, F., Patole-Edoumba, E., Shackelford, L.L., Dunn, T.E., Zachwieja, A., Duangthongchit, S., Sayavonkhamdy, T., Sichanthongtip, P., Sihanam, D., Souksavatdy, V., Hublin, J.-J. and Tütken, T., 2020, Zinc isotopes in Late Pleistocene fossil teeth from a Southeast Asian cave setting preserve paleodietary information: Proceedings of the National Academy of Sciences, v. 117, p. 4675-4681.

Bowen, J. J., 2013, The neoichnology of juliform millipedes and upper Monongahela to lower Dunkard Group paleosols: A multi-proxy approach to paleolandscape variability [M.S. thesis]: Athens, Ohio University, 305 p.

Bowman, R. E., 1986, Effect of regurgitation on stomach content data of marine fisheries: Environmental Biology of Fishes, v. 16, p. 171-181.

Boy, J. A., 1993, Synopsis of the tetrapods from the Rotliegend (Lower Permian) in the Saar-Nahe Basin (SW-Germany); *in* Heidtke, U.H.J., ed., New research on Permo-Carboniferous faunas. Bad Durkheim, Pollichia, p. 155-169.

Boy, J. A., 2003, Paläoeokologische Rekonstruktion von Wirbeltieren: Möglichkeiten und Grenzen: Paläontologische Zeitschrift, v. 77, p. 123-152.

Boy, J. A. and Sues, H.-D., 2000, Branchiosaurs: Larvae, metamorphosis and heterochrony in temnospondyls and seymouriamorphs; *in* Heatwole, H. and Carroll, R. L., eds., Amphibian biology, Volume 4, Palaeontology. Chipping Norton, Surrey Beatty and Sons, p. 1151–1197.

Boy, J. A., Schoch, R. R. and Lucas, S. G., 2001, The Moenkopi Formation in east-central New Mexico: Stratigraphy and vertebrate fauna: New Mexico Geological Society, Guidebook 52, p. 103-108.

Boyd, C., Starck, E., Welsh, E. and Householder, M., 2013, Bite marks on nimravid crania and implications for intraclade interactions within Nimravidae (Mammalia: Feliformia): Geological Society of America, Abstracts with Programs, v. 45, p. 755.

Boyd, C.A., Drumheller, S.K. and Gates, T.A., 2013, Crocodyliform feeding traces on juvenile ornithischian dinosaurs from the Upper Cretaceous (Campanian) Kaiparowits Formation, Utah: PLoS ONE, v. 8(2): e57605, doi:10.1371/journal.pone.0057605.

Boyd, D.W. and Newell, N.D., 1972, Taphonomy and diagenesis of a Permian fossil assemblage from Wyoming: Journal of Paleontology, v. 46, p.1-14.

Boylan, P. J., 1997, William Buckland and the foundations of taphonomy and palaeoecology: Archives of Natural History, v. 24, p. 361-372.

Brachaniec, T., Leko, K. and Wieczorek, A., 2016, Regurgitalite from the Silurian of Holy Cross Mountains, southern Poland: Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, v. 280, p. 331-334.

Brachaniec, T., Niedźwiedzki, R., Surmik, D., Krzykawski, T., Szopa, K., Gorzelak, P. and Salamon, M.A., 2015, Coprolites of marine vertebrate predators from the Lower Triassic of southern Poland: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 435, p.118-126.

Bradley, W.H., 1946, Coprolites from the Bridger Formation of Wyoming: Their composition and microorganisms: American Journal of Science, v. 244, p. 215-239.

Brain, C. K., 1970. New finds at the Swartkrans australopithecine site: Nature, v. 225, p.1112-1119.

Brain, C.K., 1978, Interpreting the bone accumulations from the Sterkfontein Valley caves: A case study in Quaternary research: Southern African Humanities, v. 23, p.465-68.

Brain, C. K., 1981, The hunters or the hunted? Chicago, University of Chicago Press, 384 p.

Brand, L.R., Goodwin, H.T., Ambrose, P.D. and Buchheim, H.P., 2000, Taphonomy of turtles in the middle Eocene Bridger Formation, SW Wyoming: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 162, p.171-189.

Branson, E.B., 1914, The Devonian fishes of Missouri: The University of Missouri Bulletin, Science Series, v. 2, p. 59-74.

Braunn, P. R., Fonseca, R. C. and Ferigolo, J., 2001, Evidências de possível necrofagia em costelas de *Jachaleria candelariensis* (Therapsida, Dicynodontia) do Triássico Superior do Estado do Rio Grande do Sul, Brasil: XVII Congresso Brasieiro Paleontologia, Resumos, Rio Branca, Universidade Federale do Acre, p. 49.

Braz, H. B. and Marques, O. A., 2016, Tail-first ingestion of prey by the false coral snake, *Erythrolamprus aesculapii*: Does it know where the tail is?: Salamandra, v. 52, p. 211-214.

Brazeau, M. D. and Friedman, M., 2015, The origin and early phylogenetic history of jawed vertebrates: Nature, v. 520, p. 490-497.

Brett, C.E., Walker, S.E., Kowalewski, M. and Kelley, P.H., 2002, Predators and predation in Paleozoic marine environments: Paleontological Society Papers, v. 8, p.93-118.

Briggs, D., 1992, Conodonts: A major extinct group added to the vertebrates: Science, v. 256, p. 1285–1286.

Briggs, D.E.G., Liu, H.P., Mckay, R.M. and Witzke, B.J., 2015, Bivalved arthropods from the Middle Ordovician Winneshiek Lagerstätte, Iowa, USA: Journal of Paleontology, v. 89, p. 991-1006.

Brink, K. S., Campione, N. E. and Hawthorn, J. R., 2013, Amniote faunal revision of the Pictou Group (Permo-Carboniferous), Prince Edward Island, Canada: Comptes Rendus Palevol, v. 12, p. 473-485.

Brink, K. S., Maddin, H. C., Evans, D. C. and Reisz, R. R., 2015, Re-evaluation of the historic Canadian fossil *Bathygnathus borealis* from the early Permian of Prince Edward Island: Canadian Journal of Earth Sciences, v. 52, p. 1109-1120.

Brinkmann, W., 2004, Mixosaurier (Reptilia, Ichthyosauria) mit Quetschzähnen aus der Grenzbitumenzone (Mitteltrias) des Monte San Giorgio (Schweiz, Kanton Tessin): Schweizerische Paläontologische Abhandlungen, v. 124, p. 1-84.

Brochu, C. A., 2003, Osteology of *Tyranosaurus rex*: Insights from a nearly complete skeleton and high-resolution tomagraphic analysis of the skull: Journal of Vertebrate Paleontology, v. 22, (supplement 4), p. 1-138.

Brochu, C.A., Njau, J., Blumenschine, R.J., Densmore, L.D., 2010, A new horned crocodile from the Plio-Pleistocene hominid sites at Olduvai Gorge, Tanzania: PLoS ONE, v. 5(2): e9333, doi:10.1371/journal.pone.0009333.

Broda, K., Wolny, M. and Zatoń, M., 2015, Palaeobiological significance of damaged and fragmented thylacocephalan carapaces from the Upper Devonian of Poland: Proceedings of the Geologists' Association, v. 126, p. 589-598.

Broili, E., 1938, Beobachtungen an *Pterodactylus*: Sitzungberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, v. 1938, p. 139-154.

Bromley, R.G., 1996, Trace fossils: Biology and taphonomy (Second Edition). London, Unwin Hyman, 361 p.

Bromley, R.G. and Jacobsen, A.R., 2008, Ichnotaxa for bite traces of tetrapods: A new area of research or a total waste of time?; *in* Uchman, A., ed., Abstract Book and the Intra-Congress Field Trip Guidebook, Second International Congress on Ichnology, p. 20.

Brooks, M. J., Moore, C. R. and Ivester, A. H., 2012, From gizzards to gastroliths: Early to mid-Holocene intensive harvest and processing of migratory waterfowl at a Carolina Bay in the upper coastal plain of South Carolina: Legacy, v. 16, p. 22-25.

Broughton, P.L., 1981, Casts of vertebrate internal organs from the Upper Cretaceous of western Canada: Journal of Geology, v. 89, p. 741-749.

Broughton, P.L., 2017, Enigmatic origin of massive Late Cretaceous-to-Neogene coprolite-like deposits in North America: A novel palaeobiological alternative to inorganic morphogenesis: Lethaia, v. 50, p. 194–216.

Broughton, P. L., Simpson, F. and Whitaker, S. H., 1977, Late Cretaceous coprolites from southern Saskatchewan: Comments on excretion, plasticity and nomenclature: Bulletin of Canadian Petroleum Geology, v. 25, p. 1097-1099.

Broughton, P.L., Simpson, F. and Whitaker, S.H., 1978, Late Cretaceous coprolites from western Canada: Palaeontology, v. 21, p. 443-453.

Brown, B., 1904, Stomach stones and the food of plesiosaurs: Science, v. 20, p. 184-185.

Brown, B., 1907, Gastroliths: Science, v. 25, p. 392.

Brown, B., 1941, The last dinosaurs: Natural History, v. 48, p. 290, 294-95.

Brown, B., 1943, Flying reptiles: Natural History, v. 52, p. 104-111.

Brown, C., 1900, Ober das Genus *Hybodus* und seine systematische Stellung: Palaeontographica, v. 46, p. 149-174.

Brown, C.M., 2017, An exceptionally preserved armored dinosaur reveals the morphology and allometry of osteoderms and their horny epidermal coverings: PeerJ, v. 5: e4066, doi: 10.7717/peerj.4066.

Brown, C. M., Currie, P. J. and Therrien, F., 2021a, Intraspecific bite marks in tyrannosaurids provide insight into sexual maturity and evolution of bird-like intersexual display: Paleobiology, 2021, p. 1-32, doi: 10.1017/pab.2021.29.

Brown, C.M., Tanke, D.H. and Hone, D.W.E., 2021b, Rare evidence for 'gnawing-like' behavior in a small-bodied theropod dinosaur: PeerJ, v. 9: e11557, doi:org/10.7717/peerj.11557.

Brown, C.M., Greenwood, D.R., Kalyniuk, J.E., Braman, D.R., Henderson, D.M., Greenwood, C.L. and Basinger, J.F., 2020, Dietary palaeoecology of an Early Cretaceous armoured dinosaur (Ornithischia; Nodosauridae) based on floral analysis of stomach contents. Royal Society Open Science, v. 7: 200305. http://dx.doi.org/10.1098/rsos.200305.

Brown, R. and Lyell, C., 1845, On the geology of Cape Breton: Quarterly Journal of the Geological Society, v. 1, p. 207-213.

Brown, R.W., 1962, Paleocene flora of the Rocky Mountains and Great Plains: U. S. Geological Survey, Professional Paper 375, 119 p.

Brown, S., Higham, T., Slon, V., Pääbo, S., Meyer, M., Douka, K., Brock, F., Comeskey, D., Procopio, N., Shunkov, M. and Derevianko, A., 2016, Identification of a new hominin bone from Denisova Cave, Siberia using collagen fingerprinting and mitochondrial DNA analysis: Scientific Reports, v. 6, p. 1-8, 23559 (2016), doi: org/10.1038/srep23559.

Brown-Sarracino, J., Peckol, P., Curran, A. and Robbart, M., 2007, Spatial variation in sea urchins, fish predators, and bioerosion rates on coral reefs of Belize: Coral Reefs, v. 26, p. 71-78.

Brownstein, C.D., 2018, Trace fossils on dinosaur bones reveal ecosystem dynamics along the coast of eastern North America during the latest Cretaceous: PeerJ, v. 6: e4973, doi:10.7717/peerj.4973.

Brownstein, C.D. and Bissell, I., 2021, An elongate hadrosaurid forelimb with biological traces informs the biogeography of the Lambeosaurinae: Journal of Paleontology, v. 95, p. 367-375.

Brunnschweiler, J.M., Andrews, P.L.R., Southall, E.J., Pickering, M. and Sims, D.W., 2005, Rapid voluntary stomach eversion in a free-living shark: Journal of Marine Biology, v. 85, p. 1141-1144.

Brunton, C.H.C., 1966, Predation and shell damage in a Visean brachiopod fauna: Palaeontology, v. 9, p. 355-359.

Brusatte, S.L., Young, M.T., Challands, T.J., Clark, N.D., Fischer, V., Fraser, N.C., Liston, J.J., MacFadyen, C.C., Ross, D.A., Walsh, S. and Wilkinson, M., 2015, Ichthyosaurs from the Jurassic of Skye, Scotland: Scottish Journal of Geology, v. 51, p. 43-55.

Bryan, K., 1931, Wind-worn stones or ventifacts–a discussion and bibliography: Reprint and Circular Series National Research Council [Report on Sedimentation 1929-1930], v. 98, p. 29-50.

Bryant, H. N. and Russell, A. P., 1992, The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa: Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, v. 337, p. 405-418.

Bryant, V. M., 1969, Late full-glacial, and post-glacial pollen analysis of Texas sediments [Ph.D. dissertation]: Austin, University of Texas, 148 p.

Bryant, V. M., 1974, Prehistoric diet in southwest Texas. The coprolite evidence: American Antiquity, v. 39, p. 407-420.

Bryant, V. M., 1975, Pollen as an indicator of prehistoric diets in Coahuila, Mexico: Bulletin of the Texas Archaeological Society, v. 46, p. 87-106.

Bryant, V. M., 1994, Callen's legacy; *in* Sobolik, K.D., ed., The diet and health of prehistoric Americans: Carbondale, Southern Illinois University Press, Center for Archaeological Investigations, Occasional Paper No. 22. p. 151-160.

Bryant, V. M., Jr. and Reinhard, K. J., 2012, Coprolites and archaeology: The missing links in understanding human health: New Mexico Museum of Natural History and Science, Bulletin 57, p. 379-387.

Buatois, L.A. and Mángano, M G. 2011, Ichnology: Organism-substrate interactions in space and time. Cambridge, Cambridge University Press, 358 p.

Buatois, L.A. and Mángano, M.G., 2016a, Ediacaran ecosystems and the dawn of animals; *in* Mángano, M.G. and Buatois, L.A., eds., The trace-fossil record of major evolutionary events. Volume 1: Precambrian and Paleozoic. Topics in Geobiology 40. Dordrecht, Springer, p. 27-72.

Buatois, L.A. and Mángano, M.G., 2016b, Recurrent patterns and processes: The significance of ichnology in evolutionary paleoecology; *in* Mángano, M. G. and Buatois, L. A., eds., The trace-fossil record of major evolutionary events. Volume 2: Mesozoic and Cenozoic. Topics in Geobiology 40. Dordrecht, Springer, p. 449-473.

Buatois, L.A., Carmona, N.B., Curran, H.A., Netto, R.G., Mángano, M.G. and Wetzel, A., 2016, The Mesozoic marine revolution; *in* Mángano, M.G. and Buatois, L.A., eds., The trace-fossil record of major evolutionary events. Volume 2: Mesozoic and Cenozoic. Topics in Geobiology 40. Dordrecht, Springer, p. 19-134.

Buchy, M.C., 2007, Mesozoic marine reptiles from north-east Mexico: Description, systematics, assemblages and palaeobiogeography [Ph.D. dissertation]: Karlsruhe, University of Karlsruhe, 87 p.

Buchy, M.C., Taugourdeau, P. and Janvier, P., 2004, Stomach contents of a Lower Triassic ichthyosaur from Spitzbergen: Oryctos, v. 5, p. 47-55.

Buchy, M.-C., Vignaud, P., Frey, E., Stinnesbeck, W. and González, A.H., 2006, A new thalattosuchian crocodyliform from the Tithonian (Upper Jurassic) of north-eastern Mexico: Comptes Rendus Palevol, v. 5, p. 785-794.

Buckland, W., 1822, Account of an assemblage of fossil teeth and bones of elephant, rhinoceros, hippopotamus, bear, tiger and hyaena, and sixteen other animals; discovered in a cave at Kirkdale, Yorkshire, in the year 1821; with a comparative view of five similar caverns in various parts of England, and others on the continent: Philosophical Transactions of the Royal Society of London, v. 112, p. 171-236.

Buckland, W., 1824, Reliquiae diluvianae; or, Observations on the organic remains contained in caves, fissures, and Diluvial Gravel, and on other geological phenomena, attesting the action of an Universal Deluge. London, J. Murray, 303 p.

Buckland, W., 1827, Observations on the bones of hyaenas and other animals on the cavern of Lunel near Montpelier, and in the adjacent strata of marine formation: Proceedings of the Geological Society of London, v. 1, p. 3-6.

Buckland, W., 1829, [A paper by Dr. Buckland]: Proceedings of the Geological Society of London, v. 1, p. 142-143.

Buckland, W., 1830, On the discovery of a new species of Pterodactyle, and of fossil inks and pens, in the Lias of Lyme Regis; also of coprolites or fossil faeces in the Lias at Lyme Regis, and Westbury-on-Severn, and elsewhere, in formations of all ages, from the Carboniferous Limestone to the Diluvium: Edinburgh New Philosophical Journal, v. January-April 1830, p. 21-26.

Buckland, W., 1835, On the discovery of coprolites, or fossil faeces, in the Lias at Lyme Regis, and in other formations: Transactions of the Geological Society of London, v. 3 (series 2), p. 223-238.

Buckland, W., 1836, Geology and mineralogy considered with reference to natural theology. The Bridgewater Treatises on the power, wisdom and goodness of God as manifested in the Creation. London, Pickering, 2 volumes, 599 p. and 128 p.

Buckland, W., 1858, Geology and Mineralogy considered with reference to Natural Theology. The Bridgewater Treatises on the power, wisdom and goodness of God as manifested in the Creation (Third Edition). Treatise VI. London, Pickering, 2 volumes, 552 p. and 143 p.

Budziszewska-Karwowska E., Bujok, A. and Sadlok, G., 2010, Bite marks on an Upper Triassic dicynodontid tibia from Zawiercie, Kraków-Częstochowa Upland, southern Poland: Palaios, v. 25, p. 415-421.

Buffetaut, E., 1979, The evolution of the crocodilians: Scientific American, v. 241(4), p. 124-132.

Buffetaut, E., 1982, Radiation évolutive, paléoécologie et biogéographie des crocodiliens mesosuchiens: Mémoires de la Sociéte Géologique de France, v. 60(142), 88 p.

Buffetaut, E., 1983, Wounds on the jaw of an Eocene mesosuchian crocodilian as possible evidence for the antiquity of crocodilian intraspecific fighting behavior: Paläontologische Zeitschrift, v. 57(1-2), p. 143-145.

Buffetaut, E. and Ingavat, R., 1980, A new crocodilian from the Jurassic of Thailand, *Sunosuchus thailandicus* n. sp. (Mesosuchia, Goniopholididae), and the palaeogeographical history of South-East Asia in the Mesozoic: Geobios, v. 13, p. 879-889.

Buffetaut, E., Martill, D. and Escuillié, F., 2004, Pterosaurs as part of a spinosaur diet: Nature, v. 430, p. 33-33.

Buffetaut, E., Suteethorn, V., Khansubha, S. and Tantiwanit, W., 2007, The ceratopsian dinosaur *Psittacosaurus* in the Early Cretaceous of Southeast Asia: A review of old and recent finds; *in* Tantiwanit, W., ed., Proceedings of the International Conference on Geology of Thailand: Towards Sustainable Development and Sufficiency Economy. Bangkok, Department of Mineral Resources, p. 338-43.

Bukowski, F. and Bond, P., 1989, A predator attacks *Sphenodiscus*: The Mosasaur, v. 4, p. 69-74.

Bunn, H.T. III, 1982, Meat-eating and human evolution: Studies on the diet and subsistence patterns of Plio-Pleistocene hominids in East Africa [Ph.D. dissertation]: Berkeley, University of California, 514 p.

Bunn, H.T., 1983, Comparative analysis of modern bone assemblages from a San hunter gatherer camp in the Kalahari Desert, Botswana, and from a spotted hyena den near Nairobi, Kenya; *in* Clutton-Brock, J. and Grigson, C., eds., Animals and archaeology. Volume I: Hunters and their prey. BAR International Series 283. Oxford, British Archaeological Reports, p. 143–148.

Bunn, H.T., Kroll, E.M., Ambrose, S.H., Behrensmeyer, A.K., Binford, L.R., Blumenschine, R.J., Klein, R.G., McHenry, H.M., O'Brien, C.J. and Wymer, J.J., 1986, Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania [and comments and reply]: Current Anthropology, v. 27, p. 431-452.

Burgin, T., 2000, *Euthynotus* cf. *incognitus* (Actinopterygii, Pachycormidae) als Mageninhalt eines Fischsauriers aus dem Posidonienschiefer Süddeutschlands (Unterer Jura, Lias epsilon): Eclogae Geologicae Helvetiae, v. 93, p. 491-496.

Burmeister, K.C., Flynn, J.J., Parrish, J.M. and Wyss, A.R., 2006, Paleogeographic and biostratigraphic implications of new early Mesozoic vertebrates from Poamay, central Morondava basin, Madagascar: New Mexico Museum of Natural History and Science, Bulletin 37, p. 457-475.

Burney, D.A., Robinson, G.S. and Burney, L.P., 2003, S*porormiella* and the late Holocene extinctions in Madagascar: Proceedings of the National Academy of Sciences of the United States of America, v. 100(19), p. 10800-10805.

Burnham, D.A., 2008, A review of the Early Cretaceous Jehol Group in northeastern China and a revision of the origin of flight paradigm: ORYCTOS, v. 7, p. 27-43.

Burrow, C.J. and Turner, S., 2010, Reassessment of "*Protodus*" *scoticus* from the Early Devonian of Scotland; *in* Elliott, K, Maisey, J. G., Yu, X. and Miao, D., eds., Morphology, phylogeny and paleobiogeography of fossil fishes. Munich, Verlag Dr. Friedrich Pfeil, p. 123-44.

Burrows, C., McCulloch, B. and Trotter, M., 1981, The diet of moas based on gizzard contents samples from Pyramid Valley, North Canterbury, and Scaifes Lagoon, Lake Wanaka, Otago: Records of the Canterbury Museum, v. 9, p. 309-336.

Busbey, A.B., 1995, The structural consequences of skull flattening in crocodilians; *in* Thomason, J.J., ed., Functional morphology in vertebrate paleontology. Cambridge, Cambridge University Press, p. 173-192.

Buscalioni, A.D., Alcalá, L., Espílez, E., Mampel, L., 2013, European Goniopholididae from the Early Albian Escucha Formation in Ariño (Teruel, Aragon, España): Spanish Journal of Paleontology, v. 28, p. 103-122.

Buskirk, B.L., Hunt, A.P. and Lucas, S.G., 2015, Who's eating who? Preliminary analysis of enigmatic bromalites from the Eocene Florissant Formation, Colorado: Geological Society of America, Abstracts with Programs, v. 47(7), p. 346.

Cadena, E.A., Anaya, F. and Croft, D.A., 2015, Giant fossil tortoise and freshwater chelid turtle remains from the middle Miocene, Quebrada Honda, Bolivia: Evidence for lower paleoelevations for the southern Altiplano: Journal of South American Earth Sciences, v. 64, p. 190-198.

Cadena, E.A., Ksepka, D.T., Jaramillo, C.A. and Bloch, J. I., 2012, New pelomedusoid turtles from the late Palaeocene Cerrejón Formation of Colombia and their implications for phylogeny and body size evolution: Journal of Systematic Palaeontology, v. 10, p. 313-331.

Caldwell, J., 1875, Notes on the zoology of Rodriguez: Proceedings of the Zoological Society of London, v. 1875, p. 644-647.

Calkins, D.G., 1978, Feeding behavior and major prey species of the sea otter, *Euhydra lutris*, in Montague Strait, Prince William Sound, Alaska: Fishery Bulletin, v. 76, p. 125-131.

Callen, E. O., 1963, Diet as revealed by coprolites; *in* Brothwell, D. and E. Higgs, E, eds., Science in archeology. London, Basic Books, p. 186-194.

Callen, E. O., 1965, Food habits of some pre-Columbian Indians: Economic Botany, v. 19, p. 335-343.

Callen, E.O., 1967a, Analysis of the Tehuacan coprolites; *in* Byers, D., ed., The prehistory of the Tehuacan Valley: Environment, and subsistence, volume 1: Austin, University of Texas Press, p. 261-289.

Callen, E.O., 1967b, The first new world cereal: American Antiquity, v. 32, p. 535-538.

Callen, E.O., l968, Plants, diet, and early agriculture of some cave dwelling pre-Columbian Mexican Indians: Actas y Memorias del 37 Congreso Internacional de Americanistas, v. 2, p. 641-656.

Callen, E.O., 1969, Les coprolithes de la cabane acheuleenne du Lazaret: Analyse et diagnostic: Memoires de la Societe Prehistorique Francaise, v. 7, p. 123-124.

Callen, E.O. and Cameron, T.W.M., 1955, The diet and parasites of prehistoric Huaca Prieta Indians as determined by dried coprolites: Proceedings of the Royal Society of Canada, v. 1955, p. 51.

Callen, E. O. and Cameron, T. W. M., 1960, A prehistoric diet revealed in coprolites: The New Scientist, v. 8(190), p. 35-40.

Callen, E.O. and Martin, P.S., 1969, Plant remains in some coprolites from Utah: American Antiquity, v. 34, p. 329-331.

Calvo, J. O., 1994, Gastroliths in sauropod dinosaurs: Gaia, v. 10, p. 205-208.

Calvo, J. O. and Salgado, L., 1995, *Rebbachisaurus tessonei* sp. nov. a new sauropod from the Albian-Cenomanian of Argentina; new evidence on the origin of the Diplodocidae: Gaia, v. 11, p. 13-33.

Calvo, J.M., Gil, E. and Meléndez, G., 1987, *Megaplanolites ibericus* (ichnogen. et ichnosp. nov.), a new trace fossil from the Upper Jurassic (uppermost Oxfordian) of Bueña (Teruel Province, Iberian Chain, Spain): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 61, p. 199-204.

Camacho, M. and Reinhard, K.J., 2020, Pinworm research in the Southwest USA: Five decades of methodological and theoretical development and the epidemiological approach: Archaeological and Anthropological Sciences, v. 12, doi: 10.1007/s12520-019-00994-2.

Camarós, E., Cueto, M., Lorenzo, C., Villaverde, V. and Rivals, F., 2016, Large carnivore attacks on hominins during the Pleistocene: A forensic approach with a Neanderthal example: Archaeological and Anthropological Sciences, v. 8, p. 635-646.

Camens, A.B. and Carey, S.P., 2013, Contemporaneous trace and body fossils from a Late Pleistocene Lakebed in Victoria, Australia, allow assessment of bias in the fossil record: PLoS ONE, v. 8: e52957, doi:10.1371/journal.pone.0052957.

Camp, C.L., 1930, A study of phytosaurs: Memoirs of the University of California, v. 10, 174 p.

Camp, C.L. 1942. California mosasaurs: Memoirs of the University of California, v. 3, 68 p.

Camp, C.L., 1980, Large ichthyosaurs from the Upper Triassic of Nevada: Palaeontographica, Abteilung A, v. 170, p. 139-200.

Campagna, T., 2000, The PT interview: Michael Triebold: Prehistoric Times, v. 40, p.18-19.

Canfield, P. J. and Fairburn, A. J., 1983, Effect of various diets on faecal analysis in normal dogs: Research in Veterinary Science, v. 34, p. 24-27.

Cannon, G. L., 1906, Sauropodan gastroliths: Science, v. 24, p. 116.

Cantrell, A.K., Suazo, T.L., Spielmann, J.A. and Lucas, S.G., 2012, Vertebrate coprolites from the lower Permian (lower Wolfcampian) Gallina Well locality, Joyita Hills, Socorro County, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 57, p. 197-201.

Canudo, J.I., Cruzado-Caballero, P. and Moreno-Azanza, M., 2005, Possible theropod predation evidence in hadrosaurid dinosaurs from the upper Maastrichtian (Upper Cretaceous) of Arén (Huesca, Spain): Kaupia, Darmstädter Beiträge zur Naturgeschichte, v. 14, p. 9-13.

Capasso, L., 1998, Cranial pathology of *Ursus spelaeus* Rosenmüller & Heinroth from Chateau Pignon, Basque Territories (Spain): International Journal of Osteoarchaeology, v. 8, p. 107-115.

Capasso, L., 2019a, First direct evidence of the spiral valve intestine of sturgeons in an exceptionally well preserved Early Cretaceous fossil: Bollettino del Museo Civico di Storia Naturale di Verona, v. 43, p. 23–27.

Capasso, L., 2019b, Palaentological evidence of piscivorous habits of some pycnodonts from the middle Cenomanian of Lebanon: Thalassia Salentina, v. 41, p. 91-110.

Capasso, L., Bacchia, F., Rabottini, N., Rothschild, B.M. and Mariani-Costantini, R., 1996, Possible intraspecific aggressive behavior of Devonian giant fishes (Arthrodira, Dinichthydae): Journal of Paleopathology, v. 8, p. 153-160.

Cardia, D.F., Bertini, R.J., Camossi, L.G. and Letizio, L.A., 2019, First record of Acanthocephala parasites eggs in coprolites preliminary assigned to Crocodyliformes from the Adamantina Formation (Bauru Group, upper Cretaceous), Sao Paulo, Brazil: Anais da Academia Brasileira de Ciências, Earth Sciences, v. 91(supplement 2), https://doi.org/10.1590/0001-3765201920170848.

Cardia, D.F.F., Bertini, R.J., Camossi, L.G., Richini-Pereira, V.B., Losnak, D.O., Francischini, H. and Dentzien-Dias, P., 2021, Paleoparasitological analysis of a coprolite assigned to a carnivoran mammal from the upper Pleistocene Touro Passo Formation, Rio Grande do Sul, Brazil: Anais da Academia Brasileira de Ciências, v. 93 (supplement 2), p. 1-13: e20190876, doi: 10.1590/0001-3765202120190876.

Carlini, S. C., Vizcaíno, S. F. and Scillato-Yané, G. J., 1997, Armored xenathrans: A unique taxonomic and taphonomic assemblage; *in* Kay, R. F., Madden, R.D., Cifelli, R.L. and Flynn, J.J., eds., Vertebrate paleontology in the neotropics: The Miocene fauna of La Venta, Colombia. Washington, D. C., Smithsonian Institution Press, p. 213-226.

Carnevale, G. and Pietsch, T.W., 2006, Filling the gap: A fossil frogfish, genus *Antennarius* (Teleostei, Lophiiformes, Antennariidae), from the Miocene of Algeria: Journal of Zoology, v. 270, p. 448-457.

Carpenter, K., 1987, Ankylosaurs; *in* Farlow, J.O. and Brett-Surman, M.K., eds., The complete dinosaur. Bloomington, Indiana University Press, p. 307-316.

Carpenter, K., 1990, Ankylosaurs systematics: Example using *Panoplosaurus* and *Edmontonia* (Ankylosauria, Nodosauridae); *in* Carpenter, K. and Currie, P. J., eds., Dinosaur systematics: Perspectives and approaches. Cambridge, Cambridge University Press, p. 281-298.

Carpenter, K., 1998, Evidence of predatory behavior by carnivorous dinosaurs: Gaia, v. 15, p. 135-144.

Carpenter, K. and Lindsey, D., 1980, The dentary of *Brachychampsa montana* Gilmore (Alligatorinae; Crocodylidae), a Late Cretaceous turtle-eating alligator: Journal of Paleontology, v. 54, p. 1213–1217.

Carpenter, K., Sanders, F., McWhinney, L.A. and Wood, L., 2005, Evidence for predator-prey relationships: Examples for *Allosaurus* and *Stegosaurus; in* Carpenter K., ed., The carnivorous dinosaurs. Bloomington, Indiana University Press, p. 325-350.

Carr, R., Lindgren, J., Schweitzer, M. Woodward, H. and Scannella, J., 2020, Soft tissue preservation and paleoecology of a new giant plioplatecarpine mosasaur from the Bearpaw Shale of Montana (U.S.A.): Society of Vertebrate Paleontology, 80th Annual Meeting, Virtual 2020, October 12-16 2020 www.vertpaleo.org Conference Program, unnumbered page.

Case, E.C., 1911, A revision of the Cotylosauria of North America: Publications of the Carnegie Institution of Washington, v. 145, p. 1-122.

Case, G.R., 1982, A pictorial guide to fossils. New York, Van Nostrand Reinhold, 514 p.

Casier, E., 1960, Les Iguanodons de Bernissart. Brussels, Institute Royal d'Histoire Naturelle de Belgique, 134 p.

Casier, E., 1978, Les Iguanodons de Bernissart. Brussels, Institute Royal d'Histoire Naturelle de Belgique, 166 p.

Caster, K.E. and Kjellesyig-Waering, E. N., 1964, Upper Ordovician eurypterids from Ohio: Palaeontographica Americana, v. 4, p. 297-358.

Castro, A.C.J., Fernandes, A.C.S. and Carvalho I.S., 1988, Coprólitos de aves da Bacia de Taubaté, SP: Anais do Congresso Brasileiro do Geologia, Belém, v. 35, p. 2358-2370.

Cate, A. S. and Evans, I., 1994, Taphonomic significance of the biomechanical fragmentation of live molluscan shell material by a bottom-feeding fish (*Pogonias cromis*) in Texas coastal bays: Palaios, v. 9, p. 254-274.

Cau, A. and Arduini, P., 2008, *Enantiophoenix electrophyla* gen. et sp. nov. (Aves, Enantiornithes) from the Upper Cretaceous (Cenomanian) of Lebanon and its phylogenetic relationships: Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, v. 149, p. 293-324.

Caviedes-Vidal, E., McWhorter, T.J., Lavin, S.R., Chediack, J.G., Tracy, C.R. and Karasov, W. H., 2007, The digestive adaptation of flying vertebrates: High intestinal paracellular absorption compensates for smaller guts: Proceedings of the National Academy of Sciences of the United States of America, v. 104, p. 19132–19137.

Cavin, L., 1999, Occurrence of a juvenile teleost, *Enchodus* sp., in a fish gut content from the Upper Cretaceous of Goulmima, Morocco: Palaeontology, v. 60, p. 57-72.

Cavin, L. and Forey, P.L., 2007, Using ghost lineages to identify diversification events in the fossil record: Biology Letters, v. 3, p. 201-204.

Cavin, L., Forey, P.L. and LéCuyer, C., 2007, Correlation between environment and late Mesozoic ray-finned fish evolution: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 245, p. 353-367.

Cenizo, M., Soibelzon, E. and Magnussen Saffer, M., 2016, Mammalian predator–prey relationships and reoccupation of burrows in the Pliocene of the Pampean Region (Argentina): New ichnological and taphonomic evidence: Historical Biology, v. 28, p. 1026-1040.

Cerda, I. A., 2008, Gastroliths in an ornithopod dinosaur: Acta

Palaeontologica Polonica, v. 53, p. 351-355.

Cerda, I. A. and Salgado, L., 2008, Gatrolítos en un plesiosaurio (Sauropterygia) de la Formación Allen (Campaniano-Maastrictiano), Provincia de Río Negro, Patagonia, Argentina: Ameghiniana, v. 45, p. 529-536.

Chabreck, R.H., 1996, Regurgitation by the American alligator: Herpetological Review, v. 27, p. 185-186.

Chame, M., 2003, Terrestrial mammal feces: A morphometric summary and description: Memórias do Instituto Oswaldo Cruz, v. 98, supplement 1, p. 71-94.

Chapman, F., 1884, Notes on the moa remains in the MacKenzie County, and other localities: Transactions of the New Zealand Institute, v. 16, p. 172-178.

Charig, A.J. and Milner, A.C., 1986, *Baryonyx*, a remarkable new theropod dinosaur: Nature, v. 324, p. 359–361.

Charig, A.J. and Milner, A.C., 1997, *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey: Bulletin of the British Museum (Natural History) Geology, v. 53, p. 11-70.

Chatelain, E.E., 1991, Surface textures on gastroliths as a key to origin: Vertebrate gastric mills or stream abraded gravel: Bulletin of Georgia Academy of Sciences, v. 49, p. 35.

Chatelain, E.E., 1993, Surface textures produced by tumbling chert nodules derived from the Kaibab Formation (Permian) of Utah; Characteristic of gastroliths or stream gravels?: Geological Society of America, Abstracts with Programs, v. 25, p. 7.

Chatterjee, S., 1978, A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India: Palaeontology, v. 21, p. 83–127.

Chatterjee, S., 1980, *Malerisaurus*, a new eosuchian reptile from the Late Triassic of India: Philosophical Transactions of the Royal Society of London, Series B, v. 291, p. 163-200.

Chatterjee, S., and Small, B., 1989, New plesiosaurs from, the Upper Cretaceous of Antarctica: Geological Society, London, Special Publications 47, 197-215.

Chen, M. and Chen, Y., 1980, Note on a possible coprolite from the lowest Cambrian strata of Yangtze Gorge: Scientia Geologica Sinica, v. 10, p. 406–407.

Chen, P.J., Dong, Z.M. and Zhen, S.N., 1998, An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China: Nature, v. 391, p. 147-152.

Cheng, L., Wings, O., Chen, X. and Sander, P. M., 2006, Gastroliths in the Triassic ichthyosaur *Panjiangsaurus* from China: Journal of Paleontology, v. 80, p. 583-588.

Chevrinais, M., Jacquet, C. and Cloutier, R. 2017, Early establishment of vertebrate trophic interactions: Foodweb structure in Middle to Late Devonian fish assemblages with exceptional fossilization: Bulletin of Geosciences, v. 92, p. 491–510.

Chiappe, L.M. and Meng, Q.-J., 2016, Birds of stone. Baltimore, Johns Hopkins University Press, 304 p.

Chiappe, L.M., Bo, Z., O'Connor, J.K., Gao, C., Wang, X., Habib, M., Marugan-Lobon, J., Meng, Q. and Cheng, X., 2014, A new specimen of the Early Cretaceous bird *Honghsanornis longicresta*: Insights into the aerodynamics and diet of a basal ornithuromorph: Peerj, v. 2: e234, doi: 10.7717/peerj.234.

Chin, K., 1996, The paleobiological implications of herbivorous dinosaur coprolites: Ichnologic, petrographic, and organic geochemical investigations [Ph.D. dissertation]: Santa Barbara, University of California, 162 p.

Chin, K., 1997, What did dinosaurs eat? Coprolites and other direct evidence of dinosaur diets; *in* Farlow, J.O. and Brett-Surman, M.K., eds., The complete dinosaur. Bloomington, Indiana University Press, p. 371-382.

Chin, K., 2007, The paleobiological implications of herbivorous dinosaur coprolites from the Upper Cretaceous Two Medicine Formation of Montana: Why eat wood?: Palaios, v. 22, p. 554-566.

Chin, K. and Bishop J., 2004, Traces within traces: Evidence for coprophagy in a probable theropod coprolite from the Jurassic Morrison Formation of Utah, USA: First International Congress on Ichnology, Abstract Book, p. 26.

Chin, K. and Bishop J.R., 2007, Exploited twice: Bored bone in a theropod coprolite from the Jurassic Morrison Formation of Utah, U.S.A.: SEPM Special Publication, v. 88, p. 379–387.

Chin, K. and Gill, B.D., 1996, Dinosaurs, dung beetles, and conifers: Participants in a Cretaceous food web: Palaios, v. 11, p. 280-285.

Chin, K. and Kirkland, J.I., 1998, Probable herbivore coprolites from the Upper Jurassic Mygatt-Moore Quarry, western Colorado: Modern Geology, v. 23, p. 249-275.

Chin, K., Feldmann, R.M. and Tashman, J.N., 2017, Consumption of crustaceans by megaherbivorous dinosaurs: Dietary flexibility and dinosaur life history strategies: Scientific Reports, v. 7, 11163, doi.org/10.1038/s41598-017-11538-w.

Chin, K., Hartman, J.H. and Roth, B., 2009, Opportunistic exploitation of dinosaur dung: Fossil snails in coprolites from the Upper Cretaceous Two Medicine Formation of Montana: Lethaia, v. 42, p. 185-198.

Chin, K., Eberth, D.A., Schweitzer, M.H., Rando, T.A., Sloboda, W.J. and Horne, J.R., 2003, Remarkable preservation of undigested muscle tissue within a Late Cretaceous tyrannosaurid coprolite from Alberta, Canada: Palaios, v. 18, p. 286-294.

Chipman, M.D., 2017, Fish coprolites of the Joggins Formation and coastal trophicrelationships in a Late Carboniferous sea [B.Sc. with Honours thesis]: Wolfville, Acadia University, 34 p.

Chipman, M., Grey, M. and Pufahl, P.K., 2020, Coprolites from a brackish ecosystem in the Pennsylvanian Joggins Formation, Nova Scotia, Canada and their palaeoecological implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 538, p.109407, doi.org/10.1016/j.palaeo.2019.109407.

Choo, B., 2012, Revision of the actinopterygian genus *Mimipiscis* (= *Mimia*) from the Upper Devonian Gogo Formation of western Australia and the interrelationships of the early Actinopterygii: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 102, p. 77-104.

Choo, B., Long, J.A. and Trinajstic, K., 2009, A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of western Australia: Acta Zoologica, v. 90, p. 194-210.

Chow, M.M., 1955, Two specimens of mammalian coprolites from the Sanmen Rapids, Shanshi and Singtsai, Honan: Acta Paleontologica Sinica, v. 3, p. 283-286.

Christiansen, P., 1996, The evidence for and implications of gastroliths in sauropods (Dinosauria, Sauropoda): Gaia, v. 12, p. 1-7.

Chrzastek, A., 2008, Vertebrate remains from the Lower Muschelkalk of Raciborowice Górne (North-Sudetic Basin, SW Poland): Geological Quarterly, v. 52, p. 225–238.

Chumakov, N.M., Dronov, A.V. and Mikuláš, R., 2013, New ichnospecies of scratching traces from phosphatic nodules (Cenomanian, England): Stratigraphy and Geological Correlation, v. 21, p. 291-299.

Chure, D.J., Fiorillo, A.R. and Jacobsen, A., 1998, Prey bone utilization by predatory dinosaurs in the Late Jurassic of North America, with comments on prey bone use by dinosaurs throughout the Mesozoic: Gaia, v. 15, p. 227-232.

Cicimurri, D.J. and Everhart, M.J., 2001, An elasmosaur with stomach contents and gastroliths from the Pierre Shale (Late Cretaceous) of Kansas: Transactions of the Kansas Academy of Science, v. 104, p. 129-143.

Cicimurri, D.J. and Knight, J.L., 2009, Two shark-bitten whale skeletons from Coastal Plain deposits of South Carolina: Southeastern Naturalist, v. 8, p. 71-83.

Cicimurri, D.J., Parris, D.C. and Everhart, M.J., 2008, Partial dentition of a chimaeroid fish (Chondrichthyes, Holocephali) from the Upper Cretaceous Niobrara Chalk of Kansas, USA: Journal of Vertebrate Paleontology, v. 28, p. 34-40.

Cigala-Fulgosi F., 1990, Predation (or possible scavenging) by a great white shark on an extinct species of bottlenosed dolphin in the Italian Pliocene: Tertiary Research, v. 12, p. 17-36.

Cione, A.L., Hospitaleche, C.A., Pérez, L.M., Laza, J.H., César, I., 2010, Trace fossils on penguin bones from the Miocene of Chubut, southern Argentina: Alcheringa, v. 34, p. 433-454.

Cisneros, J.C., 2005, New Pleistocene vertebrate fauna from El Salvatore: Revista Brasileira de Paleontologia, v. 8, p. 239–255.

Citton, P., Sacchi, E. and Nicosia, U., 2012, Sometimes they come back: Recovery and reinterpretation of a trackway slab from the Permian Coconino Sandstone of the southwestern United States: Ichnos, v. 19, p. 3, 165-174.

Clark, J., Beerbower, J.R. and Kietzke, K.K., 1967, Oligocene sedimentation, stratigraphy, paleoecology and paleoclimatology in the Big Badlands of South Dakota: Fieldiana, Geological Memoirs, v. 5, 157 p.

Clark, J.M. and Fastovsky, D.E., 1986, Vertebrate biostratigraphy of the Glen Canyon Group in northern Arizona; *in* Padian, K., ed., The beginning of the age of dinosaurs: Faunal change across the Triassic-Jurassic boundary. Cambridge, Cambridge University Press, p. 285-301.

Clark, N. D. L., 1989, A study of a Namurian crustacean-bearing shale from the western Midland Valley of Scotland [Ph.D. dissertation]: Glasgow, University of Glasgow, 372 p.

Clarke, M.R., Pailiza, O. and Aguayo, A., 1998, Sperm whales of the southeast Pacific. Part IV: Fatness, food and feeding; *in* Pilleri G, ed., Investigations on Cetacea. Berne, University of Berne, Brain Anatomy Institute, p. 53–195.

Clarke, R., 2006, The origin of ambergris: The Latin American Journal of Aquatic Mammals, v. 5, p. 7-21.

Clément G., 2005, A new coelacanth (Actinistia, Sarcopterygii) from the Jurassic of France, and the question of the closest relative fossil to *Latimeria*: Journal of Vertebrate Paleontology, v. 25, p. 481-491.

Clément, G., 2006, *Swenzia*, n. nov., a replacement name for the preoccupied coelacanth genus *Wenzia* Clément: Journal of Vertebrate Paleontology, v. 26, p. 461.

Clifton, H. E., 1965, Tectonic polish of pebbles: Journal of Sedimentary Research, v. 35, p. 867-873.

Clouter, F., Mitchell, T., Rayner, D. and Rayner, M., 2000, London clay fossils of the Isle of Sheppey: A collectors guide to the fossil animals of the London Clay between Minster and Warden Point, Sheppey. Medway, Medway Fossil and Mineral Society, 100 p.

Cloutier, R., 2013. Great Canadian Lagerstätten 4. The Devonian Miguasha biota (Québec): UNESCO World Heritage Site and a time capsule in the early history of vertebrates: Geoscience Canada, v. 40, p. 149-163.

Coates, M.I. and Sequeira, S.E.K., 2001, A new stethacanthid chondrichthyan from the lower Carboniferous of Bearsden, Scotland: Journal of Vertebrate Paleontology, v. 21, p. 438-459.

Cockerill, T.D.A., 1915, A visit to Oeningen: Science Monthly, v. 1, p. 287-291.

Coco, G.E.L., Agnolín, F.L. and Carrión, J.L.R., 2020, Late Pleistocene owls (Aves, Strigiformes) from Ecuador, with the description of a new species: Journal of Ornithology, v. 161, p. 713-721.

Codorniú, L., Chiappe, L. M., Cid, F. D., 2013, First occurrence of stomach stones in pterosaurs: Journal of Vertebrate Paleontology, v. 33, p. 647-654.

Codrea, V.A. and Solomon, A., 2012, Peculiar fossilization and taphonomy in Maastrichtian terrestrial deposits of Pui (Haţeg Basin, Romania): Studii și cercercetări (Geol-Geogr), v. 17, p. 51-69.

Codrea, V., Barbu, O., and Jipa-Murzea, C., 2010, Upper Cretaceous (Maastrichtian) land vertebrate diversity in Alba District (Romania): Bulletin of the Geological Society of Greece, v. 43, p. 594-601.

Codrea, V., Godefroit, P. and Smith, T., 2012, First discovery of Maastrichtian (latest Cretaceous) terrestrial vertebrates in Rusca Montană Basin (Romania); *in* Godefroit P., ed., Bernissart dinosaurs and Early Cretaceous terrestrial cosystems. Bloomington, Indiana University Press, p. 570-581.

Codrea, V., Vremir, M., Jipa, C., Godefroit, P., Csiki, Z., Smith, T. and Fărcaş, C., 2010, More than just Nopcsa's Transylvanian dinosaurs: A look outside the Haţeg Basin: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 293, p. 391-405.

Cohen, B., 2003, Actualistic investigation of bone modification on leporids by Caracal (*Caracal caracal*) and Honey Badger (*Mellivora capensis*); An insight to the taphonomy of Cooper's Cave, South Africa [M.S. thesis]: Johannesburg, University of the Witwatersrand, 160 p.

Cohen, B.F. and Kibii, J.M., 2015, Experimental study of bone modification by captive caracal (*Caracal caracal*); A model for fossil assemblage analysis: Journal of Archaeological Science, v. 62, p. 92-104.

Collareta, A., Caasati, S. and Di Cencio, A., 2017a. A pristid sawfish from the lower Pliocene of Lucciolabella (Radicofani basin, Tuscany, central Italy): Atti della Società Toscana di Scienze Naturali, Memorie Serie A, v. 124, p. 49-55.

Collareta, A., Cigala Fulgosi, F., and Bianucci, G. 2019a, A new kogiid sperm whale from northern Italy supports psychrospheric conditions in the early Pliocene Mediterranean Sea: Acta Palaeontologica Polonica, v. 64, p. 609–626.

Collareta, A., Gemelli, M., Varola, A. and Bianucci, G., 2019b, Trace fossils on a trace fossil: A vertebrate-bitten vertebrate coprolite from the Miocene of Italy: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 293, p. 117-126.

Collareta, A., Lambert, O., Landini, W., Di Celma, C., Malinverno, E., Varas-Malca, R., Urbina, M. and Bianucci, G., 2017b, Did the giant extinct shark *Carcharocles megalodon* target small prey? Bite marks on marine mammal remains from the late Miocene of Peru: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 469, p. 84-91.

Collareta, A., Landini, W., Augusto, C., Budiel, C., Vera, W. V., Sierra, A., Ali, J., Schmitt, M. U. and Bianucci, G., 2017c, A well preserved skeleton of the fossil shark *Cosmopolitodus hastalis* from the late Miocene of Peru, featuring fish remains as fossilized stomach contents: Rivista Italiana di Paleontologia e Stratigrafia, v. 123, p. 11-22

Collareta, A., Landini, W., Lambert, O., Post, K., Tinelli, C., Di Celma, C., Panetta, D., Tripodi, M., Salvadori, P.A., Caramella, D. and Marchi, D., 2015. Piscivory in a Miocene Cetotheriidae of Peru: First record of fossilized stomach content for an extinct baleen-bearing whale: The Science of Nature, v. 102, p. 1-12, doi: 10.1007/s00114-015-1319-y.

Collinson, M.E., 1990, Plant evolution and ecology during the Early Cainozoic diversification: Advances in Botanical Research, v. 17, p. 1-98.

Collinson, M.E., 1999, Plants and animal diets; *in* Jones, T.P. and Rowe, N.P., eds., Fossil plants and spores: Modern techniques. London, Geological Society of London, p. 316-319.

Collinson, M.E. and Hooker, J.J., 2000, Gnaw marks on Eocene seeds: Evidence for early rodent behavior: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 157, p. 127-149.

Contreras, V.H., 1995, Datos preliminares de estrucuturas biodeposicionales (coprólitos) de La Formacion Ischigualasto (Triásico superior, Temprano), en su localidad tipo (Ischigualasto, San Juan, Argentina): 2 Reunión Argentina de Icnologia, San Juan, p. 7-8.

Conway Morris, S., 1976, A new Cambrian lophophorate from the Burgess Shale of British Columbia: Palaeontology, v. 19, p. 199-222.

Conway Morris, S., 1990, *Typhloesus wellsi* (Melton and Scott, 1973), a bizarre metazoan from the Carboniferous of Montana, U.S.A.: Philosophical Transactions of the Royal Society of London, Series B, v. 327, p. 595–624.

Conway Morris, S. and Robison, R.A., 1986, Middle Cambrian priapulids and other softbodied fossils from Utah and Spain: The University of Kansas Paleontological Contributions, Paper 117, 22 p.

Cook, D.O., 1971, Depressions in shallow marine sediment made by benthic fish: Journal of Sedimentary Research, v. 41, p. 577-578.

Cook, P.J. and McElhinny, M.W., 1979, A re-evaluation of the spatial and temporal distribution of phosphorites in the light of plate tectonics: Economic Geology, v. 74, p. 315-330.

Coombs, M.C., 1983, Large mammalian clawed herbivores: A comparative study: Transactions of the American Philosophical Society, v. 73, p. 1-96.

Cooper, M., 1981, The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: Its biology, mode of life and phylogenetic significance: Occasional Papers of the National Museums and Monuments of Rhodesia, Series B, Natural Sciences, v. 6, p. 690-840.

Cope, E.D., 1868, [Remarks on a new enaliosaurian, *Elasmosaurus platyurus*.]: Proceedings of the Academy of Natural Sciences, Philadelphia, v. 20, p. 92-93.

Cope, E.D., 1872, [On a species of *Clidastes* and on *Plesiosaurus gulo* Cope]: Proceedings of the Academy of Natural Sciences, Philadelphia, v. 24, p. 127-129.

Corral, J.C., Pereda Suberbiola, X. and Bardet, N., 2004, Marcas de ataque atribuidas a un selacio en una vertebra de mosasaurio del Cretácico Superior de Álava (Region Vasco-Cantábrica): Revista Española de Paleontología, v. 19, p. 23-32.

Cortés, D., De Gracia, C., Carrillo-Briceño, J.D., Aguirre-Fernández, G., Jaramillo, C., Benites-Palomino, A. and Atencio-Araúz, J.E., 2019, Shark-cetacean trophic interactions during the late Pliocene in the Central Eastern Pacific (Panama): Palaeontologia Electronica, v. 22(2), pp.1-13, doi.org/10.26879/953.

Cosmidis, J., Benzerara, K., Gheerbrant, E., Esteve, I., Bouya, B. and Amaghzaz, M., 2013, Nanometer-scale characterization of exceptionally preserved bacterial fossils in Paleocene phosphorites from Ouled Abdoun (Morocco): Geobiology, v. 11, p.139-153.

Cott, H., 1961, Scientific results of an inquiry into the ecology and economic status of the Nile crocodile in Uganda and Northern Rhodesia: Transactions of the Zoological Society of London, v. 29, p. 236-245.

Courville, C.B., 1953, Cranial injuries in prehistoric animals; with special notes on a healed wound of the skull in the dire wolf (*Canis* [*Aenocyon*] *dirus* [Leidy]) and a mortal wound in the California black bear (*Ursus americanus*): Bulletin of the Los Angeles Neurological Society, v. 18, p. 117-126.

Covert, H.H. and Kay, R.F., 1981, Dental microwear and diet: implications for determining the feeding behaviors of extinct primates, with a comment on the dietary pattern of *Sivapithecus*: American Journal of Physical Anthropology, v. 55, p. 331-336.

Cox, T.D., 1994, The formation of gastrolith derived stone-lines in deep loess upland soils: Mid-continental USA [M.S. thesis]: Champaign, University of Illinois, 198 p.

Cox, T.D., 1997, Gastrolith-derived stone concentration in deep loess soil of the middle and lower Mississippi River valley, U. S. A.; *in* Goodyear, A. C., Foss, J. E. and Sassaman, K. E., eds., Proceedings of the Second International Conference on Pedo-archaeology. University of South Carolina, South Carolina Institute of Archaeology and Anthropology, Anthropology Studies, v. 10, p. 27-33.

Cox, T.D., 1998, Origin of stone concentration in loess-derived interfluve soils: Quaternary International, v. 51-52, p. 74-75.

Coy, C.E., 1995, The first record of spiral coprolites from the Dinosaur Park Formation (Judith River Group, Upper Cretaceous) southern Alberta, Canada: Journal of Paleontology, v. 69, p. 1191-1194.

Cozzuol, M.A. and Aguilera, O.A., 2008, Cetacean remains from the Neogene of northwestern Venezuela: Paläontologische Zeitschrift, v. 82, p. 196-203.

Crandall, B. D. and Stahl, P. W., 1995, Human digestive effects on a micromammalian skeleton: Journal of Archaological Science, v. 22, p. 789-797.

Crane, J.M., Jr., 1996, Late Tertiary radiation of viperfishes (Chauliodontidae) based on a comparison of Recent and Miocene species: Contributions in Science, Los Angeles County Museum, v. 115, 29 p.

Crompton, A.W. and Hotton, N., 1967, Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida): Postilla, v. 109, p. 1-51.

Cruickshank, A. R. I., 1986, Archosaur predation on an East African Middle Triassic dicynodont: Palaeontology, v. 29, p. 415-422.

Cueille, M., Green, E., Duffin, C.J. Hildebrand, C. and Benton, M.J., 2020, Fish and crab coprolites from the latest Triassic of the UK: From Buckland to the Mesozoic Marine Revolution: Proceedings of the Geologists' Association, v. 131, p. 699-721.

Cumbaa, S.L., Schröder-Adams, C., Day, R.G. and Phillips, A.J., 2006, Cenomanian bonebed faunas from the northeastern margin, Western Interior Seaway, Canada: New Mexico Museum of Natural History and Science, Bulletin 35, p. 139-155.

Cunningham, C.R., Feldman, H.R., Franseen, E.K., Gastaldo, R.A., Mapes, G., Maples, C.G. and Schultze, H.P., 1993, The upper Carboniferous Hamilton Fossil-Lagerstätte in Kansas: A valley-fill, tidally influenced deposit: Lethaia, v. 26 p. 225-236.

Currie, P. J., 1981, *Hovasaurus boulei*: an aquatic eosuchian from the upper Permian of Madagascar: Palaeontologica Africana, v. 24, p. 99-168.

Currie, P.J., 1985, Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds: Canadian Journal of Earth Sciences, v. 22, p. 1643-1658.

Currie, P.J., 1997, Gastroliths; *in* Currie, P. J. and Padian, K., eds., Encyclopedia of dinosaurs. San Diego, Academic Press, p. 270.

Currie, P.J. and Chen, P.J., 2001, Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China: Canadian Journal of Earth Sciences, v. 38, p. 1705-1727.

Currie, P.J. and Eberth, D.A., 2010, On gregarious behavior in *Albertosaurus*: Canadian Journal of Earth Sciences, v. 47, p. 1277-1289.

Currie, P.J. and Jacobsen, A.R., 1995, An azhdarchid pterosaur eaten by a velociraptorine theropod: Canadian Journal of Earth Sciences, v. 32, p. 922-925.

Currie, P.J., Koppelhus, E.B. and Muhammad, A.F., 1995, Stomach contents of a hadrosaur from the Dinosaur Park Formation (Campanian, Upper Cretaceous) of Alberta, Canada; *in* Sun, A. and Wang, Y., eds., Sixth symposium on Mesozoic terrestrial ecosystems and biota, short papers. Beijing, China Ocean Press, p. 111-114.

Currie, P.J., Wilson, J.A., Fanti, F., Mainbayar, B. and Tsogtbaatar, K., 2018, Rediscovery of the type localities of the Late Cretaceous Mongolian sauropods *Nemegtosaurus mongoliensis* and *Opisthocoelicaudia skarzynskii*: Stratigraphic and taxonomic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 494, p. 5-13.

Cuvier, G., 1812, Recherches sur les Ossemens Fossiles de Quadrupèdes, ou l'on Rétablit les Caractères de Plusieurs Espècies d'animaux que les Révolutions du Globe Paroissent Avoir Détruites. Tome quatrième. Contenant les ruminans, les onguiculés et les reptiles fossiles. Paris, Déterville Libraire, 523 p.

Cuvier, G., 1818, Essay on the theory of the Earth: With mineralogical notes, and an account of Cuvier's geological discoveries by Professor Jameson. New York, Kirk and Mercein, 431 p.

Cuvier, G., 1829, Le Règne Animal, Distribué d'après son Organisation, Pour Servir de Base a l'histoire Naturelle des Animaux et d'introduction a l'anatomie Comparée. Tome II. Paris, Déterville Libraire, 406 p.

Czaplewski, N.J., 2011, An owl-pellet accumulation of small Pliocene vertebrates from the Verde Formation, Arizona, USA: Palaeontologia Electronica, v. 14, no. 3, p. 1-33.

Dachroth, W., 1985, Fluvial sedimentary styles and associated depositional environments in the Buntsandstein west of River Rhine in Saar area and Pfalz (F.R. Germany) and Vosges (France); *in* Mader, D., ed., Aspects of fluvial sedimentation in the Lower Triassic Buntsandstein of Europe: Lecture Notes in Earth Sciences, v. 4. Berlin, Springer, p. 197-248.

Dalla Vecchia, F.M., 2003, New morphological observations on Triassic pterosaurs; *in* Buffetaut, E. and Mazin, J.-M., eds., Evolution and palaeobiology of pterosaurs: Geological Society of London, Special Publications 217, p. 23-44.

Dalla Vecchia, F.M. and Chiappe, L.M., 2002, First avian skeleton from the Mesozoic of northern Gondwana: Journal of Vertebrate Paleontology, v. 22, p. 856-860.

Dalla Vecchia, F.M., Muscio, G., and Wild, R., 1989, Pterosaur remains in a gastric pellet from the Upper Triassic (Norian) of Rio Seazza Valley (Udine, Italy): Gortania Atti Museo Friuli Storia Naturale, v. 10, p. 121–132.

Dalman, S.G. and Lucas, S.G., 2018, New evidence for predatory behavior in tyrannosaurid dinosaurs from the Kirtland Formation (Late Cretaceous, Campanian), northwestern New Mexico: New Mexico Museum of Natural History and Science, Bulletin 79, p. 113-124.

Dalman, S.G. and Lucas, S.G., 2021, New evidence for cannibalism in tyrannosaurid dinosaurs from the Upper Cretaceous (Campanian/Maastrichtian) San Juan Basin of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 82, p. 39-56.

D'Amore, D.C., 2009, A functional, behavioral, and taphonomic analysis of ziphodont dentition: Novel methodology for the evaluation of carnivorous dinosaur feeding paleoecology [Ph.D. dissertation]: New Brunswick, Rutgers University-New Brunswick, 221 p.

Dal Sasso, C. and Signore, M., 1998, Exceptional soft-tissue preservation in a theropod dinosaur from Italy: Nature, v. 392, p. 383-387.

Dal Sasso C. and Maganuco S., 2011, *Scipionyx samniticus* (Theropoda: Compsognathidae) from the Lower Cretaceous of Italy. Osteology, ontogenetic assessment, phylogeny, soft tissue anatomy, taphonomy and palaeobiology: Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, v. 37, p. 1-281.

Dalsätt, J., Zhou, Z., Zhang, F. and Ericson, P.G., 2006, Food remains in *Confuciusornis sanctus* suggest a fish diet: Naturwissenschaften, v. 93, p. 444-446.

Dana, S. L., 1845, Analysis of coprolites from the New Red Sandstone Formation of New England: American Journal of Science, v. 48, p. 46-60.

Dantas, P., Freitas, C., Azevedo, T., Carvalho A. G. de, Santos, D., Ortego, F., Santos, V., Sanz, J.L., Silva, C.M. da, Cachão, M., 1998, Estudo dos gastrólitos do dinossáurio *Lourinhasaurus* do Jurássico superior portugués: Communicaçãoes do Instituto Geológico e Mineiro V Congreso Nacional do Geologia (Lisbon), v. 84, p. 87-90.

Darby, D. and Ojakangas, R., 1980, Gastroliths from an Upper Cretaceous plesiosaur: Journal of Paleontology, v. 54, p. 548-556.

Darroch, S.A.F., Fraser, D. and Casey, M.M., 2021, The preservation potential of terrestrial biogeographic patterns: Proceeding of the Royal Society, Series B, 288: 20202927. https://doi.org/10.1098/rspb.2020.2927.

Dart, R., 1957, The osteodontokeratic culture of *Australopithecus promethius*: The total contents of the breccia hitherto: Transvaal Museum Memoirs, v. 10, p. l-105.

Darwin, C., 1881, The formation of vegetable mould through the action of worms, with observations on their habits. London, John Murray, 326 p.

da Silva Marinho, T., Marinho, T.S. and Iori, F.V., 2011, A large titanosaur (Dinosauria, Sauropoda) osteoderm with possible bite marks from Ibirá, São Paulo State, Brazil: Paleontologia: Cenários de Vida, v. 4, p. 369-379.

Daujeard, C., Geraads, D., Gallotti, R., Lefèvre, D., Mohib, A., Raynal, J.-P., and Hublin, J.-J., 2016, Pleistocene hominins as a resource for carnivores: A c.500,000-year-old human femur bearing tooth marks in North Africa (Thomas Quarry I, Morocco): PLoSOne, v. 11(4):e0152284, doi:10.1371/journal. pone.0152284.

Davidson, I. and Soloman, S., 1990, Was OH7 the victim of a crocodile attack?; *in* Solomon, S., Davidson, I. and Watson, D., eds., Problem solving in taphonomy: Archaeological and palaeontological studies from Europe, Africa and Oceania. St. Lucia, Tempus, p. 197-206.

Davidson, R.G. and Trewin, N.H. 2005, Unusual preservation of the internal organs of acanthodian and actinopterygian fish in the Middle Devonian of Scotland: Scottish Journal of Geology, v. 41, p. 129-134.

Davis, J. W., 1887, The fossil fish of the Chalk of Mount Lebanon in Syria: Scientific Transactions of the Royal Society of Dublin, Series 2, v. 3, p. 457-636.

Davis, O.K., 1987, Spores of the dung fungus *Sporormiella*: Increased abundance in historic sediments and before Pleistocene megafaunal extinction: Quaternary Research, v. 28, p. 290-294.

Davis, O.K., Kolva, D.A. and Mehringer, P.J. 1977, Pollen analysis of Wildcat Lake, Whitman County, Washington: The last 1000 years: Northwest Science, v. 51, p. 13–30.

Davis, O.K. and Shafer, D.S., 2006, *Sporormiella* fungal spores, a palynological means of detecting herbivore density: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 40-50.

Dawkins, W.B., 1863, Wookey Hole hyaena den: Proceedings of the Somersetshire Archaeological Natural History Society, v. 11, p. 197–219.

Dawson, J.W., 1854, On the coal measures of the South Joggins, Nova Scotia: Quarterly Journal of the Geological Society of London, v. 10, p. 1-42.

Dawson, J.W., 1862, Notice of the discovery of additional remains of land animals in the coal-measures of the South Joggins, Nova Scotia: Quarterly Journal of the Geological Society of London, v. 18, p. 5-7.

Dawson, S. D. and Gottfried, M. D., 2002, Paleopathology in a Miocene kentriodontid dolphin (Cetacea: Odontoceti): Smithsonian Contributions to Paleontology, v. 93, p. 263-270.

de Araújo Júnior, H.I. and da Silva Marinho, T., 2013, Taphonomy of a *Baurusuchus* (Crocodyliformes, Baurusuchidae) from the Adamantina Formation (Upper Cretaceous, Bauru Basin), Brazil: Implications for preservational modes, time resolution and paleoecology: Journal of South American Earth Sciences, v. 47, p. 90-99.

de Araújo-Júnior, H.I., Porpino, K.O., Bergqvist, L.P., 2011, Marcas de dentes de carnívoros/carniceiros em mamíferos pleistocênicos do Nordeste do Brasil: Revista Brasileira de Paleontologia, v.14, p. 291–296.

de Araújo-Júnior, H.I., de Souza Barbosa, F.H. and Medeiros da Silva, L.H., 2017, Overlapping paleoichnology, paleoecology and taphonomy: Analysis of tooth traces in a Late Pleistocene-early Holocene megafaunal assemblage of Brazil and description of a new ichnotaxon in hard substrate: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 468, p. 122-128.

De Baets, K., Dentzien-Dias, P., Harrison, G.W.M., Littlewood, D.T.J. and Parry, L.A., 2021, Fossil constraints on the timescale of parasitic helminth evolution; *in* De Baets, K. and Huntley, J., eds., The evolution and fossil record of parasitism: Identification and macroevolution of parasites. Topics in Geobiology, v. 49. Cham, Springer, p. 231-271.

DeBakey, M. and Ochsner, A., 1939, Bezoars and concretions: Surgery, v. 5, p. 132-160

Debrenne, F. and Zhuravlev, A.Y., 1997, Cambrian food web: A brief review: Geobios, v. 30, p. 181-188.

DeKay, J.E., 1830a, On the discovery of coprolites in North America: Philosophical Magazine, new series, v.10, p. 321-322.

DeKay, J.E., 1830b, On the extinct reptiles of the genera *Mosasaurus* and *Geosaurus* found in the secondary formation of New Jersey; and on the occurrence of a substance recently named coprolite by Dr. Buckland in the same locality: Annals of the Lyceum of Natural History of New York, v. 3, p. 134-141.

De Klerk, W. J., Forster, C. A., Sampsoin, S. D., Chinsamy, A., Ross-Callum, I., 2000, A new coelurosaurian dinosaur from the Early

Cretaceous of South Africa: Journal of Vertebrate Paleontology, v. 20, p. 324-332.

de los Reyes, M., Poiré, D., Soibelzon, L., Zurita, A. E. and Arrouy, M.J., 2013, First evidence of scavenging of a glyptodont (Mammalia, Glyptodontidae) from the Pliocene of the Pampean region (Argentina): Taphonomic and paleoecological remarks: Palaeontologia Electronica, v. 16 (2); 15A; 13p; palaeo-electronica.org/content/2013/434-scavenging-of-a-glyptodont.

Delson, E., Faure, M., Guérin, C., Aprile, L., Argant, J., Blackwell, B.A.B., Debard, E., Harcourt-Smith, W., Martin-Suarez, E., Monguillon, A., Parenti, F., Pastre, J. F., Sen, S., Skinner, A.R., Swisher, C.C. and Valli, A.M.F., 2006, Franco-American renewed research at the Late Villafranchian locality of Senèze (Haute-Loire, France); *in* Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations. Proceedings of the 18th International Senckenberg Conference (VI IPCW) Volume I, p. 275-290.

de Lumley, H., 1969, A Paleolithic camp at Nice: Scientific American, v. 220, p. 42-50.

De Mendoza, R.S. and Haidr, N.S., 2018, Predation trace fossils in a new specimen of *Cayaoa bruneti* Tonni (Aves, Anseriformes) from the Gaiman Formation (early Miocene, Chubut, Argentina): Ameghiniana, v. 55, p. 483-488.

Deméré T. A. and Cerutti R. A., 1982, A Pliocene shark attack on a cetotheriid whale: Journal of Paleontology, v. 56, p. 1480–1482.

Demírcan, H. and Uchman, A., 2010, Kiss of death of a hunting fish: Trace fossil *Osculichnus labialis* igen. et isp. nov. from late Eocene–early Oligocene prodelta sediments of the Mezardere Formation, Thrace Basin, NW Turkey: Acta Geologica Polonica, v. 60, p. 29-38.

Demírcan, H. and Uchman, A., 2016, Ichnology of the Mezardere Formation (Late Eocene-early Oligocene) in the Gökçeada island, western Turkey: Geodinamica Acta, v. 28 (1-2), p. 86-100.

Deng, T. and Tseng, Z.J., 2010, Osteological evidence for predatory behavior of the giant percrocutid (*Dinocrocuta gigantea*) as an active hunter: Chinese Science Bulletin, v. 55, p. 1790-1794.

Dennell, R.W., Coard, R. and Turner, A., 2008, Predators and scavengers in early Pleistocene southern Asia: Quaternary International, v. 192, p. 78-88.

Denison, R.H., 1956, A review of the habitat of the earliest vertebrates: Fieldiana Geology, v. 11, p. 361-457.

Dennis, K. and Miles, R. S., 1981, A pachyosteomorph arthrodire from Gogo, western Australia: Zoological Journal of the Linnaean Society, v. 73, p. 213-258.

Denton, R. K., Dobie, J. L. and Parris, D. C., 1997, The marine crocodilian *Hyposaurus* in North America; *in* Callaway, J. M. and Nicholls, E. L., eds., Ancient marine reptiles. San Diego, Academic Press, p. 375-397.

Dentzien-Dias, P.C., Poinar, G. and Francischini, H. 2017: A new actinomycete from a Guadalupian vertebrate coprolite from Brazil: Historical Biology, v. 29, p. 770-776.

Dentzien-Dias, P., Carrillo-Briceño, J.D., Francischini, H. and Sánchez, R., 2018, Paleoecological and taphonomical aspects of the Late Miocene vertebrate coprolites (Urumaco Formation) of Venezuela: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 490, p. 590-603.

Dentzien-Dias, P., Hunt, A.P., Lucas, S.G., Francischini, H. and Gulotta, M., 2021, Coprolites from shallow marine deposits of the Nanjemoy Formation, Lower Eocene of Virginia, USA: Lethaia, v. 54, p. 26-39.

Dentzien-Dias, P.C., Figueiredo, A.E.Q., Horn, B., Cisneros, J.C. and Schultz, C.L., 2012, Paleobiology of a unique vertebrate coprolite concentration from Rio do Rasto Formation (middle/upper Permian), Paraná Basin, Brazil: Journal of South American Earth Sciences, v. 40, p. 53 –62.

Dentzien-Dias, P.C., Poinar, G., De Figueiredo, A.E.Q., Pacheco, A.C.L., Horn, B.L.D. and Schultz, C.L., 2013, Tapeworm eggs in a 270 million-year-old shark coprolite: PLoS ONE, v. 8, doi: 10.1371/journal.pone.0055007.

Denys, C., 2011, Des référentiels en taphonomie des petits vertébrés: Bilan et perspectives; *in* Laroulandie, V., Mallye, J.B. and Denys, C., eds., Taphonomie des petits vertébrés référentiels et transferts aux fossils: British Archaeological Reports, International Series 2269, p. 7–22.

Denys, C., Viriot, L., Daams, R., Pelaez-Campomanes, P., Vignaud, P., Andossa, L. and Brunet, M., 2003, A new Pliocene xerine sciurid (Rodentia) from Kossom Bougoudi, Chad: Journal of Vertebrate Paleontology, v. 23, p. 676-687.

Denys, C., Stoetzel, E., Andrews, P., Bailon, S., Rihane, A., Huchet, J.B., Fernández-Jalvo, Y., and Laroulandie, V., 2018, Taphonomy of small predators multi-taxa accumulations: Palaeoecological implications: Historical Biology, v. 30, p. 868–881.

de Oliveira, F. A., Santucci, R. M., de Oliveira, C. E. M., and de Andrade, M. B., 2021, Morphological and compositional analyses of coprolites from the Upper Cretaceous Bauru Group reveal dietary habits of notosuchian fauna: Lethaia, doi:org/10. 1111/let.12431.

DePalma, R.A., Burnham, D.A., Martin, L.D., Rothschild, B.M. and Larson, P.L., 2013, Physical evidence of predatory behavior in *Tyrannosaurus rex*: Proceedings of the National Academy of Sciences, v. 110, p. 12560-12564.

de Queiroz, A. and de Queiroz, K., 1987, Prey handling behavior of *Eumeces gilberti* with comments on headfirst ingestion in squamates: Journal of Herpetology, v. 21, p. 57-63.

de Rooij, J., 2020, Bite marks on *Triceratops* ribs attributed to crocodilian scavenging: Society of Vertebrate Paleontology, 80th Annual Meeting Virtual 2020, October 12-16 2020. www.vertpaleo.org Conference Program, unnumbered page.

de Saint Seine, P., 1949, Les poisons des calcaires lithographiques de Cerin (Ain): Nouvelles Archives de Muséum d'histoire naturelle de Lyon, v. 2, 1-351 p.

DeSantis, L.R. G., 2016, Dental microwear textures: Reconstructing diets of fossil mammals: Surface Topography: Metrology and Properties, v. 4, https://iopscience.iop.org/article/10.1088/2051-672X/4/2/023002.

de Valais, S., Apesteguía, S. and Garrido, A.C., 2012, Cretaceous small scavengers: Feeding traces in tetrapod bones from Patagonia, Argentina: PLoS ONE, v. 7(1): e29841, doi:10.1371/journal.pone.0029841.

de Valais, S., Díaz-Martínez, I., Citton, P., Maniel, I. and de la Fuente, M., 2020, A predation attempt in a Late Cretaceous pleurodire turtle from Patagonia: Cretaceous Research, 107, p.104290. https://doi.org/10.1016/j.cretres.2019.104290

De Vasconcellos, F.M., and Carvalho, I.S., 2010, Paleoichnological assemblage associated with *Baurusuchus salgadoensis* remains, a Baurusuchidae Mesoeucrocodylia from the Bauru Basin, Brazil (Late Cretaceous): New Mexico Museum of Natural History and Science, Bulletin 51, p. 227-237.

Diamond, J., Bishop, K.D. and Gilardi, J.D., 1999, Geophagy in New Guinea birds: Ibis, v. 141, p. 181-193.

DiBenedetto, J.N., 2002, Phytoliths extracted from Oligocene carnivore coprolites: Geological Society of America, Abstracts with Programs, v. 34, p. 47.

Dick, D.G., Schweigert, G. and Maxwell, E.E., 2016, Trophic niche ontogeny and palaeoecology of early Toarcian *Stenopterygius* (Reptilia: Ichthyosauria): Palaeontology, v. 59, p. 423-431.

Diedrich, C., 2006, By Ice Age spotted hyenas protracted, cracked, nibbled and chewed skeleton remains of *Coelodonta antiquitatis* (Blumenbach 1799) from the Lower Weichselian (Upper Pleistocene) freeland prey deposit site Bad Wildungen-Biedensteg (Hesse, NW Germany): Journal of Taphonomy, v. 4, p. 95–127.

Diedrich, C., 2008, The food of the miosiren *Anomotherium langenwieschei* (Siegfried–indirect proof of seaweed or seagrass by xenomorphic oyster fixation structures in the Upper Oligocene (Neogene) of the Doberg, Bünde (NW Germany) and comparisons to modern *Dugong dugon* (Müller) feeding strategies:

Senckenbergiana Maritima, v. 38, p. 59-73.

Diedrich, C.G., 2011, Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss, 1810) footprints and bone records from open air sites in northern Germany–evidence of hyena-lion antagonism and scavenging in Europe: Quaternary Science Reviews, v. 30, p. 1883-1906.

Diedrich, C.G., 2012a, An Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss 1823) population, their excrements and prey from the late Pleistocene hyena den of the Sloup Cave in the Moravian Karst, Czech Republic: Historical Biology, v. 24, p.161-185.

Diedrich, C.G., 2012b, Stomach and gastrointestinal tract contents in Late Cenomanian (Upper Cretaceous) teleosts from black shales of Germany and analysis of fish mortality and food chains in the upwelling-influenced Pre-North Sea Basin of Europe: New Mexico Museum of Natural History and Science, Bulletin 57, p. 241-256.

Diedrich, C.G., 2012c, Typology of Ice Age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) coprolite aggregate pellets from the European Late Pleistocene and their significance at dens and scavenging sites: New Mexico Museum of Natural History and Science, Bulletin 57, p. 369-377.

Diedrich, C.G., 2013, Extinctions of late Ice Age cave bears as a result of climate/habitat change and large carnivore lion/hyena/wolf predation stress in Europe: ISRN Zoology Volume 2013, ArticleID138319, 25 p., http://dx.doi: org/10.1155/2013/138319.

Diedrich, C.G., 2014, Ice Age spotted hyenas as Neanderthal exhumers and scavengers in Europe: Chronicles of Science, v. 1(1), p. 1-34.

Diedrich, C.G., 2015, The vertebrates from the Lower Ladinian (Middle Triassic) bonebed of Lamerden (Germany) as palaeoenvironment indicators in the Germanic Basin: Open Geosciences, v. 7, issue 1, id.62, 28 p. 10.1515/geo-2015-0062.

Diedrich, C.G. and Felker, C.D.H., 2012, Middle Eocene shark coprolites from shallow marine and deltaic coasts of the pre-North Sea Basin in central Europe: New Mexico Museum of Natural History and Science, Bulletin 57, p. 311-318.

Diefenbach, C.O., and Emslie, S.G., 1971, Cues influencing the direction of prey ingestion of the Japanese snake, *Elaphe climacophora*: Herpetologica, v. 27, p. 461-466.

Dietl, G. and Schweigert, G., 2001, Im Reich der Meerengel. München, Pfeil, 144 p.

Diffendal, R., Jr., (compiler), 2003, Field trip Ash Fall Historic Park: Field Trip 5: Association of American State Geologists, 95th Annual Meeting, Lincoln Nebraska, 37 p.

Dilger, W. C., 1957, The loss of teeth in birds: Auk, v. 74, p. 103-104.

Dinter, C., 2013, Crocodyliform bite marks on an articulated *Gryposaurus* (Dinosauria: Hadrosauridae) cranium from the Upper Cretaceous of southern Utah: Journal of Vertebrate Paleontology, v. 33 (supplement to no. 3), p. 116.

Dobkins, J.E. and Folk, R.L., 1970, Shape development on Tahiti-Nui: Journal of Sedimentary Petrology, v. 40, p. 1167-1203.

Dodson, P., 1973, The significance of small bones in paleoecological interpretation: Rocky Mountain Geology, v. 12, p. 15-19.

Dodson, P. and Wexlar, D., 1979, Taphonomic investigations of owl pellets: Paleobiology, v. p. 5, p. 275-284.

Doherty, J.M., 2009, Comparison of digestion through examination of fecal contents over differing feeding regimens in *Elaphe guttata*, *Elaphe obsoleta*, and *Chelydra serpentina* [M.S. thesis]: Boulder, University of Colorado, 42 p.

Dolowy, W.C., Fisher, L.E. and Williamson, W., 1960, Some observations on vomiting in animals: Journal of the American Veterinary Medical Association, v. 137, p. 426-427.

Dollo, L., 1887a, Le hainosaure et les nouveaux vertébrés fossiles du Musée de Bruxelles: Revue des Questions Scientifiques, v. 21, p. 504-539.

Dollo, L., 1887b, On some Belgian fossil reptiles: Geological Magazine, v. 4, p. 392-396.

Dollo, L., 1913, *Globidens fraasi*, mosasaurien mylodonte nouveau du Maestrichtien (Crétacé supérieur) du Limbourg, et l'éthologie de la nutrition chez les mosasauriens: Archives de Biologie, v. 28, p. 609-626.

Dominato, V.H.S., Mothé, D., Costa-da-Silva, R., Avilla, L.S., 2011, Evidence of scavenging on remains of the gomphothere *Haplomastodon waringi* (Proboscidea: Mammalia) from the Pleistocene of Brazil: Taphonomic and paleoecological remarks: Journal of South American Earth Science, v. 31, p. 171-177.

Domínguez-Rodrigo, M. and Piqueras, A., 2003, The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours: Journal of Archaeological Science, v. 30, p. 1385–1391.

Domínguez-Rodrigo, M., Gidna, A., Yravedra, J. and Musiba, C., 2012, A comparative neotaphonomic study of felids, hyenids and canids: An analogical framework based on long bone modification patterns: Journal of Taphonomy, v. 10, p. 147–164.

Dominici, S., Cioppi, E., Danise, S., Betocchi, U., Gallai, G., Tangocci, F., Valleri, G. and Monechi, S., 2009, Mediterranean fossil whale falls and the adaptation of mollusks to extreme habitats: Geology, v. 37, p. 815-818.

Dong, L. P., Huang, D. Y. and Wang, Y., 2012, Two Jurassic salamanders with stomach contents from Inner Mongolia, China: Chinese Science Bulletin, v. 57, p. 72-76.

Dong, Z. and Chen, P., 2000, A tiny fossil lizard in the stomach content of the feathered dinosaur *Sinosauropteryx* from northeastern China: Verebrata PalAsiatica, v. 38 (supplement), p. 10.

Donoghue, P. C. J. and Purnell, M. A., 2009, Distinguishing heat from light in debate over controversial fossils: BioEssays, v. 31, p. 178-189.

Donoghue P. C. J. and Smith M. P., 2001, The anatomy of *Turinia pagei* (Powrie) and the phylogenetic status of the Thelodonti: Transactions of the Royal Society of Edinburgh (Earth Sciences), v. 92, p. 15-37.

Donovan, S. K., Jagt, J. W. M. and Lewis, D. N., 2008, Ichnology of Late Cretaceous echinoids from the Maastrichtian type area (The Netherlands, Belgium) – 1. A healed puncture wound in *Hemipneustes striatoradiatus* (Leske): Bulletin of the Mizunami Fossil Museum, v. 34, p. 73–76.

Dornbos, S.Q., 2011, Phosphatization through the Phanerozoic; *in* Allison, P. A. and Bottjer, D. J., eds., Taphonomy: Process and bias through time, Topics in Geobiology 32. New York, Springer, p. 435-456.

Dorr, J., Jr., 1966, Wind-polished stones: Two similar sites: Papers of the Michigan Academy of Science, Arts and Letters, v. 51, p. 265-273.

Dortangs, R.W., 1998, Ichnofossielen; *in* Jagt J.W.M., Leloux J. and Dhondt A.V., eds., Fossielen van de St. Pietersberg. Grondboor & Hamer, v. 52, p. 150-151.

Dortangs, R.W., Schulp, A.S., Mulder, E.W., Jagt, J.W., Peeters, H.H. and De Graaf, D.T., 2002, A large new mosasaur from the Upper Cretaceous of The Netherlands: Netherlands Journal of Geosciences, v. 81, p. 1-8.

Dortch, J., Cupper, M., Grün, R., Harpley, B., Lee, K. and Field, J., 2016, The timing and cause of megafauna mass deaths at Lancefield Swamp, south-eastern Australia: Quaternary Science Reviews, v. 145, p. 161-182.

Doyle, P. and MacDonald, D.I., 1993, Belemnite battlefields: Lethaia, v. 26, p. 65-80.

Druckenmiller, P.S. and Russell, A.P., 2008, Skeletal anatomy of an exceptionally complete specimen of a new genus of plesiosaur from the Early Cretaceous (early Albian) of northeastern Alberta, Canada: Palaeontographica A, v. 283, p. 1-33.

Druckenmiller, P.S. and Russell, A.P., 2009, Earliest North American occurrence of Polycotylidae (Sauropterygia: Plesiosauria) from the Lower Cretaceous (Albian) Clearwater Formation, Alberta, Canada: Journal of Paleontology, v. 83, p. 981-989.

Druckenmiller, P.S., Daun, A.J., Skulan, J.L. and Pladziewicz, J.C., 1993, Stomach contents in the Upper Cretaceous shark *Squalicorax falcatus*: Journal of Vertebrate Paleontology, v. 13 (supplement to no. 3), p. 33A-34A.

Druckenmiller, P.S., Hurum, J.H., Knutsen, E.M. and Nakrem, H.A., 2012, Two new ichthyosaurs (Ichthyosauria: Ophthalmosauridae) from the Agardhfjellet Formation (Upper Jurassic: Volgian), Svalbard, Norway: Norwegian Journal of Geology, v. 92, p. 311-339.

Druckenmiller, P.S., Kelley, N., Whalen, M.T., Mcroberts, C. and Carter, J.G., 2014, An Upper Triassic (Norian) ichthyosaur (Reptilia, Ichthyopterygia) from northern Alaska and dietary insight based on gut contents: Journal of Vertebrate Paleontology, v. 34, p. 1460-1465.

Drumheller, S.K. and Boyd, C., 2011, Direct evidence of crocodyliform predation on small dinosaurians from the Kaiparowits Formation of Utah: Journal of Vertebrate Paleontology, v. 31 (supplement to no. 3), p. 101.

Drumheller, S.K. and Brochu, C.A., 2014, A diagnosis of *Alligator mississippiensis* bite marks with comparisons to existing crocodilian datasets: Ichnos, v. 21, p. 131-146.

Drumheller, S.K. and Brochu, C.A., 2016, Phylogenetic taphonomy: A statistical and phylogenetic approach for exploring taphonomic patterns in the fossil record using crocodylians: Palaios, v. 31, p. 463-478.

Drumheller, S.K., Stocker, M.R. and Nesbitt, S.J., 2014, Direct evidence of trophic interactions among apex predators in the Late Triassic of western North America: Naturwissenschaften, v. 101, p. 975-987.

Drumheller, S.K., McHugh, J.B., Kane, M., Riedel, A. and D'Amore, D.C., 2020, High frequencies of theropod bite marks provide evidence for feeding, scavenging, and possible cannibalism in a stressed Late Jurassic ecosystem: PLoS ONE, v. 15(5): e0233115, doi:org/10.1371/journal. pone.0233115.

Drumheller-Horton, S.K., 2012, An actualistic and phylogenetic approach to identifying and interpreting crocodylian bite marks [Ph.D. dissertation]: Iowa City, University of Iowa, 170 p.

Drymala, S.M. and Bader, K., 2012, Assessing predator–prey interactions through the identification of bite marks on an aetosaur (Archosauria, Suchia) osteoderm from the Upper Triassic (Norian) Chinle Formation in Petrified Forest: Journal of Vertebrate Paleontology, v. 32 (supplement to no. 3) p. 89.

Drymala, S.M., Bader, K. and Parker, W.G., 2021, Bite marks on an aetosaur (Archosauria, Suchia) osteoderm: Assessing Late Triassic predator-prey ecology through ichnology and tooth morphology: Palaios, v. 36, p. 28-37.

Duarte, A.N., Verde, M., Ubilla, M., Araújo, A., Martins, P.C., Reinhard, K.J. and Ferreira, L.F., 1999, Note on parasite eggs in mineralized Carnivora coprolites from the upper Pleistocene Sopas Formation, Uruguay: Paleopathology News, v. 107, p. 6-8.

Dubois, A., Grosjean, S. and Paicheler, J.C., 2009, Strange tadpoles from the lower Miocene of Turkey: Is paedogenesis possible in anurans?: Acta Palaeontologica Polonica, v. 55, p. 43-55.

Duff, R.S., 1949, Pyramid Valley. Christchurch, Pegasus Press for the Association of Friends of the Canterbury Museum, 48 p.

Duffin, C.J., 1979, Coprolites: A brief review with reference to specimens from the Rhaetic bone beds of England and South Wales: Mercian Geologist, v. 7, p. 191-204.

Duffin, C.J., 2009, "Records of warfare…embalmed in the everlasting hills:" A history of early coprolite research: Mercian Geologist, v. 2009, p. 101-111.

Duffin, C.J., 2010, Coprolites; *in* Lord, A.R. and Davis, P.G., ed., Fossils from the Lower Lias of the Dorset Coast: Palaeontological Association, Field Guides to Fossils, no. 13, p. 395-400.

Duffin, C.J., 2012a, Coprolites and characters in Victorian Britain: New Mexico Museum of Natural History and Science, Bulletin 57, p. 45-59.

Duffin, C.J., 2012b, The earliest published records of coprolites: New Mexico Museum of Natural History and Science, Bulletin, 57, p. 25-29.

Duffin, C.J. and Ward, D.J., 2020, Coprolites in an early Carboniferous microvertebrate fauna from Derbyshire, UK: Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, v. 297, p. 1-10.

Duke, G.E., 1997, Gastrointestinal physiology and nutrition in wild birds: Proceedings of the Nutrition Society, v. 56, p. 1049–1056.

Duke, G.E., Jegers, A.A., Loff, G. and Evanson, 0.A., 1975, Gastric digestion in some raptors: Comparative Biochemistry and Physiology, Part A Physiology, v. 50, p. 649-656.

Duke, G.E., Evanson, O.A., Redig, P.T. and Rhoades, D.D., 1976, Mechanism of pellet egestion in great horned owls (*Bubo virginianus*): American Journal of Physiology, v. 231, p. 1824-1829.

Dzik, J., Sulej, T. and Niedźwiedzki, G., 2008, A dicynodont-theropod association in the latest Triassic of Poland: Acta Palaeontologica Polonica, v. 53, p. 733-738.

Eaton, T.H., 1964, A captorhinomorph predator and its prey (Cotylosauria): American Museum Novitates, v. 2169, p. 1-3.

Eastman, C. R., 1904, A recent paleontological induction: Science, v. 20, p. 465-466.

Eastman, C. R., 1906, Sermons in stomach stones: Science, v. 23, p. 983.

Eastman, C. R., 1911, Jurassic saurian remains ingested within fish: Annals of the Carnegie Museum, v. 8, p. 182-187.

Ebert, M., Kölbl-Ebert, M. and Lane, J.A., 2015, Fauna and predator-prey relationships of Ettling, an actinopterygian fish-dominated Konservat Lagerstätte from the Late Jurassic of Southern Germany: PLoS ONE, v. 10(1):e0116140, doi:10.1371/ journal. pone.0116140.

Eberth, D.A. and Getty, M.A., 2005, Ceratopsian bonebeds: Occurrence, origins, and significance; *in* Currie, P.J. and Koppelhus, E.B., eds., Dinosaur Provincial Park: a spectacular ancient ecosystem revealed. Bloomington, Indiana University Press, p. 501–536.

Edwards, P., 1973a, A qualitative comparison of the chemical composition of recent feces and coprolites: Proceedings of the 83rd Nebraska Academy of Sciences, p. 12.

Edwards, P., 1973b, Qualitative x-ray diffraction fluorescence analysis of some Oligocene coprolites: Contributions to Geology, v. 12, p. 25.

Edwards, P., 1976, Fish coprolites from Fossil Butte, Wyoming: Rocky Mountain Geology, v. 14, p. 115-117.

Edwards, P. and Yatkola, D., 1974, Coprolites of White River (Oligocene) carnivorous mammals: Origin and paleoecologic and sedimentologic significance: Contributions to Geology, v. 13, p. 67-73.

Eichler, B. and Werneburg, R., 2010, Neufunde von *Branchiosauriern* aus dem Rotliegend von Frietal bei Dresden im UV-Licht: Geologica Saxonica, v. 56, p. 137-157.

Effinger, J.A., 1998, Entelodontidae; *in* Janis, C.M., Scott, K.M. and Jacobs, L.L., eds., Evolution of Tertiary mammals of North America, Volume 1, Terrestrial carnivores, ungulate and ungulate-like mammals. Cambridge, Cambridge University Press, p. 375-380.

Ehret, D.J. and Harrell, T.L., Jr., 2018, Feeding traces on a *Pteranodon* (Reptilia: Pterosauria) bone from the Late Cretaceous (Campanian) Mooreville Chalk in Alabama, USA: Palaios, v. 33, p. 414-418.

Ehret, D.J., MacFadden, B.J. and Salas-Gismondi, R., 2009, Caught in the act: Trophic interactions between a 4-million-year-old white shark (*Carcharodon*) and mysticete whale from Peru: Palaios, v. 24, p. 329-333.

Einarsson, E., Lindgren, J., Kear, B. P. and Siverson, M., 2010, Mosasaur bite marks on a plesiosaur propodial from the Campanian (Late Cretaceous) of southern Sweden: GFF, v. 132, p. 123-138.

Ekrt, B., Mikuláš, R., Wagner, J., Čermák, S., Procházková, K., Kadlecová, E. and Fejfar, O., 2016, New contribution to the palaeoichnology and taphonomy of the Ahníkov fossil site, Early Miocene, Most Basin (the Czech Republic): Fossil Imprint, v. 72, p. 202-214.

Elder, R.L., 1985, Principles of aquatic taphonomy with examples from the fossil record [Ph.D. dissertation]: Ann Arbor, University of

Michigan, 336 p..

Elder, R.L. and Smith, G.R., 1988, Fish taphonomy and environmental inference in paleolimnology: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 62, p. 577-592.

Elliott, D.K. and Petriello, M.A., 2011, New poraspids (Agnatha, Heterostraci) from the Early Devonian of the western United States: Journal of Vertebrate Paleontology, v. 31, p. 518-530.

Emery, K., 1941, Transportation of rock particles by sea mammals: Journal of Sedimentary Petrology, v. 11, p. 92-93.

Engesser, B. and Storch, G., 1999, Eomyiden (Mammalia, Rodentia) aus dem Oberoligozän von Enspel im Westerwald (Westdeutschland): Eclogae Geologicae Helvetiae, v. 92, p. 483–493.

Erickson, B.R., 1967, Fossil bird tracks from Utah: Museum Observor (Science Museum of Minnesota), v. 5, p. 1-7.

Erickson, B.R., 1984, Chelonivorous habits of the Paleocene crocodile *Leidysuchus formidabilis*: Scientific Publications of the Science Museum of Minnesota, New Series, v. 5, p. 1-9.

Erickson, G.M. and Olson, K.H., 1996, Bite marks attributable to *Tyrannosaurus rex*: Preliminary description and implications: Journal of Vertebrate Paleontology, v. 16, p. 175-178.

Erickson, G. M., van Kirk, S. D., Su, J.-T., Levenston, M.E., Caler, W. E. and Carter, D. R., 1996, Bite force estimation for *Tyrannosaurus rex* from tooth marked bone: Nature, v. 302, p. 706-708.

Eriksson, M.E. and Terfelt, F., 2007, Anomalous facies and ancient faeces in the latest middle Cambrian of Sweden: Lethaia, v. 40, p. 69-84.

Eriksson, M.E., Lindgren, J., Chin, K. and Månsby, U., 2011, Coprolite morphotypes from the Upper Cretaceous of Sweden: Novel views on an ancient ecosystem and implications for coprolite taphonomy: Lethaia, v. 44, p. 455-468.

Ernst, G., Kohring, R. and Rehfeld, U., 1996, Gastrolithe aus dem Mittel-Cenmomanium von Baddeckenstedt (Harzvorland) und ihre paläogeographische Bedeutung fur eine prällsedische Harzinsel: Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, v. 77, p. 503-543.

Esperante, R., Guinea, F.M. and Nick, K.E., 2009, Taphonomy of a Mysticeti whale in the Lower Pliocene Huelva Sands Formation (southern Spain): Geologica Acta, v. 7, p. 489-505.

Esperante, R., Brand, L.R., Chadwick, A. and Poma, O., 2002, Taphonomy of fossil whales in the diatomaceous sediments of the Miocene/Pliocene Pisco Formation, Peru; *in* Current topics on taphonomy and fossilization: Valencia, Spain, Ajuntament de Valencia, International Conference, Taphos 2002, 3rd Meeting on Taphonomy and Fossilization, p. 337-343.

Esperante, R., Brand, L.R., Chadwick, A.V. and Poma, O., 2015, Taphonomy and paleoenvironmental conditions of deposition of fossil whales in the diatomaceous sediments of the Miocene/Pliocene Pisco Formation, southern Peru– A new fossil-Lagerstätte: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 417, p. 337-370.

Esteban-Nadal, M., Cáceres, I. and Fosse, P., 2010, Characterization of a current coprogenic sample originated by *Canis lupus* as a tool for identifying a taphonomic agent: Journal of Archaeological Science, v. 37, p. 2959-2970.

Eudes-Deslongchamps, J. A., 1838, Mémoire sur le *Poikilopleuron bucklandii*, grand saurien fossile, intermédiaire entre les crocodiles et les lézards: Mémoire de la Société Linéene de Normandie, v. 6, p. 37-146.

Evans, S. E., 2016, Urodela; *in* Poyato-Ariza, F.J. and Buscalioni, Á.D., eds., Las Hoyas: A Cretaceous wetland: A multidisciplinary synthesis after 25 years of research on an exceptional fossil Lagerstätte from Spain: Volume dedicated to the late Jordi María de Gibert. Munich, Verlag Dr. Friedrich Pfeil, p. 138-142.

Everhart, M.J., 1999, Evidence of feeding on mosasaurs by the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*: Journal of Vertebrate Paleontology v. 17 (supplement to no. 3), p. 43-44.

Everhart, M.J., 2000, Gastroliths associated with plesiosaur remains in the Sharon Springs Member of the Pierre Shale (Late Cretaceous), western Kansas: Transactions of the Kansas Academy of Science, v. 103, p. 58-69.

Everhart, M.J., 2002, New data on cranial measurements and body length of the mosasaur, *Tylosaurus nepaeolicus* (Squamata; Mosasauridae), from the Niobrara Formation of western Kansas: Kansas Academy of Science, Transactions, v. 105, p. 33–43.

Everhart, M.J., 2003, First records of plesiosaur remains in the lower Smoky Hill Chalk Member (Upper Coniacian) of the Niobrara Formation in western Kansas: Kansas Academy of Sciences, Transactions, v. 106, p. 139-148.

Everhart, M.J., 2004a, Conchoidal fractures preserved on elasmosaur gastroliths are evidence for use in processing food: Journal of Vertebrate Paleontology, v. 24 (supplement to no. 3), p. 56A.

Everhart, M.J., 2004c, Late Cretaceous interaction between predators and prey. Evidence of feeding by two species of shark on a mosasaur: PalArch, Vertebrate Palaeontology Series, v. 1, p. 1-7.

Everhart, M.J., 2004b, Plesiosaurs as the food of mosasaurs: New data on the stomach contents of a *Tylosaurus proriger* (Squamata; Mosasauridae) from the Niobrara Formation of western Kansas: The Mosasaur, v. 7, p. 41-46.

Everhart, M.J., 2005a, Bite marks on an elasmosaur (Sauropterygia; Plesiosauria) paddle from the Niobrara Chalk (Upper Cretaceous) as probable evidence of feeding by the lamniform shark, *Cretoxyrhina mantelli*: PalArch, Vertebrate Paleontology, v. 2, p. 14-24.

Everhart, M.J., 2005b, Earliest record of the genus *Tylosaurus* (Squamata: Mosasauridae) from the Fort Hays Limestone (Lower Coniacian) of western Kansas: Kansas Academy of Science, Transactions, v. 108, p. 149-155.

Everhart, M. J., 2005c, Elasmosaurid remains from the Pierre Shale (Upper Cretaceous) of western Kansas. Possible missing elements of the type specimen of *Elasmosaurus platyurus* Cope, 1868?: PalArch, Vertebrate Palaeontology, v. 4, p. 19-32.

Everhart, M.J., 2005e, Oceans of Kansas– A natural history of the Western Interior sea. Bloomington, Indiana University Press, 322 p.

Everhart, M.J., 2005f, Probable plesiosaur gastroliths from the basal Kiowa Shale (Early Cretaceous) of Kiowa County, Kansas: Kansas Academy of Science, Transactions, v. 108, p. 109-115.

Everhart, M. J., 2005g, *Tylosaurus kansasensis*, a new species of tylosaurine (Squamata: Mosasauridae) from the Niobrara Chalk of western Kansas, U.S.A.: Netherlands Journal of Geosciences, v. 84, p. 231-240.

Everhart, M.J., 2006, The occurrence of elasmosaurids (Reptilia: Plesiosauria) in the Niobrara Chalk of western Kansas: Paludicola, v. 5, p. 170-183.

Everhart, M.J., 2008. A bitten skull of *Tylosaurus kansasensis* (Squamata: Mosasauridae) and a review of mosasaur-on-mosasaur pathology in the fossil record: Transactions of the Kansas Academy of Science, v. 111, p. 251-262.

Everhart, M.J., 2013, A new specimen of the marine turtle, *Protostega gigas* Cope (Cryptodira, Protostegidae), from the Late Cretaceous Smoky Hill Chalk of Western Kansas: Transactions of the Kansas Academy of Sciences, v. 116, p. 73.

Everhart, M.J., 2017, Oceans of Kansas–A natural history of the Western Interior sea (Second Edition). Bloomington, Indiana University Press, 427 p.

Everhart, M.J. and Everhart, P.A., 1994, Evidence of predation on the rare plethodid *Martinichthys* in the Smoky Hill Chalk (Upper Cretaceous) of western Kansas: Kansas Academy of Science, Abstracts, v. 13, p. 36.

Everhart, M.J. and Ewell, K., 2006, Shark-bitten dinosaur (Hadrosauridae) caudal vertebrae from the Niobrara Chalk (Upper Coniacian) of western Kansas: Transactions of the Kansas Academy of Science, v. 109, p. 27-36.

Everhart, M.J. and Hamm, S.A., 2005, A new nodosaur (Dinosauria: Nodosauridae) from the Smoky Hill Chalk (Upper Cretaceous) of western Kansas: Kansas Academy of Science, Transactions, v.

108, p. 15–21.

Everhart, M.J., Everhart, P.A. and Shimada, K., 1995, New specimen of shark bitten mosasaur vertebrae from the Smoky Hill Chalk (Upper Cretaceous) in western Kansas: Kansas Academy of Science Transactions, v. 14, p. 19.

Everhart, M.J., Hageman, S.A. and Hoffman, B.L., 2010, Another Sternberg "fish-within-a-fish" discovery: First report of *Ichthyodectes ctenodon* (Teleostei; Ichthyodectiformes) with stomach contents: Transactions of the Kansas Academy of Science, v. 113, p. 197-205.

Fahlke, J. M., 2012, Bite marks revisited – evidence for middle-to-late Eocene *Basilosaurus isis* predation on *Dorudon atrox* (both Cetacea, Basilosauridae): Palaeontologia Electronica, v. 15, issue 3; 32A, 16p; palaeo-electronica.org/content/2012-issue-3-articles/339-archaeocete-predation.

Falcon-Lang, H.J., Benton, M.J., Braddy, S.J. and Davies, S.J., 2006, The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Nova Scotia, Canada: Journal of the Geological Society, v. 163, p. 561-576.

Falk, A.R., 2004, Foot and hindlimb morphology, soft tissues, and tracemaking behaviors of Early Cretaceous birds from China and the Republic of Korea with a comparison to modern avian morphology and behavior [Ph.D. dissertation]: Lawrence, University of Kansas, 750 p.

Falk, A.R., Hasiotis, S.T. and Martin, L.D., 2010, Feeding traces associated with bird tracks from the Lower Cretaceous Haman Formation, Republic of Korea: Palaios, v. 25, p. 730-41.

Falk, A.R., Lim, J.D. and Hasiotis, S.T., 2014, A behavioral analysis of fossil bird tracks from the Haman Formation (Republic of Korea) shows a nearly modern avian ecosystem: Vertebrata Palasiatica, v. 52, p. 129-152.

Falk, D., Mccoy, V. and Wings, O., 2019, Ichnofossils of the Eocene Fossillagerstätte Geiseltal (Saxony-Anhalt, Germany): Hallesches Jahrbuch für Geowissenschaften, Beiheft, v. 46, p. 15-16.

Fan, R.Y., Zong, R.W. and Gong, Y.M., 2019, Fish hunting trace *Osculichnus* and the oldest *Sinusichnus sinuosus* from the Upper Devonian of South China: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 530, p. 103-112.

Fanti, F., Currie, P.J. and Burns, M.E., 2015, Taphonomy, age, and paleoecological implication of a new *Pachyrhinosaurus* (Dinosauria: Ceratopsidae) bonebed from the Upper Cretaceous (Campanian) Wapiti Formation of Alberta, Canada: Canadian Journal of Earth Sciences, v. 52, p. 250-260.

Fanti, F., Minelli, D., Conte, G.L. and Miyashita, T., 2016, An exceptionally preserved Eocene shark and the rise of modern predator–prey interactions in the coral reef food web: Zoological Letters, 2(1), p. 9. doi: 10.1186/s40851-016-0045-4.

Farlow, J.O., 1985, Notes; *in* Bird, R.T., Bones for Barnum Brown. Fort Worth, Texas Christian University Press, p. 209-211.

Farlow, J.O., 1987a, Lower Cretaceous dinosaur tracks, Paluxy River Valley, Texas. Field Trip Guidebook, South Central Section, Geological Society of America, Waco, Texas, Baylor University, 50 p.

Farlow, J., 1987b, Speculations about the diet and digestive physiology of herbivorous dinosaurs: Paleobiology, v. 13, p. 60-72.

Farlow, J.O. and Holtz, T.R., 2002, The fossil record of predation in dinosaurs: Paleontological Society Papers, v. 8, p. 251-266.

Farlow, J.O., O'Brien, M., Kuban, G.J., Dattilo, B.F., Bates, K.T., Falkingham, P.L., Piñuela, L., Rose, A., Freels, C. Kumagai, C., Libben, C., Smith, J. and Whitcraft, J., 2012, Dinosaur tracksites of the Paluxy River Valley (Glen Rose Formation, Lower Cretaceous), Dinosaur Valley State Park, Somervell County, Texas: Actas de V Jornadas Internacionales sobre Paleontologia de Dinosaurios y su Entorno, Salas de los Infantes, Burgos. Proceedings of the V International Symposium on Dinosaur Palaeontology and their Environment, p. 41-69.

Fea, N. and Harcourt, R., 1997, Assessing the use of fecal and regurgitate analysis as a means of determining the diet of New Zealand Fur Seals; *in* Hindell, M. and Kemper, C., eds., Marine mammal research in the Southern Hemisphere. Volume 1: Status, ecology and medicine. Chipping Norton, Beatty, p. 143-150.

Feibel, C.S., 1987, Fossil fish nests from the Koobi Fora Formation (Plio-Pleistocene) of northern Kenya: Journal of Paleontology, v. 61, p. 130–134.

Fejfar, O., Dvorák, Z. and Kadlecová, E., 2003, New record of early Miocene (MN3a) mammals in the open brown coal pit Merkur, North Bohemia, Czech Republic: Deinsea, v. 10, p. 163-182.

Fernándes, M.A., Fernandes, L.B. dos R. and Souto, P.R. de F., 2004, Occurrence of urolites related to dinosaurs in the Lower Cretaceous of the Botucatu Formation, Paraná Basin, São Paulo State, Brazil: Revista Brasileira de Paleontologia, v. 7, p. 263-268.

Fernández, V., Abdala, F., Carlson, K.J., Cook, D.C., Rubidge, B.S, Yates, A. and Tafforeau, P., 2013, Synchrotron reveals Early Triassic odd couple: Injured amphibian and aestivating therapsid share burrow: PLoS ONE, v. 8(6): e64978, doi:10.1371/journal.pone.0064978.

Fernández-Jalvo, Y., and Andrews, P. 1992. Small mammal taphonomy of Gran Dolina, Atapuerca (Burgos), Spain: Journal of Archaeological Science, v. 19, p. 407–428.

Fernández-Jalvo, Y. and Andrews, P., 2016, Atlas of taphonomic identifications: 1001+ images of fossil and recent mammal bone modification. New York, Springer, 359 p.

Fernández-Jalvo, Y., Andrews, P., Sevilla, P. and Requejo V., 2014, Digestion versus abrasion features in rodent bones: Lethaia, v. 4, p. 323-336.

Fernández–Jalvo, Y., Sánchez–Chillón, B., Andrews, P., Fernández–López, S. and Alcalá Martínez, L., 2002, Morphological taphonomic transformations of fossil bones in continental environments, and repercussions on their chemical composition: Archaeometry, v. 44, p. 353-361.

Fernández-Jalvo, Y., Andrews, P., Denys, C., Sese, C., Stoetzel, E., Marin-Monfort, D. and Pesquero, D., 2016, Taphonomy for taxonomists: Implications of predation in small mammal studies: Quaternary Science Reviews, v. 139, p. 138-157.

Fernándéz-Rodrìguez, C., Ramil, P. and Martìnez Cortizas, A., 1995, Characterization and depositional evolution of hyaena (*Crocuta crocuta*) coprolites from La Valina Cave (northwest Spain): Journal of Archaeological Science, v. 22, p. 597-607.

Ferreira, L.F., Araújo, A. and Duarte, A.N., 1993, Nematode larvae in fossilized animal coprolites from lower and middle Pleistocene sites, central Italy: Journal of Parasitology, v. 79, p. 440-442.

Ferreira, L. F., Araújo, A., Confalonieri, U., Chame, M. and Gomes, D.C., 1991, *Trichuris* eggs in animal coprolites dated from 30,000 years ago: Journal of Parasitology, v. 77, p. 491-493.

Ferreira, D.F., Bertini, R.J., Camossi, L.G. and Letizio, L.A., 2019, The first record of ascaridoidea eggs discovered in crocodyliformes hosts from the Upper Cretaceous of Brazil: Revista Brasileira de Paleontologia, v. 21, p. 238-244.

Figueirido, B., Tseng, Z.J. and Martín-Serra, A., 2013, Skull shape evolution in durophagous carnivorans: Evolution, v. 67, p. 1975-1993.

Fikentscher, R., 1933, Koproporphyrin in tertiären Krokodilkot: Zoologische Anzeiger, v. 103, p. 289-295.

Fiorelli, L.E., 2010, Predation bite-marks on a peirosaurid crocodyliform from the Upper Cretaceous of Neuquén Province, Argentina: Ameghiniana, v. 47, p. 387-400.

Fiorelli, L.E., Ezcurra, M.D., Hechenleitner, E.M., Arganaraz, E., Taborda, J.R., Trotteyn, M.J., von Baczko, M.B. and Desojo, J.B., 2013, The oldest known communal latrines provide evidence of gregarism in Triassic megaherbivores: Scientific Reports, v. 3, 3348 (2013), doi: org/10.1038/srep03348.

Fiorillo, A.R., 1991a, Prey bone utilization by predatory dinosaurs: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 88, p. 157-166.

Fiorillo, A.R., 1991b, Taphonomy and depositional setting of Careless Creek Quarry (Judith River Formation), Wheatland

County, Montana, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 81, p. 281-311.

Fiorillo, A.R., 1998, Dental micro wear patterns of the sauropod dinosaurs *Camarasaurus* and *Diplodocus*: Evidence for resource partitioning in the Late Jurassic of North America: Historical Biology, v. 13, p. 1-16.

Fiorillo, A.R., 2011, Microwear patterns on the teeth of northern high latitude hadrosaurs with comments on microwear patterns in hadrosaurs as a function of latitude and seasonal ecological constraints: Palaeontologia Electronica, v. 14, Issue 3; 20A:7 p.; palaeo-electronica.org/2011_3/7_fiorillo/index.html.

Fiorillo, A.R., McCarthy, P.J. and Flaig, P.P., 2010, Taphonomic and sedimentologic interpretations of the dinosaur-bearing Upper Cretaceous strata of the Prince Creek Formation, northern Alaska: Insights from an ancient high-latitude terrestrial ecosystem: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 295, p. 376-388.

Fischer, C.E., 1856, Die Fischreste aus den Plänerschichten von Plauen, Strehlen, Weinböhla und Gross-Sedlitz: Allgemeine deutsche naturhistorische Zeitung, v. 2, p. 134-145.

Fischer, W.A., 1978, The habitat of the early vertebrates: Trace and body fossil evidence from the Harding Formation (Middle Ordovician), Colorado: The Mountain Geologist, v. 15, p. 1-26.

Fisher, D.C., 1981a, Crocodilian scatology, microvertebrate concentrations, and enamel-less teeth: Paleobiology, v. 7, p. 262–275.

Fisher, D.C., 1981b, Taphonomic interpretation of enamel-less teeth in the Shotgun local fauna (Paleocene, Wyoming): Contributions of the Museum of Paleontology, University of Michigan, v. 25, p. 259–275.

Fleming, C., 1951, Sea lions as geological agents: Journal of Sedimentary Petrology, v. 21, p. 22-25.

Fluckiger, F. A., 1861, Über Koprolithen aus Baselland: Schweizer Zeitschrift Pharmacie, v. 3, p. 189-195.

Forbes, H. O., 1892, On the recent discovery of the remains of extinct birds in New Zealand: Nature, v. 45, p. 416-418.

Fordyce, N., Smith, R. and Chinsamy, A., 2012, Evidence of a therapsid scavenger in the late Permian Karoo Basin, South Africa: South African Journal of Science, v. 108, p. 114-118.

Forrest, R., 2000, A large rhomaleosaurid pliosaur from the Upper Lias of Rutland: Mercian Geologist, v. 15, p. 37-40.

Forrest, R., 2003, Evidence for scavenging by the marine crocodile *Metriorhynchus* on the carcass of a plesiosaur: Proceedings of the Geologists' Association, v. 114, p. 363-366.

Fortelius, M., and Solounias, N., 2000, Functional characterization of ungulate molars using the abrasion-attrition wear gradient: A new method for reconstructing paleodiets: American Museum Novitates, no. 3301, p. 1–36.

Fowler, D.W., and Sullivan, R.M., 2006, A ceratopsid pelvis with toothmarks from the Upper Cretaceous Kirtland Formation, New Mexico: Evidence of Late Campanian tyrannosaurid feeding behavior: New Mexico Museum of Natural History and Science, Bulletin 35, p. 127-130.

Fowler, D.W., Woodward, H.N., Freedman, E.A., Larson, P.L. and Horner, J.R., 2011, Reanalysis of "*Raptorex kriegsteini*": A juvenile tyrannosaurid dinosaur from Mongolia: PLoS ONE, v. 6(6): e21376, doi:10.1371/journal.pone.0021376.

Fraas, E., 1891, Die Ichthyosaurier der Süddeutschen Trias- und Jura-Ablagerungen: Tubingen, 81 p.

Fraas, E., 1910, Plesiosaurier aus der oberen Lias von Holzmaden: Palaeontographica, v. 57, p. 105-140.

Francischini, H., Dentzien-Dias, P. and Schultz, C.L., 2018, A fresh look at ancient dungs: The Brazilian Triassic coprolites revisited: Lethaia, v. 51, p. 389-405.

Frandsen, G., 2020, Coprolites of the world. Monee, Poozeum, 92 p.

Frandsen, G. and Godfrey, S. J., 2019, A gar-bitten coprolite from the Eocene Green River Formation near Kemmerer, Wyoming, U.S.A.: The Ecphora, v. 34(1), p. 2-4.

Franzen, J. L., 1976, Senckenburgs Grabungskampagne 1975 in Messel: erste Ergebnisse und Ausblick: Natur und Museum Frankfurt, v. 106, p. 217-223.

Franzen, J. L., 1977, Die Entstehung der Fossilfundstelle Messel: Berichte Naturforschende Gesellschaft zu Freiburg, v. 67, p. 53-58.

Franzen, J. L., 1984, Die Stammesgeschichte der Pferde in ihrer wissenschafthistorischen Entwickung: Natur und Museum Frankfurt, v. 114, p. 149-162.

Franzen, J.L., 1985, Exceptional preservation of Eocene vertebrates in the lake deposit of Grube Messel (West Germany): Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, v. 311, p. 181-186.

Franzen, J.L., 2001, Taphonomic analysis of the Messel Formation (Germany); *in* Gunnell, G. F. ed., Eocene biodiversity: Unusual occurrences and rarely sampled habitats. Boston, Kluwer Academic/Plenum Press, p. 197-214.

Franzen, J.L. Wilde, V., 2003, First gut contents of a fossil primate: Journal of Human Evolution, v. 44, p. 373-378.

Franzen, J.L. and Frey, E., 1993, *Europolemur* completed: Kaupia, v. 3, p. 130.

Franzen, J.L. and Wilde, V., 2003, First gut contents of a fossil primate: Journal of Human Evolution, v. 44, p. 373-378.

Franzen, J.L., Gingerich, P.D., Habersetzer, J., Hurum, J.H., von Koenigswald, W. and Smith, H., 2009, Complete primate skeleton from the middle Eocene of Messel in Germany: PLOS ONE, v. 4, et al. (2009)

Franzen, J.L., Gingerich, P.D., Habersetzer, J., Hurum, J.H., von Koenigswald, W. and Smith, H., 2009, Complete primate skeleton from the middle Eocene of Messel in Germany: PLOS ONE, v. 4(7): 10.1371/annotation/18555b51-1fd1-47b6-a362-acaaa24a53da, https://doi.org/10.1371/annotation/18555b51-1fd1-47b6-a362-acaaa24a53da.

Frei, S., Ortmann, S., Reutlinger, C., Kreuzer, M., Hatt, J.M. and Clauss, M., 2014, Comparative digesta retention patterns in ratites: The Auk, v. 132, p. 119–131.

Freimuth, W. J., 2020, Paleoecological utility of feeding traces at Egg Mountain, a rich terrestrial vertebrate locality of the Upper Cretaceous Two Medicine Formation, Montana, U.S.A. [M.S. thesis]: Bozeman, Montana State University, 209 p.

Freimuth, W. J., Varricchio, D.J., Brannick, A.L.,Weaver, L.N., Wilson Mantilla, G., 2021, Mammal-bearing gastric pellets potentially attributable to *Troodon formosus* at the Cretaceous Egg Mountain locality, Two Medicine Formation, Montana, USA: Palaeontology, 2021: doi: 10.1111/pala.12546.

Frenguelli, J., 1928, A proposito di alcune incisioni sull'omero di uno Squalodonte del Miocene della Patagonia: Bollettino della Società Geologica Italiana, v. 47, p. 1-9.

Frentzen, K., 1936, Ein fossiler Mageninhalt aus dem Lias Delta (Amaltheen-Schichten) von Reichenbach, Aalen: Beitrage Naturkund Forschungshefte S. W. Deutschland, v. 1, p. 153-156.

Frerichs, U., 2012, Bissspuren an einem *Echinocorys* aus dem Obercampan von Misburg: Arbeitskreis Paläontologie Hannover, v. 40, p. 91-92.

Freschi, A. 2017, New *Carcharodon* scavenging evidence on Pliocene whale bones remains from Northern Appennines: Quaderni del Museo Civico di Storia Naturale di Ferrara, v. 5, p. 33-36.

Frey, E. and Tischlinger, H., 2012, The Late Jurassic pterosaur *Rhamphorhynchus*, a frequent victim of the ganoid fish *Aspidorhynchus*?: PLoS ONE 7:e31945, doi: 10.1371/journal.pone.0031945.

Frey, E., Martill, D.M. and Buchy, M.C., 2003, A new crested ornithocheirid from the Lower Cretaceous of northeastern Brazil and the unusual death of an unusual pterosaur; *in* Buffetaut, E. and Mazin, J.M., eds., Evolution and palaeobiology of pterosaurs. Geological Society of London, Special Publications, v. 217, p. 55-63.

Frey, E., Buchy, M.C., Stinnesbeck, W. and López-Oliva, J.G., 2002, *Geosaurus vignaudi* n. sp. (Crocodyliformes: Thalattosuchia), first evidence of metriorhynchid crocodilians in the Late Jurassic (Tithonian) of central-east Mexico (State of Puebla): Canadian Journal of Earth Sciences, v. 39, p. 1467-1483.

Friedman, M. and Carnevale, G., 2018, The Bolca Lagerstätten: Shallow marine life in the Eocene: Journal of the Geological Society, v. 175, p. 569-579.

Friedman, M. and Sallan, L.C., 2012, Five hundred million years of extinction and recovery: A Phanerozoic survey of large-scale diversity patterns in fishes: Palaeontology, v. 55, p. 707-742.

Friedman, V., 2012, Vertebrate coprolites from the lower Eagle Ford Group of north central Texas and their paleoecological significance: New Mexico Museum of Natural History and Science, Bulletin 57, p. 221-228.

Frison, R.E., 1939, Hunting dinosaurs in Wyoming: Mineralogist, v. 7(7), p. 263-264.

Fritsch, A., 1895, Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, Band 3. Prague, F. Řivnáč 132 p.

Fritsch, A., 1907, Miscellanea Palaeontologica. I Palaeozoica. Prague, Rivnac, 23 p.

Fritz, F., Hummel, J., Kienzle, E., Arnold, C., Nunn, C., and Clauss, M., 2009, Comparative chewing efficiency in mammalian herbivores: Oikos, v. 11, p. 1623-1632.

Fritz, J., 2007, Allometrie der Kotpartikelgröße von pflanzenfressenden Säugern, Reptilien und Vögeln [Inaugural-Dissertation]: München, Ludwig-Maximilians-Universität, 272 p.

Fritz, J., Hummel, J., Kienzle, E., Wings, O., Streich, W.J., Clauss, M., 2011, Gizzard vs. teeth; it's a tie: Food-processing efficiency in herbivorous birds and mammals and implications for dinosaur feeding strategies: Paleobiology, v. 37, p. 577-586.

Frizzell, D. L. and Exline, H., 1958, Crustacean gastroliths from the Claiborne Eocene of Texas: Micropaleontology, v. 4, p. 273-280.

Frizzell, D. L. and Horton, W. C., 1961, Crustacean gastroliths from the Jackson Eocene of Louisiana: University of Missouri Columbia School of Mines and Metallurgy Bulletin, v. 99, p. 3-6.

Frost, S. R., Saanane, C., Starkovich, B. M., Schwartz, H., Schrenk, F. and Harvati, K., 2017, New cranium of the large cercopithecid primate *Theropithecus oswaldi leakeyi* (Hopwood, 1934) from the paleoanthropological site of Makuyuni, Tanzania: Journal of Human Evolution, v. 109, p. 46-56.

Froyd, C.A., Coffey, E.E.D., Van Der Knaap, W.O., Van Leeuwen, J.F.N., Tye, A. and Willis, K.J., 2013, The ecological consequences of megafaunal loss: Giant tortoises and wetland biodiversity: Ecology Letters. http://dx.doi.org/10.1111/ele.12203.

Fry, G.F., 1969, Prehistoric diet at Danger Cave, Utah as determined by the analysis of coprolites [M.A. thesis]: Salt Lake City, University of Utah, 69 p.

Fuentes, E.J., 2003, Predación crocodiliana a quelonios. Un *Neochelys* (Pelomedusidae), del Eoceno de Zemora, lisiando por un *Asiatosuchus*: Studia Geologica Salmanticensia, v. 39, p. 11-23.

Gagnier, P.-Y., Blieck, A.R. and Rodrigo, S.G., 1986, First Ordovician vertebrate from South America: Geobios, v. 19, p. 629-634.

Gahn, F. J., 2004, Parasitism and predation on Paleozoic crinoids [Ph.D. dissertation]: Ann Arbor, The University of Michigan, 120 p.

Gale, A.S. 1987, Goniasteridae (Asteroidea, Echinodermata) from the Late Cretaceous of north-west Europe. 1. Introduction. The genera *Metopaster* and *Recurvaster*: Mesozoic Research, v. 1, p. 1-69.

Gale, A.S., Kennedy, W.J. and Martill, D., 2017, Mosasauroid predation on an ammonite–*Pseudaspidoceras*–from the early Turonian of south-eastern Morocco: Acta Geologica Polonica, v. 67, p. 31-46.

Gall, J.-C., 1971, Faunes et paysages du Grès à Voltzia du nord des Vosges. Essai paleoecologique sur le Buntsandstein superieur: Mémoires du Service de la Carte Géologique d'Alsace et de Lorraine, v. 34, p. 1-138.

Gall, J-C and Grauvogel-Stamm, L., 1993, Paleoecology of terrestrial ecosystems from the Buntsandstein (Lower Triassic) of eastern France: New Mexico Museum of Natural History and Science, Bulletin 3, p. 141-145.

Gallagher, W.B., Tumanova, T.A. and Dodson, P., 1998, CT Scanning Asian ankylosaurs: Paleopathology in a *Tarchia* skull: Journal of Vertebrate Paleontology, v. 18 (supplement to no. 3), p. 44-45.

Galle, A. and Mikuláš, R., 2003. Evidence of predation on the rugose coral *Calceola sandalina* (Devonian, Czech Republic): Ichnos, v. 10, p. 41-45.

Galton, P. M., 1976, Prosauropod dinosaurs (Reptilia; Saurischia) of North America: Postilla, v. 169, p. 1-98.

Galton, P., 1985, Diet of prosauropod dinosaurs from the Late Triassic and Early Jurassic: Lethaia, v. 18, p. 116.

Galton, P. M., 1986, Herbivorous adaptations of Late Triassic and Early Jurassic dinosaurs; *in* Padian, K., ed., The beginning of the age of dinosaurs. Cambridge, Cambridge University Press, p. 204-221.

Gambaryan, P.P. and Kielan-Jaworowska, Z., 1995, Masticatory musculature of Asian taeniolabidoid multituberculate mammals: Acta Palaeontologica Polonica, v. 40, p. 45-108.

Gangloff, R.A. and Fiorillo, A.R., 2010, Taphonomy and paleoecology of a bonebed from the Prince Creek Formation, North Slope, Alaska: Palaios, v. 25, p. 299-317.

Gangloff, R.A., May, K.C. and Pasch, A.D., 1999, Dinosaur ichnofossils of the Nanushuk and Colville Groups, Northern Alaska: The Alaska Geological Society 1999 Science and Technology Conference, p. 14.

Gans, C., 1952, The functional morphology of the egg-eating adaptations in the snake genus: *Dasypeltis*: Zoologica, v. 37, p. 209–244.

Gans, C., 1974, Biomechanics: An approach to vertebrate biology. Ann Arbor, University of Michigan Press, 261 p.

Gao, K.Q. and Shubin, N.H., 2003, Earliest known crown-group salamanders: Nature, v. 422, p. 424-428.

Garassino, A. and Donovan, D.T., 2000, A new family of coleoids from the Lower Jurassic of Osteno, northern Italy: Palaeontology, v. 43, p. 1019-1038.

Gaudry, A., 1887, L'Actinodon: Mémoire extrait des Nouvelles Archives du Muséum National d'Histoire naturelle, Serie 2, v. 10, 30 p.

Gautier, A., 1993, Trace fossils in archaeozoology: Journal of Archaeological Science, v. 20, p. 511-523.

Gawne, C.E., 1975, Rodents from the Zia Sand Miocene of New Mexico: American Museum Novitates, no. 2586, 25 p.

Gebo, D.L., and Simons, E. S., 1984, Puncture marks on early African anthropoids: American Journal of Physical Anthropology, v. 63, p. 31-35.

Geinitz, H.B., 1842, Über einige Petrfakte des Zechsteins und Muschelkalks: Neues Jahrbuch für Mineralogie, Geognosie und Petrefactenkunde, v. 1842, p. 576-579.

Geister, J., 1998, Lebensspuren von Meersauriern und ihren beutetieren im mittleren Jura (Callovien) von Liesberg, Schweiz: Facies, v. 39, p.105-124.

Gekker, E. L. and Gekker, R. F., 1955, [Remains of Teuthoidea from the White Lias and Lower Cretaceous of the Volga region]. Voprosi Palaeontologii, v. 1955(2), p. 36-44. [In Russian]

Georgalis, G.L., Rage, J.C., de Bonis, L. and Koufos, G.D., 2018, Lizards and snakes from the late Miocene hominoid locality of Ravin de la Pluie (Axios Valley, Greece): Swiss Journal of Geosciences, v. 111, p. 169-181.

Gerts, O. F., 1902, Report of the leader of the expedition of the Imperial Academy of Sciences to the Berezovka to dig up a mammoth carcass. Izvestiya Imperial Akademy Nauk [Proceedings of the Imperial Academy of Sciences], v. 16, p. 137-174. [In Russian].

Ghosh, P., Bhattacharya, S.K. Sahni, A., Kar, R.K., Mohabey, D.M. and Ambwani, K., 2003, Dinosaur coprolites from the Late Cretaceous (Maastrichtian) Lameta Formation of India: Isotopic and other markers suggesting a C3 plant diet: Cretaceous Research, v. 24, p. 743-750.

Gianechini, F.A. and de Valais, S., 2016, Bioerosion trace fossils on bones of the Cretaceous South American theropod *Buitreraptor gonzalezorum* Makovicky, Apesteguía and Agnolín, 2005

(Deinonychosauria): Historical Biology, v. 28, p. 533-549.

Gignac, P.M. and Erickson, G.M., 2017, The biomechanics behind extreme osteophagy in *Tyrannosaurus rex*: Scientific Reports, v. 7, 2012 (2017), doi: org/10.1038/s41598-017-02161-w.

Gignac, P. M., Makovicky, P. J., Erickson, G. M. and Walsh, R. P., 2010, A description of *Deinonychus antirrhopus* bite marks and estimates of bite force using tooth indentation simulations: Journal of Vertebrate Paleontology, v. 30, p. 1169-1177.

Gilardi, J.D., Duffey, S.S., Munn, C.A. and Tell, L.A., 1999, Biochemical functions of geophagy in parrots: Detoxification of dietary toxins and cytoprotective effects: Journal of Chemical Ecology, v. 25, p. 897-922.

Gilbert, C.C., McGraw, W.S. and Delson, E., 2009, Plio-Pleistocene eagle predation on fossil cercopithecids from the Humpata Plateau, southern Angola: American Journal of Physical Anthropology, v. 139, p. 421-429.

Gilfillian, A.M. and Olsen, P.E., 2000, The coelacanth *Diplurus longicaudatus* as the origin of the large coprolites occurring in the Triassic-Jurassic lacustrine strata of eastern North America: Geological Society of America, Abstracts with Programs, v. 32(1), p. 20.

Gill, J.L., Mclauchlan, K.K., Skibbe, A.M., Goring, S., Zirbel, C.R. and Williams, J.W., 2013, Linking abundances of the dung fungus *Sporormiella* to the density of bison: Implications for assessing grazing by megaherbivores in palaeorecords: Journal of Ecology, v. 101, p. 1125-1136.

Gillette, D.D., 1990, Gastroliths of a sauropod dinosaur from New Mexico: Journal of Vertebrate Paleontology, v. 10 (supplement to no. 3), p. 24A.

Gillette, D.D., 1991, *Seismosaurus halli,* gen. et sp. nov., a new sauropod dinosaur from the Morrison Formation (Upper Jurassic/ Lower Cretaceous) of New Mexico, USA: Journal of Vertebrate Paleontology, v. 11, p. 417-433.

Gillette, D.D., 1994, *Seismosaurus*: The Earth Shaker. New York, Columbia University Press, 205 p.

Gillette, D.D., 1995, True grit: Natural History, v. 104(6), p. 41-43.

Gilmore, B., 1992, Scroll coprolites from the Silurian of Ireland and the feeding of early vertebrates: Palaeontology, v. 35, p. 319-333.

Gilmore, C.W., 1920, Osteology of the carnivorous Dinosauria in the United States National Museum: With special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*: Proceedings of United States National Museum, v. 60, 1-154.

Gilpin, E., 1886, The Geology of Cape Breton Island, Nova Scotia: Quarterly Journal of the Geological Society, v. 42, p. 515-526.

Gingerich, P.D., 1977, A small collection of fossil vertebrates from the middle Eocene Kuldana and Kohat formations of Punjab (Pakistan): Contributions from the Museum of Paleontology, The University of Michigan, v. 24, p. 190-203.

Gingerich, P.D., 1987, Early Eocene bats (Mammalia, Chiroptera) and other vertebrates in freshwater limestones of the Willwood Formation, Clark's Fork Basin, Wyoming: Contributions from the Museum of Paleontology, The University of Michigan, v. 27, p. 275-320.

Gingerich, P.D., 1994, New species of *Apheliscus*, *Haplomylus*, and *Hyopsodus* (Mammalia, Condylarthra) from the late Paleocene of southern Montana and early Eocene of northwestern Wyoming: Contributions from the Museum of Paleontology, The University of Michigan, v. 29, p. 119-134

Gingras, M.K., Armitage, I.A., Pemberton, S.G. and Clifton, H.E., 2007, Pleistocene walrus herds in the Olympic Peninsula area: Trace-fossil evidence of predation by hydraulic jetting: Palaios, v. 22, p. 539-545.

Gionfriddo, J.P. and Best, L.B., 1999, Grit use by birds: A review: Current Ornithology, v. 15, 89-148.

Girod P., and Rösner T., 2013, Spurenfossilien (Ichnofossilien); *in* Schneider, C., ed., Fossilien aus dem Campan von Hannover, 3, komplett überarbeitete Auflage. Hannover, Arbeitskreis Paläontologie Hannover, p. 280–286.

Girotti, O., Capasso Barbato, L., Esu, D., Kotsakis, A., Martinetto, E., Petronio, C., Sardella, R. and Squazzini, E., 2004, The section of Torre Picchio (Terni, Umbria, Central Italy): A Villafranchian site rich in mammals, molluscs, ostracods and plants: Revista Italiana di Paleontologia e Stratigrafia, v. 109, p. 77-98.

Glinskiy, V.N. and Mark-Kurik, E., 2016, Revision of *Psammosteus livonicus* Obruchev (Agnatha, Heterostraci) from the Devonian Amata Regional Stage of the NW of the East European Platform: Estonian Journal of Earth Sciences, v. 65, p. 1-18.

Glowiak, E. M., 2007, Gypsum Cave revisited: Faunal and taphonomic analysis of a Rancholabrean to Holocene fauna in southern Nevada [M.S. thesis]: Las Vegas, University of Nevada at Las Vegas, 132 p.

Gobetz, K.E., 2006, Possible burrows of mylagaulids (Rodentia: Aplodontoidea: Mylagaulidae) from late Miocene (Barstovian) Pawnee Creek Formation of northeastern Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 119–136.

Gobetz, K.E., and Hattin, D.E., 2002, Rodent-gnawed carbonate rocks from Indiana: Proceedings of the Indiana Academy of Science, v. 111, p. 1-8.

Gobetz, K.E. and Martin, L.D., 2006, Burrows of a gopher-like rodent, possibly *Gregorymys* (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 305-314.

Godfrey, S.J., 1997, Tetrapods (amphibians and reptiles); *in* Shabica, C. W. and Hay, A. A., eds., Richardson's guide to the fossil fauna of Mazon Creek. Chicago, Northeastern Illinois University, p. 256-269.

Godfrey, S., 2003, Miocene sharks and smoking guns…: Bugeye Times (Quarterly Newsletter of Calvert Marine Museum), v. 28(1), p. 1, 5-7.

Godfrey, S. J., 2021, Shark-bitten Miocene baleen whale ulna: The Ecphora, v. 36(3), p. 11.

Godfrey, S.J. and Altman, J., 2005, A Miocene cetacean vertebra showing a partially healed compression fracture, the result of convulsions or failed predation by the Giant White Shark, *Carcharodon megalodon*: Jeffersoniana: Contributions from the Virginia Museum of Natural History, v. 16, p. 1-12.

Godfrey, S. J. and Frandsen, G., 2016, Vertebrate-bitten coprolite from South Carolina: The Ecphora, v. 31(1), p. 12-14.

Godfrey, S.J. and Palmer, B.T., 2015, Gar-bitten coprolite from South Carolina, USA: Ichnos, v. 22, p. 103–108.

Godfrey, S.J. and Smith, J., 2010, Shark-bitten vertebrate coprolites from the Miocene of Maryland: Naturwissenschaften, v. 97, p. 461–467.

Godfrey, S.J., Nance, J.R. and Riker, N.L., 2021, *Otodus*-bitten sperm whale tooth from the Neogene of the Coastal Eastern United States: Acta Palaeontologica Polonica, doi:https://doi.org/10.4202/app.00820.2020.

Godfrey, S.J, Alford, A., Collareta, A. and Weems, R.E., 2020, A Paleocene vertebrate-bitten crocodilian coprolite from Liverpool Point, Maryland, USA: Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, v. 296, p. 237-244.

Godfrey, S.J., Ellwood, M., Groff, S. and Verdin, M.S., 2018, *Carcharocles*-bitten odontocete caudal vertebrae from the Coastal Eastern United States: Acta Palaeontologica Polonica, v. 63, p. 463-468.

Godoy, P.L., Montefeltro, F.C., Norell, M.A. and Langer, M.C., 2014, An additional baurusuchid from the Cretaceous of Brazil with evidence of interspecific predation among Crocodyliformes: PLoS ONE, v. 9(5): e97138, doi:10.1371/journal.pone.0097138.

Goldring, R., Pollard, J.E. and Radley, J.D., 2005, Trace fossils and pseudofossils from the Wealden strata (non-marine Lower Cretaceous) of southern England: Cretaceous Research, v. 26, p. 665–685.

Gommery, D., Pickford, M. and Senut, B., 2007, A case of carnivore-inflicted damage to a fossil femur from Swartkrans, comparable to that on a hominid femur representing *Orrorin tugenensis,* BAR 1003'00 (Kenya): Annals of the Transvaal Museum, v. 44, p. 215-218.

Gônet, J., Rozada, L., Bourgeais, R. and Allain, R., 2019, Taphonomic study of a pleurosternid turtle shell from the Early Cretaceous of Angeac-Charente, southwest France: Lethaia, v. 52, p. 232-243.

Gong, Y., Zhang, L. and Wu, Y., 2010, Carboniferous coprolites from Qinhuangdao, North China: Science China Earth Sciences, v. 53, p. 213-219.

Goodman-Lowe, G.D., 1998, Diet of the Hawaiian monk seal (*Monachus schauinslandi*) from the Northwestern Hawaiian Islands during 1991 to 1994: Marine Biology, v. 132, p. 535–546.

Gordon, C.M., Roach, B.T., Parker, W.G. and Briggs, D.E., 2020, Distinguishing regurgitalites and coprolites: A case study using a Triassic bromalite with soft tissue of the pseudosuchian archosaur *Revueltosaurus*: Palaios, v. 35, p. 111-121.

Górecki, A., Barbacka, M., Niedźwiedzki, G., Jarzynka, A., Pacyna, G. and Ziaja, J., 2019, Plant remains from fossil faeces (coprolites) of a large predator from the Early Jurassic of Poland (Sołtyków); *in* Fekete, K., Michalík, J. and Reháková, D., eds*.,* XIV Jurassica Conference and Workshop of the ICS Berriasian Group, Field Trip Guide and Abstracts Book, Earth Science Institute, Slovak Academy of Sciences and Faculty of Natural Sciences, Comenius University, Bratislava, p. 105-106.

Gorzelak, P., Niedźwiedzki, G. and Skawina, A., 2010, Pathologies of non-marine bivalve shells from the Late Triassic of Poland: Lethaia, v. 43, p. 285-289.

Gorzelak, P., Salamon, M.A. and Baumiller, T.K., 2012, Predator-induced macroevolutionary trends in Mesozoic crinoids: Proceedings of the National Academy of Sciences, v. 18, p. 7004–7007.

Gorzelak, P.L., Rakowicz, L., Salamon, M.A. and Szrek, P., 2011, Inferred placoderm bite marks on Devonian crinoids from Poland: Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, v. 259, p. 105-112.

Götzinger, G. and Becker, H., 1932, Zur geologischen Gliederung des Wienerwaldflysches (Neue Fossilfunde): Jahrbuch der Geologischen Bundesanstalt, Vienna, v. 82, p. 343-395.

Govender R., 2015, Shark-cetacean trophic interaction, Duinefontein, Koeberg, (5 Ma), South Africa: South African Journal of Science, v. 111, p. 11-12.

Govender, R., 2019, Early Pliocene fossil cetaceans from Hondeklip Bay, Namaqualand, South Africa: Historical Biology, p.1-20, doi: org/10.1080/08912963.2019.1650273.

Govender, R. and Chinsamy, A., 2013, Early Pliocene (5 Ma) shark-cetacean interaction from Langebaanweg, western coast of South Africa: Palaios, v. 28, p. 27-77.

Grande, L., 1980, Paleontology of the Green River Formation, with a review of the fish fauna. Geological Survey of Wyoming, Bulletin 63, 333 p.

Grande, L., 1984, Paleontology of the Green River Formation, with a review of the fish fauna (Second Edition): Wyoming State Geological Survey, Bulletin 63, 333 p.

Grande, L., 2013, The lost world of fossil lake: Snapshots from deep time. Chicago, University of Chicago Press, 425 p.

Grandstaff, B.S., 1998, Mosasaur bite marks on a turtle plastron from the Late Maastrichtian Hornerstown Formation of New Jersey: Journal of Vertebrate Paleontology, v. 18 (supplement to no. 3), p. 47A.

Grange, D.R., Storrs, G.W., Carpenter, S. and Etches, S., 1996, An important marine vertebrate-bearing locality from the Lower Kimmeridge Clay (Upper Jurassic) of Westbury, Wiltshire: Proceedings of the Geologists' Association, v. 107, p. 107-116.

Grawe-Baumeister, J., Schweigert, G. and Dietl, G., 2000, Echiniden aus dem Nusplinger Plattenkalk (Ober-Kimmeridgium, Südwestdeutschland): Stuttgarter Beiträge zur Naturkunde (B), v. 286, p. 1-39.

Greb, S.F., Storrs, G.W., Garcia, W.J. and Eble, C.F., 2015, Late Mississippian vertebrate palaeoecology and taphonomy, Buffalo Wallow Formation, western Kentucky, USA: Lethaia, v. 49, p. 99-218.

Green, J.L. and Croft, D.A., 2018, Using dental mesowear and microwear for dietary inference: A review of current techniques and applications; *in* Croft, D.A, Su, F. and Simpson, S.W., eds., Methods in paleoecology: Reconstructing Cenozoic terrestrial environments and ecological communities. Cham, Springer International Publishing, p. 53–73.

Green, M., 1948, A new species of dog (*Tomarctus*) from the lower Pliocene of California: University of California, Department of Geological Sciences, Bulletin, v. 28, p. 81-90.

Greene, H.W., 1976, Scale overlap, a directional sign stimulus for prey ingestion by ophiophagous snakes: Zeitschrift für Tierpsychologie, v. 41, p. 113-120.

Greene, H.W., 1983, Dietary correlates of the origin and radiation of snakes: American Zoologist, v. 23, p. 431-441.

Greene, W.D., 1956, Dinosaur gizzard stones Wyoming: The Mineralogist, v. 24, p. 51-55.

Greenwood, P.H., 1951, Fish remains from Miocene deposits of Rusinga Island and Kavirondo Province, Kenya: Annals and Magazine of Natural History, v. 4, p. 1192-1201.

Gregor, H.J., 1982, *Pinus aurimontana* N. Sp.-eine neue Kiefernart aus dem Jungtertiaer des Goldbergs (Ries.): Stuttgarter Beitrage zur Naturkunde, Series B, Geologie und Palontologie, v. 83, p. 1-19.

Gregory, M.R., 1991, New trace fossils from the Miocene of Northland, New Zealand: *Rorschachichnus amoeba* and *Piscichnus waitemata*: Ichnos, v. 1, p. 195-205.

Gregory, M.R., Balance, P.F., Gibson, G.W. and Ayling, A.M., 1979, On how some rays (Elasmobranchia) excavate feeding depressions by jetting water: Journal of Sedimentary Petrology, v. 49, p. 1125-1130.

Grigg, G.C. and Kirshner, D., 2015, Biology and evolution of crocodylians. Ithaca, Cornell University Press, 649.

Grigorescu, D., 1992, Nonmarine Cretaceous formations of Romania; *in* Mateer, N.J. and Chen, P., eds., Aspects of nonmarine Cretaceous geology. Special volume of ICGP Project 245. Beijing, China Ocean Press, p. 142-164.

Gripp, K., 1929, Über Verletzungen an Seeigeln aus der Kreide Norddeutschlands: Paläontologische Zeitschrift, v. 11, 238–245.

Gudger, E.W., 1949, Natural history notes on tiger sharks, *Galeocerdo tigrinus*, caught at Key West, Florida, with emphasis on food and feeding habits: Copeia, v. 1949, p. 39-47.

Guinot, G., Adnet, S. and Cappetta, H., 2012, An analytical approach for estimating fossil record and diversification events in sharks, skates and rays: PLoS ONE, v. 7(9): e44632, doi:10.1371/journal.pone.0044632.

Gunnell, G.F., Lehmann, T., Ruf, I., Habersetzer, J., Morlo, M., Rose, K.D., 2018, Ferae—Animals that eat animals; *in* Smith, K.T., Schaal, S.F.K. and Habersetzer, J., eds., Messel—An ancient greenhouse ecosystem. Stuttgart, Schweizerbart, p. 271-283.

Guth, C., 1962, Un insectivore de Menat: Annales de Paléontologie, v. 48, p. 1-10.

Gutherz, S.B., Groenke, J.R., Sertich, J.J.W., Burch, S.H. and O'Connor, P.M., 2020, Paleopathology in a nearly complete skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) Cretaceous Research, v. 115, doi.org/10.1016/j.cretres.2020.104553.

Guthörl, P., 1959, Hundert Jahre Pälaontologie und Karbonstratigraphie im Saarbrückener Steinkohlengbiet: Bergfreiheit, v. 24, p. 111-129.

Guthrie, R.D., 1990, Frozen fauna of the mammoth steppe: The story of Blue Babe. Chicago, University of Chicago Press, 323 p.

Habersetzer, J., Rabenstein, R. and Gunnell, G. F., 2018, Bats – highly specialized nocturnal hunters with echolocation; *in* Smith, K.T., Schaal, S.F.K. and Habersetzer, J., eds., Messel – ancient greenhouse ecosystem. Frankfurt am Main, Senckenberg

Gesellschaft für Naturforschung, p. 249-261.

Habersetzer, J., Richter, G. and Storch, G., 1994, Paleoecology of early middle Eocene bats from Messel, FRG: Aspects of flight, feeding and echolocation: Historical Biology, v. 8, p. 235-260.

Häntzschel, W., El-Baz, F. and Amstutz, G.C., 1968, Coprolites: An annotated bibliography: Geological Society of America Memoir, v. 108, 132 p.

Hall, H.J., 1969, Rehydration and concentration of parasite ova in human coprolites from the Great Basin [Honor's Thesis, Department of Anthropology]: Salt Lake City, University of Utah, 68 p

Hamilton, R.F.M. and Trewin, N.H., 1988, Environmental controls on fish faunas of the Middle Devonian Orcadian Basin; *in* McMillan, N.J., Embry, A.F. and Glass, D.J., eds., Devonian of the world. Canadian Society of Petroleum Geologists, Memoir, v. 14, p. 589-600.

Hamilton, R.F.M. and Trewin, N.H., 1994, Taphonomy of fish beds from the Upper Flagstone Group of the Middle Old Red Sandstone, Caithness: Scottish Journal of Geology, v. 30, p. 175-181.

Hamm, S.A. and Shimada, K., 2007, The Late Cretaceous anacoracid shark, *Pseudocorax laevis* (Leriche), from the Niobrara Chalk of western Kansas: Transactions of the Kansas Academy of Science, v. 110, p. 44-52.

Hammer, W.R. and Hickerson, W.J., 1993, A brief review of Mesozoic terrestrial vertebrates from the Transantarctic Mountains including evidence of scavenging theropod: Antarctic Journal of the United States, v. 28, p. 33-35.

Hanks, H.D. and Shimada, K., 2002, Vertebrate fossils including non–avian remains and the first shark–bitten bird bone, from a Late Cretaceous (Turonian) marine deposit of northeastern South Dakota: Journal of Vertebrate Paleontology, v. 22 (supplement to no. 3), p. 62A.

Hansen, B.B., 2014, Description and analysis of a Rhaetian vertebrate coprolite assemblage of the Kap Stevard Formation, Jameson Land, East Greenland [M.S. thesis]: Copenhagen, University of Copenhagen, 97 p.

Hansen, B.B., Milàn, J., Clemmensen, L.B., Adolfssen, J.S., Estrup, E.J., Klein, N., Mateus, O. and Wings, O., 2016, Coprolites from the Late Triassic Kap Stewart Formation, Jameson Land, East Greenland: Morphology, classification and prey inclusions; *in* Kear, B. P., Lindgren, J., Hurum, J. H., Milàn, J. and Vajda, V., eds., Mesozoic biotas of Scandinavia and its Arctic Territories: Geological Society of London, Special Publications, v. 434, p. 49-69.

Hansen, M.C., 1990 and Mapes, R.H., 1990, A predator-prey relationship between sharks and cephalopods in the late Paleozoic; *in* Boucot, A. J., Evolutionary paleobiology of behavior and coevolution. Elsevier, Amsterdam p. 189-192.

Hansen, R.M., 1978, Shasta ground sloth food habits, Rampart Cave, Arizona: Paleobiology, v. 4, p. 302-319.

Hansen, R.M., 1980, Late Pleistocene plant fragments in the dungs of herbivores at Cowboy Cave; *in* Jennings, J. D., ed., Cowboy Cave: University of Utah, Anthropological Papers, v. 104, p. 179-189.

Hans-Volker, K. and Nyhuis, C. J., 2012, *Ctenochelys stenoporus* (Hay, 1905) (Testudines: Toxochelyidae) and *Clidastes* sp. (Squamata: Mosasauridae) from the Upper Cretaceous of NW-Germany: Studia Geologica Salmanticensia, v. 9, p. 129-142.

Happ, J., 2008, An analysis of predator–prey behavior in a head-to-head encounter between *Tyrannosaurus rex* and *Triceratops*; *in* Larson P. and Carpenter K., eds., *Tyrannosaurus rex* the tyrant king. Bloomington, Indiana University Press, p. 355–370.

Hardcastle, J., 1889, Origin of the loess deposit of the Timaru Plateau: Transactions of the New Zealand Institute, v. 22, p. 406-414.

Hares, C., 1917, Gastroliths in the Cloverly Formation: Proceedings of the Academy and Affiliated Societies, the Geological Society of Washington, v. 7, p. 429.

Hargrave, J.E., 2007, *Pteranodon* (Reptilia: Pterosauria): stratigraphic distribution and taphonomy in the lower Pierre Shale Group (Campanian), western South Dakota and eastern Wyoming; *in* Martin, J.E. and Parris, D.C., eds., The geology and paleontology of the Late Cretaceous marine deposits of the Dakotas: Geological Society of America, Special Papers, v. 427, p. 215-225.

Harington, C.R., 1996, Paleoecology of a Pliocene beaver-pond site in the Canadian Arctic Islands: 30th International Geological Congress, Beijing, China, Abstracts, v. 2, p. 114

Harington, C.R., 2002, Yukon horse: Beringian Research Notes, v. 14, p. 1-4.

Harrington, C. R., 2007, Late Pleistocene mummified mammals; *in* Elias, S. A., ed., Encyclopedia of Quaternary science. Amsterdam, Elsevier, p. 3197-3202.

Harington, C.R., Ross, R.L., Mathewes, R.W., Stewart, K.M., and Beattie, O., 2004, A late Pleistocene Steller Sea Lion (*Eumetopias jubatus*) from Courtenay, British Columbia: Its death, associated biota, and paleoenvironment: Canadian Journal of Earth Sciences, v. 41, p. 1285-1297.

Harper, E.M. and Peck, L.S., 2016, Latitudinal and depth gradients in marine predation pressure: Global Ecology and Biogeography, v. 25, p. 670-678.

Harrell, S. D. and Schwimmer, D. R., 2010, Coprolites of *Deinosuchus* and other crocodylians from the Upper Cretaceous of western Georgia, USA: New Mexico Museum of Natural History and Science, Bulletin 51, p. 209-213.

Harris, J.D., 1997, A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas [M.S. thesis]: Dallas, Southern Methodist University, 204 p.

Harris, J.D., 1998, A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status and paleobiogeographical implications, based on a new specimen from Texas: New Mexico Museum of Natural History and Science, Bulletin 13, 75 p.

Harris, J.W., Williamson, P.G., Verniers, J., Tappen, M.J., Stewart, K., Helgren, D., de Heinzelin, J., Boaz, N.T. and Bellomo, R.V., 1987, Late Pliocene hominid occupation in Central Africa: The setting, context, and character of the Senga 5A site, Zaire: Journal of Human Evolution, v. 16, p. 701-728.

Harrison, T., 2011, Coprolites: Taphonomic and paleoecological implications; *in* Harrison, H. T., ed., Paleontology and geology of Laetoli: human evolution in context geology, geochronology, paleoecology and paleoenvironment, Volume 1. Dordrecht, Springer, p. 279-292.

Hart, D. and Sussman, R.W., 2005, Man the hunted: Primates, predators, and human evolution. Boulder, Westview Press, 336 p.

Hasiotis, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177-268.

Hasiotis, S. T., Platt, B. F., Hembree, D. I. and Everhart, M. J. 2007, The trace-fossil record of vertebrates; *in* Miller, W. III, ed., Trace fossils: Concepts, problems, prospects. Elsevier, Amsterdam, p. 196-218.

Hastings, A.K., Bloch, J.I. and Jaramillo, C.A., 2015, A new blunt-snouted dyrosaurid, *Anthracosuchus balrogus* gen. et sp. nov. (Crocodylomorpha, Mesoeucrocodylia), from the Palaeocene of Colombia: Historical Biology, v. 27, p. 998-1020.

Hastings, A.K., Bloch, J.I., Jaramillo, C.A., Rincon, A.F. and MacFadden, B.J., 2013, Systematics and biogeography of crocodylians from the Miocene of Panama: Journal of Vertebrate Paleontology, v. 33, p. 239-263.

Hattin, D.E., 1996, Fossilized regurgitate from Smoky Hill Member of Niobrara Chalk (Upper Cretaceous) of Kansas, USA: Cretaceous Research, v. 17, p. 443–450.

Hattin, D. E., 1988, Rudists as historians: Fort Hays Studies, Third Series, v. 10, p. 4-22.

Haubold, H., 1990, Ein neuer Dinosaurier (Ornithischia, Thyreophora) aus dem unteren Jura des nördlichen Mitteleuropa: Revue de Paléobiologie, v. 9, p. 149-177.

Haubold, H. and Schaumberg, 1985, Die Fossilien des Kupferschiefers: Pflanzen-und Tierwelt zu Beginn des Zechsteins-eine Erzlagerstätte und ihre Paläonthologie. Wittenberg, A. Ziemsen Verlag, 223 p.

Hauff, B., 1921, Untersuchung der Fossilfundstatten in Posidonienschiefer des oberen Lias Württemberg: Palaeontographica, v. 64, p. 1-42

Haughton, S.H., 1930, Notes on the Karroo Reptilia from Madagascar: Transactions of the Royal Society of South Africa, v. 18, p. 125-136.

Havlik, P., Aiglstorfer, M., Beckmann, A.K., Gross, M. and Böhme, M., 2014, Taphonomical and ichnological considerations on the late middle Miocene Gratkorn locality (Styria, Austria) with focus on large mammal taphonomy: Palaeobiodiversity and Palaeoenvironments, v. 94, p. 171-188.

Hawkes, L., 1951, The erratics of the English Chalk: Proceedings of the Geologists Association, v. 62, p. 257-268.

Hawkins, A.D., Liu, H.P., Briggs, D.E., Muscente, A.D., McKay, R.M., Witzke, B.J. and Xiao, S., 2018, Taphonomy and biological affinity of three-dimensionally phosphatized bromalites from the Middle Ordovician Winneshiek Lagerstätte, northeastern Iowa, USA: Palaios, v. 33, p. 1-15.

Haynes, G., 1980, Evidence of carnivore gnawing on Pleistocene and Recent mammalian bones: Paleobiology, v. 6, p. 341-351.

Haynes, G., 1982, Utilization and skeletal disturbances of North American prey carcasses: Arctic, v. 35, p. 266-281.

Haynes, G., 1983, A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore long bones: Paleobiology, v. 9, p. 164-172.

Haynes, G., 1991, Mammoths, mastodonts and elephants: Biology, behavior and the fossil record. Cambridge, Cambridge University Press, 413 p.

Heidtke, U.H.J., 2007 Ein ausgestorbenes Fischkonzept: Acanthodier, schwache Krieger im Kettenhemd; *in* Schindler, T. and Heidtke, U.H.J, eds., Kohlesümpfe, Seen und Halbwüsten-Dokumente einer rund 300 Millionen Jahre alten Lebewelt zwischen Saarbrücken und Mainz: Pollichia Sonderveröffentlichung, v. 10, p. 230-238.

Heintz, A., 1938, Notes on Arthrodira: Norsk Geografisk Tidsskrift, v. 18, p. 1-27.

Heizer, R.E, and Napton, L.K., 1969, Biological and cultural evidence from Prehistoric human coprolites: Science, v. 165, p. 563-68.

Hejnol, A. and Martín-Durán, J.M., 2015, Getting to the bottom of anal evolution: Zoologischer Anzeiger, v. 256, p.61-74.

Hembree, D.I. and Blair, M.G., 2016, A paleopedological and ichnological approach to interpreting spatial and temporal variability in early Permian fluvial deposits of the lower Dunkard Group, West Virginia, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 454, p. 246-266.

Hembree, D.I. and Bowen, J.J., 2017, Paleosols and ichnofossils of the Upper Pennsylvanian–lower Permian Monongahela and Dunkard groups (Ohio, USA): A multi-proxy approach to unraveling complex variability in ancient terrestrial landscapes: Palaios, v. 32 p. 295-320.

Hembree, D.I. and Hasiotis, S.T., 2004, Using paleosols and ichnofossils to interpret the changing paleoecology, paleoenvironments and paleoclimate of the Eocene-Oligocene White River Formation, northeastern Colorado: Geological Society of America, Abstracts with Programs, v. 36(5), p. 63.

Hembree, D.I. and Hasiotis, S.T., 2007, Paleosols and ichnofossils of the White River Formation of Colorado: Insight into soil ecosystems of the North American midcontinent during the Eocene-Oligocene transition: Palaios, v. 22, p. 123-142.

Hembree, D.I., and Hasiotis, S.T., 2008, Miocene vertebrate and invertebrate burrows defining compound paleosols in the Pawnee Creek Formation, Colorado, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 270, p. 349-365,

Henderson, D.M., 2003, Effects of stomach stones on buoyancy and equilibrium of a floating crocodilian: A computational analysis: Canadian Journal of Zoology, v. 81, p. 1346-1357.

Henderson, D.M., 2006. Floating point: A computational study of buoyancy equilibrium and gastroliths in plesiosaurs: Lethaia, v. 39, p. 227-244.

Henslow, J.S., 1845, On nodules, apparently coprolitic, from the Red Crag, London Clay, and Greensand: Notices and Abstracts of the British Association for the Advancement of Science, v. 15, p. 51-52.

Hewitt, R.A. and Westermann, G.E.G., 1990, Mosasaur tooth marks on the ammonite *Placenticeras* from the Upper Cretaceous of Alberta, Canada: Canadian Journal of Earth Sciences, v. 27, p. 469-472.

Hill, C.R., 1976, Coprolites of *Ptilophyllum* cuticles from the Middle Jurassic of North Yorkshire: Bulletin of the British Museum of Natural History (Geology), v. 27, p. 289-294.

Hill, R.V., Roberts, E.M., Tapanila, L., Bouare, M.L., Sissoko, F. and O'Leary, M.A., 2015, Multispecies shark feeding in the Trans-Saharan seaway: Evidence from Late Cretaceous dyrosaurid (Crocodyliformes) fossils from northeastern Mali: Palaios, v. 30 p. 589-596.

Hilton, G.M., Furness, R.W. and Houston, D.C., 2000a, A comparative study of digestion in North Atlantic seabirds: Journal of Avian Biology, v. 31, p. 36–46.

Hilton, G.M., Furness, R.W. and Houston, D.C., 2000b, The effects of diet switching and mixing on digestion in seabirds: Functional Ecology, v. 14, p. 145–154.

Hilton, G.M., Houston, D.C. and Furness, R.W., 1998, Which components of diet quality affect retention time of digesta in seabirds?: Functional Ecology, v. 12, p. 929–939.

Hilton, G.M., Houston, D.C., Barton, N.W.H., Furness, R.W. and Ruxton, G.D., 1999, Ecological constraints on digestive physiology in carnivorous and piscivorous birds: Journal of Experimental Zoology Part A: Ecological Genetics and Physiology, v. 283, p. 365–376.

Hirsch, K.F., Kihm, A.J. and Zelenitsky, D.K., 1997, New eggshell of ratite morphotype with predation marks from the Eocene of Colorado: Journal of Vertebrate Paleontology, v. 17, p. 360-369.

Hitchcock, E., 1844, Report on ichnolithology or fossil footmarks, with a description of several new species, and the coprolites of birds from the valley of Connecticut River, and of a supposed footmark from the valley of the Hudson River: American Journal of Science, v. 47, p. 292-322.

Hockett, B.S., 1996, Corroded, thinned and polished bones created by golden eagles (*Aquila chrysaetos*): Taphonomic implications for archaeological interpretation: Journal of Archaeological Science, v. 23, 587–591.

Hodnett, J.-P. and Lucas, S. G., 2018, A nonmarine Late Pennsylvanian vertebrate assemblage in a marine bromalite from the Manzanita Mountains, Bernalillo County, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 79, p. 251-260.

Hoernes, R., 1904, Über Koprolithen und Enterolithen: Biologie Centralblatte, Leipzig, v. 24, p. 566–576.

Hoffmann, R. and Keupp, 2015, Definition of (paleo-) pathological phenomena; *in* King, C., Korn, D., De Baets, K., Kruta, I. and Mapes, R.H., eds., Ammonoid paleobiology: From anatomy to ecology. Topics in Geobiology 43. New York, Springer, p. 877-926.

Hoffmann, R., and Stevens, K., 2020, The palaeobiology of belemnites–foundation for the interpretation of rostrum geochemistry: Biological Reviews, v. 95, p. 94–123, doi: org/10.1111/brv.12557.

Hoffmann, R., Stevens, K., Keupp, H., Simonsen, S. and Schweigert, G., 2019, Regurgitalites–a window into the trophic ecology of fossil cephalopods: Journal of the Geological Society, v. 177, p. 82-102.

Hoffmann, R., Bestwick, J., Berndt, G., Berndt, R., Fuchs, D. and Klug, C., 2020, Pterosaurs ate soft-bodied cephalopods (Coleoidea): Scientific Reports, v. 10, 1230 (2020), doi.org/10.1038/s41598-020-57731-2.

Hölder, H., 1955, Ein Jura-Krokodil mit Magensteinen: Aus Heimat,

v. 63, p. 84-88.

Holgado, B., Dalla Vecchia, F.M., Fortuny, J., Bernardini, F. and Tuniz, C., 2015, A reappraisal of the purported gastric pellet with pterosaurian bones from the Upper Triassic of Italy: PLoS ONE, v. 10(11): e0141275, doi:10.1371/journal.pone.0141275.

Holland, B., Bell, P.R., Fanti, F., Hamilton, S., Larson, D.W., Sissons, R., Sullivan, C., Vavrek, M.J., Wang, Y. and Campione, N.E., 2021, Taphonomy and taxonomy of a juvenile lambeosaurine (Ornithischia: Hadrosauridae) bonebed from the late Campanian Wapiti Formation of northwestern Alberta, Canada: PeerJ 9:e11290, doi: 10.7717/peerj.11290.

Holland, T., 2018, The mandible of *Kronosaurus queenslandicus* Longman, 1924 (Pliosauridae, Brachaucheniinae), from the Lower Cretaceous of Northwest Queensland, Australia: Journal of Vertebrate Paleontology, v. 38, e1511569.

Hollocher, K. and Hollocher, T.C., 2012, Early processes in the fossilization of terrestrial feces to coprolites, and microstructure preservation: New Mexico Museum of Natural History and Science, Bulletin 57, p. 79–92.

Hollocher, K.T., Hollocher, T.C. and J. Keith Rigby, J. K., Jr., 2010, A phosphatic coprolite lacking diagenetic permineralization from the Upper Cretaceous Hell Creek Formation, northeastern Montana: Importance of dietary calcium phosphate in preservation: Palaios, v. 25, p.132–140.

Hollocher, K.T., Alcober, O.A., Colombi, C.E. and Hollocher, T.C., 2005, Carnivore coprolites from the Upper Triassic Ischigualasto Formation, Argentina: Chemistry, mineralogy, and evidence for rapid initial mineralization: Palaios, v. 20, p. 51-63.

Hollocher, T.C., Chin, K., Hollocher, K.T., and Kruge, M.A., 2001, Bacterial residues in coprolite of herbivorous dinosaurs: Role of bacteria in mineralization of feces: Palaios, v. 16, p. 547-565.

Hone, D.W. and Chure, D.J., 2018, Difficulties in assigning trace makers from theropodan bite marks: An example from a young diplodocoid sauropod: Lethaia, v. 51, p. 456-466.

Hone, D.W.E. and Tanke, D.H., 2015, Pre- and postmortem tyrannosaurid bite marks on the remains of *Daspletosaurus* (Tyrannosaurinae: Theropoda) from Dinosaur Provincial Park, Alberta, Canada: PeerJ, v. 3:e885, doi:10.7717/peerj.885.

Hone, D.W.E. and Watabe, M., 2010, New information on scavenging and selective feeding behavior of tyrannosaurids: Acta Palaeontologica Polonica, v. 55, p. 627-634.

Hone, D.W.E., Habib, M.B. and Lamanna, M.C., 2013, An annotated and illustrated catalogue of Solnhofen (Upper Jurassic, Germany) pterosaur specimens at Carnegie Museum of Natural History: Annals of Carnegie Museum, v. 82, p. 65–191.

Hone, D.W., Tanke, D.H. and Brown, C.M., 2018a, Bite marks on the frill of a juvenile *Centrosaurus* from the Late Cretaceous Dinosaur Provincial Park Formation, Alberta, Canada: PeerJ, v. 6:e5748; doi: 10.7717/peerj.5748.

Hone, D.W.E., Witton, M.P. and Habib, M.B., 2018b, Evidence for the Cretaceous shark *Cretoxyrhina mantelli* feeding on the pterosaur *Pteranodon* from the Niobrara Formation: PeerJ, v. 6:e6031, doi.org/10.7717/peerj.6031.

Hone, D., Henderson, D.M., Therrien, F. and Habib, M.B., 2015, A specimen of *Rhamphorhynchus* with soft tissue preservation, stomach contents and a putative coprolite: PeerJ, v. 3: e1191, doi.org/10.7717/peerj.1191.

Hone, D., Tsuihiji, T., Watabe, M. and Tsogtbaatr, K., 2012, Pterosaurs as a food source for small dromaeosaurs: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 331, p. 27-30.

Hoorn, C., 1994, An environmental reconstruction of the palaeo-Amazon river system (Middle–Late Miocene, NW Amazonia): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 112, p. 187-238.

Horner, J.R., 1992, Cranial morphology of *Prosaurolophus* (Ornithischia: Hadrosauridae) with descriptions of two new hadrosaurid species and an evaluation of hadrosaurid phylogenetic relationships: Museum of the Rockies, Occasional Paper No. 2, 119 p.

Horner, J. R. and Lessem, D., 1993, The complete *T. rex*. New York, Simon and Schuster, 239 p.

Horrocks, M., D'Costa, D., Wallace, R., Gardner, R. and Renzo Kondo, R., 2004, Plant remains in coprolites: Diet of a subalpine moa (Dinornithiformes) from southern New Zealand: Emu, v. 104, p. 149-156.

Horsthemke, E., Ledendecker, S. and Porada, H., 1990, Depositional environments and stratigraphic correlation of the Karoo sequence in northwestern Damaraland: Communications of the Geological Survey of South West Africa/Namibia, v. 6, p. 63-73.

Horstmann, G. and Maier, D., 1957, Neue Sauriergewölle aus dem Bielefelder Dogger: Aufschluss, v. 8, p. 17-21.

Horton, A., 2012, The occurrence of calcium phosphate in the Mesozoic and Tertiary of eastern England: Mercian Geologist, v. 18, p. 60-68.

Horton, D.R. and Wright, R.V., 1981, Cuts on Lancefield bones: Carnivorous *Thylacoleo*, not humans, the cause: Archaeology in Oceania, v. 16, p. 73-80.

Hoskin, C.M., Guthrie, R.D. and Hoffman, B. L. P. O., 1970, Pleistocene, Holocene and Recent bird gastroliths from Interior Alaska: Arctic, v. 23, p. 14-23.

Hospitaleche, C.A. 2016, Paleobiological remarks on a new partial skeleton of the Eocene Antarctic penguin *Palaeeudyptes klekowskii*: Ameghiniana, v. 53 p. 269–281.

Höss, M., Dilling, A., Currantt, A. and Pääbo, S., 1996, Molecular phylogeny of the extinct ground sloth *Mylodon darwinii*: Proceedings of the National Academy of Sciences, v. 93, p. 181-85.

Houck, K.J., Fleming, J., Guerrero, R., Heimink, N., Heberton, A., Itano, W., Titus, A. and Barrick, J.E., 2004, Paleontology of the Bassam Park fossil beds (Pennsylvanian), San Isabel National Forest, Colorado: Geological Society of America, Abstracts with Programs, v. 36, p. 413.

Houpt, T. J., C.J. Flis, C. J., Bakker, R.T. and Temple, D. T., 2020, *Dimetrodon*s disassembling prey: Multiple taphonomic signatures at Craddock Bone Bed, Seymour, TX: Society of Vertebrate Paleontology, 80th Annual Meeting Virtual 2020, October 12-16 2020 www.vertpaleo.org Conference Program, unnumbered page.

Howard, J. D., Mayou, T. V. and Heard, R.W., 1977, Biogenic sedimentary structures formed by rays: Journal of Sedimentary Petrology, v. 47, p. 339-346.

Hu, S.X., Zhang, Q.Y., Chen, Z Q., Zhou, C.Y., Lü, T., Xie, T., Wen, W., Huang, J.Y. and Benton, M.J., 2011, The Luoping biota: Exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction: Proceedings of the Royal Society of London, Series B, v. 278, p. 2274–2282.

Hu, Y., Meng, J., Wang, Y. and Li, C., 2005, Large Mesozoic mammals fed on young dinosaurs: Nature, v. 433, p. 149-152.

Hua, H., Pratt, B.R. and Zhang, L.Y., 2003, Borings in *Cloudina* shells: Complex predator-prey dynamics in the terminal Neoproterozoic: Palaios, v. 18, p. 454-459.

Hua, S., Buffetaut, E., Legall, C. and Rogron, P., 2007, *Oceanosuchus boecensis* n. gen, n. sp., a marine pholidosaurid (Crocodylia, Mesosuchia) from the Lower Cenomanian of Normandy (western France): Bulletin de la Société géologique de France, v. 178, p. 503-513.

Huber, P., 1992, Faunal distribution, seasonal deposition, and fish taphonomy at the Upper Pennsylvanian (Missourian) Kinney Brick Company Quarry, central New Mexico; *in* Zidek, J., ed., Geology and paleontology of the Kinney Brick Quarry, Late Pennsylvanian, central New Mexico: New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, p. 37-48.

Hunt, A.P., 1984, Fluvial vertebrate taphonomy: Historical perspectives: New Mexico Journal of Science, v. 24, p. 26-27.

Hunt, A.P., 1987, Phanerozoic trends in nonmarine taphonomy: Implications for Mesozoic vertebrate taphonomy and paleoecology: Geological Society of America, Abstracts with

Programs, v. 19, p. 171.

Hunt, A.P., 1991, Two phytosaur (Reptilia: Archosauria) skeletons from the Bull Canyon Formation (Late Triassic) of east-central New Mexico with preserved stomach contents: New Mexico Geology, v. 13, p. 93.

Hunt, A.P., 1992, Late Pennsylvanian coprolites from the Kinney Brick Quarry, central New Mexico, with notes on the classification and utility of coprolites; *in* Zidek, J., ed., Geology and paleontology of the Kinney Brick Quarry, Late Pennsylvanian, central New Mexico: New Mexico Bureau of Mines and Mineral Resources, Bulletin 138, p. 221-229.

Hunt, A.P. 1994, Vertebrate paleontology and biostratigraphy of the Bull Canyon Formation (Chinle Group: Norian), east-central New Mexico with revisions of the families Metoposauridae (Amphibia: Temnospondyli) and Parasuchidae (Reptilia: Archosauria) [Ph.D. dissertation]: Albuquerque, University of New Mexico, 403 p.

Hunt, A.P., 2001, The vertebrate fauna, biostratigraphy and biochronology of the type Revueltian land-vertebrate faunachron, Bull Canyon Formation (Upper Triassic), east-central New Mexico: New Mexico Geological Society, Guidebook 52, p. 123-151.

Hunt, A.P. and Lucas, S.G. 1998, Ichnological evidence for vertebrate predation in the Paleozoic: Is there any: New Mexico Museum of Natural History and Science, Bulletin 12, p. 59-62.

Hunt, A.P. and Lucas, S.G., 2003, Tetrapod ichnofacies in the Paleozoic; *in* Martin, A. J., ed., Workshop on Permo-Carboniferous Ichnology Program and Abstracts. Alabama Museum of Natural History, Alabama Geological Survey, p. 8-11.

Hunt, A.P. and Lucas, S.G., 2004, Tetrapod ichnofacies in the Paleozoic: 32nd International Geological Congress, Italia 2004, Abstracts Part 1. International Union of Geological Sciences, p. 600.

Hunt, A.P. and Lucas, S.G., 2005a, A new coprolite ichnotaxon from the early Permian of Texas: New Mexico Museum of Natural History and Science, Bulletin 30, p. 121-122.

Hunt, A.P. and Lucas, S.G., 2005b, The origin of large vertebrate coprolites from the early Permian of Texas: New Mexico Museum of Natural History and Science, Bulletin 30, p. 125-126.

Hunt, A.P. and Lucas, S.G., 2005c, Tetrapod ichnofacies and their utility in the Paleozoic; *in* Buta, R.J., Rindsberg, A.K., and Kopaska-Merkel, D.C., eds., Pennsylvanian footprints in the Black Warrior Basin of Alabama: Alabama Paleontological Society Monograph, v. 1, p. 113-119.

Hunt, A.P. and Lucas, S.G., 2007a, Cenozoic vertebrate trace fossils of North America: Ichnofaunas, ichnofacies and biochronology: New Mexico Museum of Natural History and Science, Bulletin 42, p. 17-41.

Hunt, A.P. and Lucas, S.G. 2007b, Tetrapod ichnofacies: A new paradigm: Ichnos, v. 14, p. 59-68.

Hunt, A.P. and Lucas, S.G., 2010, Crocodylian coprolites and the identification of the producers of coprolites: New Mexico Museum of Natural History and Science, Bulletin 51, p. 219-226.

Hunt, A.P. and Lucas, S.G., 2012a, Classification of vertebrate coprolites and related trace fossils: New Mexico Museum of Natural History and Science, Bulletin 57, p. 137-146.

Hunt, A.P. and Lucas, S.G., 2012b, Descriptive terminology of coprolites and recent feces: New Mexico Museum of Natural History and Science, Bulletin 57, p. 153-160.

Hunt, A.P. and Lucas, S.G., 2013, The fossil record of Carboniferous and Permian vertebrate coprolites: New Mexico Museum of Natural History and Science, Bulletin 60, p. 121-127.

Hunt, A.P. and Lucas, S.G., 2014a, Jurassic vertebrate bromalites of the western United States in the context of the global record: Volumina Jurassica, v. 12(2), p. 151-158.

Hunt, A.P. and Lucas, S.G., 2014b, Vertebrate trace fossils from New Mexico and their significance: New Mexico Museum of Natural History and Science, Bulletin 64, p. 9-40.

Hunt, A.P. and Lucas, S.G., 2016a The case for archetypal vertebrate ichnofacies: Ichnos, v. 23, p. 237-247.

Hunt, A.P. and Lucas, S.G., 2016b, The most significant record of "Middle"- Late Paleozoic vertebrate coprolites: Silurian-Carboniferous ichnoassemblages from Scotland: Geological Society of America, Abstracts with Programs*,* v. 48 (7) doi: 10.1130/abs/2016AM-284166.

Hunt, A.P. and Lucas, S.G., 2016c, The record of vertebrate coprolites across the Cretaceous/Paleogene boundary: New Mexico Museum of Natural History and Science, Bulletin 74, p. 79-93.

Hunt, A.P. and Lucas, S.G., 2017a, A new vertebrate coprolite locality from the Late Pennsylvanian of central New Mexico, USA, and the environmental context of Carboniferous bromalites: New Mexico Museum of Natural History and Science, Bulletin 77, p. 139-150.

Hunt, A.P. and Lucas, S.G., 2017b, On the probable rarity of small dinosaur coprolites: Geological Society of America, Abstracts with Programs*,* v. 49 (6), doi: 10.1130/abs/2017AM-303525.

Hunt, A. P., and Lucas, S. G., 2018a, Biochronology of Triassic vertebrate coprolites and the lack of a significant turnover in coprolite ichnofaunas at the Triassic/Jurassic boundary: Geological Society of America, Abstracts with Programs, v. 50(5), doi: 10.1130/abs/2018RM-314409.

Hunt, A.P., and Lucas, S.G., 2018b, Mosasaur coprolites from the Bearpaw Formation (Upper Cretaceous) of Saskatchewan, Canada: New Mexico Museum of Natural History and Science, Bulletin 79, p. 271–275.

Hunt, A.P., and Lucas, S.G., 2018c, The record of sloth coprolites in North and South America: Implications for terminal Pleistocene extinctions. New Mexico Museum of Natural History and Science, Bulletin 79, p. 277–298.

Hunt, A.P. and Lucas, S.G., 2019, Coprolites of bone-crushing carnivores: Abundant in the Old World, rare in the New World: Geological Society of America, Abstracts with Programs, v. 51(5), doi: 10.1130/abs/2019AM-336095.

Hunt, A.P. and Lucas, S.G., 2020a, Hyena hegemony: Biogeography and taphonomy of Pleistocene vertebrate coprolites with description of a new mammoth coprolite ichnotaxon: Ichnos, v. 27, p. 111-121.

Hunt, A.P. and Lucas, S.G., 2020b, The taphonomy of vertebrate consumulites: Taphcon 2020, Meeting Booklet, p. 30.

Hunt, A.P. and Lucas, S.G., 2021a, A review of the bromalite ichnofauna from the Kinney Brick Quarry Lagerstätte (Late Pennsylvanian) of New Mexico, USA with descriptions of new consumulites and coprolites: New Mexico Museum of Natural History and Science, Bulletin 84, p. 217-236.

Hunt, A.P. and Lucas, S.G., 2021b, Coprolites; *in*, Alderton, D. and Elias, S., eds., Encyclopedia of geology (Second Edition), volume 3. London, Elsevier, p. 532-544.

Hunt, A.P. and Lucas, S.G., 2021c, Coprolites in caves: Late Pleistocene coprofaunas of the American Southwest and their significance: New Mexico Museum of Natural History and Science, Bulletin, in press.

Hunt, A.P. and Lucas, S.G., 2021d, Coprolites of *Borophagus* (Mammalia: Canidae) from western North America and the distribution of the coprolites of bone-cracking carnivores in the late Cenozoic: New Mexico Museum of Natural History and Science, Bulletin 82, p. 151-159.

Hunt, A.P., Chin, K. and Lockley, M.G., 1994a, The paleobiology of coprolites; *in* Donovan, S.K., ed., The paleobiology of trace fossils: London, John Wiley, p. 221-240.

Hunt, A.P., Lucas, S.G. and Buskirk, B.L., 2015a, The value of vomit: The fossil record of vertebrate regurgitalites and its significance: Geological Society of America, Abstracts with Programs, v. 47(7), p. 346.

Hunt, A.P., Lucas, S.G. and Klein, H., 2018, Late Triassic nonmarine vertebrate and invertebrate trace fossils and the pattern of the Phanerozoic record of vertebrate trace fossils; *in* Tanner, L.H., ed., The Late Triassic world. Topics in Geobiology 46: New York, Springer Verlag, p. 447-543.

Hunt, A.P., Lucas, S.G. and Lichtig, A.J., 2015b, A helical coprolite from the Red Crag Formation (Plio-Pleistocene) of England: New

Mexico Museum of Natural History and Science, Bulletin 67, p. 59-61.

Hunt, A.P., Lucas, S.G. and Lockley, M.G., 1998, Taxonomy and stratigraphic and facies significance of vertebrate coprolites of the Upper Triassic Chinle Group, western United States: Ichnos, v. 5, p. 225-234.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2005a, Biochronology of early Permian vertebrate coprolites of the American Southwest: New Mexico Museum of Natural History and Science, Bulletin 31, p. 43-45.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2005b, Early Permian vertebrate coprolites from north-central New Mexico with description of a new ichnogenus: New Mexico Museum of Natural History and Science, Bulletin 31, 39-42.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2005c, The postcranial skeleton of *Revueltosaurus callenderi* (Archosauria: Crurotarsi) from the Upper Triassic of Arizona and New Mexico, USA: New Mexico Museum of Natural History and Science, Bulletin 29, p. 67-76.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2012a, New coprolite ichnotaxa from the Buckland Collection at the Oxford University Museum of Natural History: New Mexico Museum of Natural History and Science, Bulletin 57, p. 115-124.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2012b, The bromalite collection at the National Museum of Natural History (Smithsonian Institution), with descriptions of new ichnotaxa and notes on other significant coprolite collections: New Mexico Museum of Natural History and Science, Bulletin 57, p. 105-114.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2012c, The vertebrate coprolite collection at the Natural History Museum (London): New Mexico Museum of Natural History and Science, Bulletin 57, p. 125-129.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2013a, A large heteropolar coprolite from the early Permian of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 59, p. 327-329.

Hunt, A.P., Lucas, S.G. and Spielmann, J.A., 2013b, Triassic vertebrate coprolite ichnofaunas: New Mexico Museum of Natural History and Science, Bulletin 61, p. 237-258.

Hunt, A.P., Lucas, S.G., Milàn, J., and Spielmann, J.A., 2012d, Vertebrate coprolite studies: Status and prospectus: New Mexico Museum of Natural History and Science, Bulletin 57, p. 5-24.

Hunt, A.P., Lucas, S.G., Spielmann, J.A. and Lerner, A.J. 2007, A review of vertebrate coprolites of the Triassic with descriptions of new Mesozoic ichnotaxa: New Mexico Museum of Natural History and Science, Bulletin 41, p. 88-107.

Hunt, A.P., Lucas, S.G., Spielmann, J.A. and Lockley, M.G., 2012e, Bromalites from the Mississippian Bear Gulch Lagerstätte of central Montana, USA: New Mexico Museum of Natural History and Science, Bulletin 57, p. 171-174.

Hunt, A.P., Meyer, C.A., Lockley, M.G and Lucas, S.G., 1994b, Archaeology, toothmarks and sauropod taphonomy; *in* Lockley, M.G., dos Santos, V.F., Meyer, C.A. and Hunt, A.P., eds., Aspects of sauropod palaeobiology: Gaia, v. 10, p. 225-232.

Hunt, A.P., Milàn, J., Lucas, S.G. and Spielmann, J.A., eds., 2012f, Vertebrate coprolites: New Mexico Museum of Natural History and Science, Bulletin 57, 387 p.

Hunt, A.P., Santucci, V.L., Tweet, J.S. and Lucas, S.G., 2012g, Vertebrate coprolites and other bromalites in National Park Service areas: New Mexico Museum of Natural History and Science, Bulletin 57, p. 343-353.

Hunt, A.P., Spielmann, J.A., Lucas, S.G. and Durney, K., 2013c, Late Pennsylvanian coprofauna from the Finis Shale of north-central Texas: New Mexico Museum of Natural History and Science, Bulletin 60, p. 129-131.

Hunt, A.P., Lucas, S.G. Milàn, J., Lichtig, A.J. and Jagt, J.W.M., 2015c, Vertebrate coprolites from Cretaceous Chalk in Europe and North America and the Shark Surplus Paradox: New Mexico Museum of Natural History and Science, Bulletin 67, p. 63-68.

Hunt, A.P., Lucas, S.G., Spielmann, J.A., Cantrell, A. and Suazo, T., 2012g, A new marine coprofauna from the Beeman Formation (Late Pennsylvanian: Late Missourian), Sacramento Mountains, New Mexico, USA: New Mexico Museum of Natural History and Science, Bulletin 57, p. 193-196.

Hunt, A.P., Lucas, S.G., Spielmann, J.A., Suazo, T. and Cantrell, A., 2012h, A re-evaluation of Late Pennsylvanian bromalites from the Kinney Brick Quarry Lagerstätte, New Mexico, USA: New Mexico Museum of Natural History and Science, Bulletin 57, p. 185-192.

Hunt, A.P., Lucas, S.G., Spielmann, J.A., Cantrell, A., Suazo, T. and Lerner, A.J, 2012i, Bromalites from the Tinajas Lagerstätte (Late Pennsylvanian: Late Missourian), central New Mexico, USA: New Mexico Museum of Natural History and Science, Bulletin 57, p. 175-183.

Hunt, C.O. and Fiacconi, M., 2018, Pollen taphonomy of cave sediments: What does the pollen record in caves tell us about external environments and how do we assess its reliability?: Quaternary International, v. 485, p. 68-75.

Hunt, R., 1984, Extinct carnivores entombed in 20 million year old dens, Agate Fossil Beds National Monument, Nebraska: The George Wright Forum, v. 4, p. 29-39.

Hunt, R.M., Xiang-Xu, X.U.E. and Kaufman, J., 1983, Miocene burrows of extinct bear dogs: Indication of early denning behavior of large mammalian carnivores: Science, v. 221, p. 364-366.

Huntley, J.W. and Kowalewski, M., 2007, Strong coupling of predation intensity and diversity in the Phanerozoic fossil record: Proceedings of the National Academy of Sciences, v. 104, p. 15006-15010.

Hurum, J.H., Luo, Z. and Kielan-Jaworowska, Z., 2006, Were mammals originally venomous?: Acta Palaeontologia Polonica, v. 51, p. 1-11.

Hutchison, J.H. and Frye, F.L., 2001, Evidence of pathology in early Cenozoic turtles: PaleoBios, v. 21, p. 12-19.

Hutchison, J.H. and Harington, C.R., 2002, A peculiar new fossil shrew (Lipotyphla, Soricidae) from the High Arctic of Canada: Canadian Journal of Earth Sciences, v. 39, p. 439-443.

Huxley, T. H., 1866, Illustrations of the structure of the crossopterygian ganoids: Memoirs of the Geological Survey of the United Kingdom. Figures and descriptions illustrative of British Organic Remains. Decade XII, 44 p.

Huxley, T.H., 1880, The crayfish: An introduction to zoology. London, C. Kegan Paul and Co., 371 p.

Hwang, S.H., Norell, M.A., Ji, Q. and Gao, K.-Q., 2004, A large compsognathid from the Early Cretaceous Yixian Formation of China: Journal of Systematic Paleontology, v. 2, p. 13–30.

Ibiricu, L.M., Martínez, R.D., Casal, G.A. and Cerda, I.A., 2013, The behavioral implications of a multi-individual bonebed of a small theropod dinosaur: PLoS ONE, v. 8(5): e64253, doi:10.1371/journal.pone.0064253.

Ifrim, C., 2013, Paleobiology and paleoecology of the early Turonian (Late Cretaceous) ammonite *Pseudaspidoceras flexuosum*: Palaios, v. 28, p. 9-22.

Irwin-Williams, C. and Shelley, P.H., 1980, Investigations at the Salmon Site: The structure of Chacoan Society in the northern Southwest: Portales, Eastern New Mexico University Publications in Anthropology, v. 4(3), 144 p.

Izawa, K., 1993, Soil-eating in *Aoluatta* and *Ateles*: International Journal of Primatology, v. 14, p. 229-242.

Isozaki, Y. and Servais, T., 2017, The Hirnatian (Late Ordovician) and end-Guadalupian (middle Permian) mass-extinction events compared: Lethaia, v. 51, p. 173-186.

Jackson, S., 1992, Do seabird gut sizes and mean retention times reflect adaptation to diet and foraging method?: Physiological Zoology, v. 65, p. 674–697.

Jacobs, L.L., 1985, Review: The Omo micromammals: Systematics and paleoecology of early man sites from Ethiopia by Henry B. Wesselman: Journal of Vertebrate Paleontology, v. 5, p. 281-283.

Jacobs, M.L. and Martill, D.M., 2020, A new ophthalmosaurid ichthyosaur from the Upper Jurassic (Early Tithonian) Kimmeridge Clay of Dorset, UK, with implications for Late Jurassic ichthyosaur diversity: PLoS ONE, v. 15(12): e0241700, doi.org/10.1371/journal. pone.0241700.

Jacobsen, A.R., 1995, Predatory behaviour of carnivorous dinosaurs: ecological interpretations based on tooth marked dinosaur bones and wear patterns of theropod teeth [M.S. thesis]: Copenhagen, University of Copenhagen, 79 p.

Jacobsen, A.R., 1998, Feeding behavior of carnivorous dinosaurs as determined by tooth marks on dinosaur bones: Historical Biology, v.13, p. 17-26.

Jacobsen, A.R., 2001, Tooth-marked small theropod bone: An extremely rare trace; *in* Tanke, D.H. and Carpenter, K., eds., Mesozoic vertebrate life. Bloomington, Indiana University Press, p. 58–63.

Jacobsen, A.R. and Bromley, R.G., 2009, New ichnotaxa based on tooth impressions on dinosaur and whale bones: Geological Quarterly, v. 53, p. 373-382.

Jäger, M., 1991, Lias epsilon von Dotternhausen 2. Teil: Fossilien, v.1/91, p. 33–36.

Jäger, M., 2001, Das Fossilienmuseum im Werkforum. Dotternhausen, self-published, 149 p.

Jagt, J.W.M. and Salamon, M.A., 2007, Late Cretaceous bourgueticrinid crinoids from southern Poland – preliminary observations: Scripta Geologica, v. 134, p. 61-76.

Jagt, J.W., Deckers, M.J., De Leebeeck, M., Donovan, S.K. and Nieuwenhuis, E., 2020, Episkeletozoans and bioerosional ichnotaxa on isolated bones of Late Cretaceous mosasaurs and cheloniid turtles from the Maastricht area, the Netherlands: Geologos, v. 26, p. 39-49.

Jagt, J.W., van Bakel, B.W., Deckers, S.K., Donovan, R.H.B., Fraaije, E.A., Jagt-Yazykova, J.L., Nieuwenhuis, E. and Thijs, B., 2018, Late Cretaceous echinoderm 'odds and ends' from the Low Countries: Contemporary Trends in Geosciences, v. 7, p. 255-282.

Jain, S., 1983, Spirally coiled 'coprolites' from the Upper Triassic Maleri Formation, India: Palaeontology, v. 26, p. 813-829.

James, H.F. and Burney, D.A., 1997, The diet and ecology of Hawaii's extinct flightless waterfowl: Evidence from coprolites: Biological Journal of the Linnean Society, v. 62, p. 279–297.

Janensch, W., 1929, Uber Magensteine bei Dinosauriern aus Deutsch-Ostrafrika: Spitzungsberichte der Gessellschaft Naturforschender Freunde, v. 16, p. 34-36.

Janicke, V., 1970, Ein Strobilodus als Speiballen im Solnhofener Plattenkalk (Tiefes Untertithon, Bayern): Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 1970, p. 61-64.

Janicke, V. and Schairer, G., 1970, Fossilerhaltung und Problematica aus den Solnhofener Plattenkalken: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 1970, p. 452-464.

Janvier, P., 1996a, Early vertebrates. Oxford, Oxford University Press, 408 p.

Janvier, P., 1996b, The Miguasha "Anapsida"; *in* Schultze, H.-P. and Cloutier, R, eds., Devonian fishes and plants of Miguasha, Quebec, Canada. Munich, Verlag Dr. Friedrich Pfeil, p. 134-140.

Janvier, P., and Arsenault, M., 2007, The anatomy of *Euphanerops longaevus* Woodward, 1900, an anaspid-like jawless vertebrate from the Upper Devonian of Miguasha, Quebec, Canada: Geodiversitas, v. 29, p. 143-216.

Jenkins, D. and Burrows, G.O., 1980, Ecology of otters in northern Scotland. III. The use of faeces as indicators of otter (*Lutra lutra*) density and distribution: The Journal of Animal Ecology, v. 49, p. 755-774.

Jennings, D.S. and Hasiotis, S.T., 2006, Taphonomic analysis of a dinosaur feeding site using geographic information systems (GIS), Morrison Formation, southern Bighorn Basin, Wyoming, USA: Palaios, v. 21, p. 480-492.

Jensen, J.A., 1988, A fourth new sauropod dinosaur from the Upper Jurassic of the Colorado Plateau and sauropod bipedalism: The Great Basin Naturalist, v. 48, p. 121-145.

Jensen, T.Z., Niemann, J., Iversen, K.H., Fotakis, A.K., Gopalakrishnan, S., Vågene, Å.J., Pedersen, M.W., Sinding, M.H.S., Ellegaard, M.R., Allentoft, M.E. and Lanigan, L.T., 2019, A 5700 year-old human genome and oral microbiome from chewed birch pitch: Nature Communications, v. 10, 5520 (2019). https://doi.org/10.1038/s41467-019-13549-9.

Jepsen, G.L., 1963, Eocene vertebrates, coprolites and plants in the Golden Valley Formation in western North Dakota: Bulletin of the Geological Society of America, v. 74, p. 673-684.

Jepsen, G.L., 1967, Notable geobiologic moments: Geotimes, v. 12, p. 16-18.

Ji, Q., Wu, X., Cheng, Y., Ten, F., Wang, X. and Ji, Y., 2016, Fish hunting ankylosaurs (Dinosauria, Ornithischia) from the Cretaceous of China: Journal of Geology, v. 40, p. 183–190.

Ji, Q., Currie, P.J., Norrell, M.A., and Ji, S.-A., 1998, Two feathered dinosaurs from northeastern China: Nature, v. 393, p. 753-761.

JiI, Q., Lu, J.-C., Wei, X.-F. and Wang, X.-R., 2012, A new oviraptorosaur from the Yixian Formation of Jianchang, western Liaoning Province, China: Geological Bulletin of China, v. 31, p. 2102–2107.

Ji, Q., Norell, M.A., Mackovicky, P.J., Gao, K., Ji, S., Yuan, C., 2003, An early ostrich dinosaur and implications for ornithomimosaur phylogeny: American Museum Novitates, no. 3420, 19 p.

Ji, Q., Ji, S.A., Lü, J.C., You, H.L., Chen, W., Liu, Y.Q. and Liu, Y.X., 2005, First avialian bird from China: Geological Bulletin of China, v. 24, p. 197–210.

Ji, S., Ji, Q., Lü, J. and Yuan, C., 2007, A new giant compsognathid dinosaur with long filamentous integuments from Lower Cretaceous of northeastern China: Acta Geologica Sinica, v. 81, p. 8–15.

Joeckel, R.M. and Tucker, S.T., 2013, Exceptionally well preserved latest Miocene (Hemphillian) rodent burrows from the eastern Great Plains, United States, and a review of the burrows of North American rodents: Palaios, v. 28, p. 793-824.

Johanson, Z., Smith, M., Kearsley, A., Pilecki, P., Mark-Kurik, E. and Howard, C., 2013, Origins of bone repair in the armour of fossil fish: Response to a deep wound by cells depositing dentine instead of dermal bone: Biology Letters, v. 9, 92013014420130144, doi: org: 10.1098/rsbl.2013.0144.

Jones, R. L., and Hanson, H. C., 1985, Mineral licks, geophagy, and biogeochemistry of North American ungulates. Ames, The Iowa State University Press, 301 p.

Johnson, D.L., 1990, Biomantle evolution and the redistribution of Earth materials and artifacts: Soil Science, v. 149, p. 84-101.

Johnson, D.L., 1993, Dynamic denudation of tropical, subtropical and temperate landscapes with three tiered soils: Toward a general theory of landscape evolution: Quaternary International, v. 17, p. 67-78.

Johnson, D.L., 2002, Darwin would be proud: Bioturbation, dynamic denudation, and the power of theory in science: Geoarchaeology, v. 17, p. 7-40.

Johnson, D.L. and Balek, C.L., 1991, The genesis of landscapes with stone lines: Physical Geography, v. 12, p. 385-395.

Johnson, D.L. and Schaetzl, R.J., 2015, Differing views of soil and pedogenesis by two masters: Darwin and Dokuchaev: Geoderma, v. 237, p. 176-189.

Johnson, D.L., Domier, J. E. J., Johnson, D.N., 2005a, Reflections on the nature of soil and its biomantle: Annals of the Association of American Geographers, v. 95, p. 11-31.

Johnson, D.L., Domier, J. E. J., Johnson, D. N., 2005b, Animating the biodynamics of soil thickness using process vector analysis: A dynamic denudation approach to soil formation: Geomorphology, v. 67, p. 23-46.

Johnson, J.H., 1934, A coprolite horizon in the Pennsylvanian of Chafee and Park Counties, Colorado: Journal of Paleontology, v. 8, p. 477-479.

Johnston, P.A., Kase, T. and Seilacher, A., 1997, Mosasaurs, limpets and diagenesis: Alternative pathways to punctured ammonite shells: CSPG-SEPM Joint Convention, Program with Abstracts, 1997, p.

308.

Johnston, R.G. and Enter, J.A., 1999, Gastroliths; *in* Singer, R., ed., Encyclopedia of paleontology. Volume 1 A-L. Chicago, Fitzroy Dean Publishers, p. 507-508.

Johnston, R.G., Lee, W.G. and Grace, W.K., 1994, Identifying moa gastroliths using a video light scattering instrument: Journal of Paleontology, v. 68, p. 159-163

Johnston, R.G., Manley, K. and Lemanski, C.L., 1990, Characterizing gastrolith surface roughness with light scattering: Optics Communications, v. 74, p. 279-283

Jouy-Avantin, F., Combes, C., Lumley, H., Miskovsky, J.C and Moné, H., 1999, Helminth eggs in animal coprolites from a middle Pleistocene site in Europe: Journal of Parasitology, v. 85, p. 376-379.

Joyce, W.G., 2000, The first complete skeleton of *Solnhofia parsonsi* (Cryptodira, Eurysternidae) from the Upper Jurassic of Germany and its taxonomic implications: Journal of Paleontology, v. 74, p. 684-700.

Joyce, W.G., Mäuser, M. and Evers, S.W., 2021, Two turtles with soft tissue preservation from the platy limestones of Germany provide evidence for marine flipper adaptations in Late Jurassic thalassochelydians: PLoS ONE, v. 16(6): e0252355, doi: org/10.1371/journal.pone.0252355.

Kaddumi, H.F., 2006, A new genus and species of gigantic marine turtles (Chelonioidea: Cheloniidae) from the Maastrichtian of the Harrana Fauna-Jordan: PalArch, v. 3, p. 1-13.

Kaiser, S.I., Aretz, M. and Becker, R.T., 2016, The global Hangenberg crisis (Devonian–Carboniferous transition): Review of a first-order mass extinction; *in* Becker, R. T., Königshof, P. and Brett, C. E., eds. Devonian climate. Sea level and evolutionary events. Geological Society of London, Special Publications, v. 423, p. 387-437.

Kallal, R.J., Godfrey, S.J. and Ortner, D.J., 2012, Bone reactions on a Pliocene cetacean rib indicate short-term survival of predation event: International Journal of Osteoarchaeology, v. 22, p. 253–260.

Kandel, A.W. and Conard, N.J., 2012, Settlement patterns during the earlier and Middle Stone Age around Langebaan Lagoon, western Cape (South Africa): Quaternary International, v. 270, p. 15-29.

Kao, F.-T.K., 1962, Notes on coprolites from the Nihowan Series: Vertebrata Palasiatica, v. 4, p. 390-397.

Karatajute-Talimaa, V. and Predtechenskyj, N., 1995, The distribution of the vertebrates in the Late Ordovician and Early Silurian palaeobasins of the Siberian Platform: Bulletin du Muséum national d'Histoire naturelle, 4ème série, section C, Sciences de la Terre, Paléontologie, Géologie, Minéralogie, v. 17, p .39-55.

Karl, H.V., 2012, Bite traces in a turtle shell fragment from the Kimmeridgian (Upper Jurassic) of northern Germany: Studia Geologica Salmanticensia, v. 9, p. 25-30.

Karl, H.-V. and Nyhuis, C.J., 2012, *Ctenochelys stenoporus* (Hay, 1905)(Testudines: Toxochelyidae) and *Clidastes* sp. (Squamata: Mosasauridae) from the Upper Cretaceous of NW-Germany: Studia Palaeocheloniologica, v. 4 (Studia Geologica Salmanticensia, Especial v. 9), p. 129-142.

Karl, H.V. and Tichy, G., 2004, The structure of fossil teeth of chelonophagous crocodiles (Diapsida: Crocodylia): Studia Geologica Salmanticensia, v. 40, p. 115-124.

Karpinski, E., Mead, J.I. and Poinar, H.N., 2017. Molecular identification of paleofeces from Bechan Cave, southeastern Utah, USA: Quaternary International, v. 443, p. 140–146.

Kase, T., Shigeta, Y and Futakami, M., 1994, Limpet home depressions in Cretaceous ammonites: Lethaia, v. 27, p. 49-58.

Kase, T., Johnston, P.A., Seilacher, A. and Boyce, J.B., 1998, Alleged mosasaur bite marks on Late Cretaceous ammonites are limpet (patellogastropod) home scars: Geology, v. 26, p. 947-950.

Kastelein, R.A., Stephens, S., and Mousterd, P., 1989, The excavation technique for mollusks of Pacific walruses (*Odobenus rosmarus divergens*) under controlled conditions: Aquatic Mammals, v. 15, p. 3–5.

Katsura, Y., 2004, Paleopathology of *Toyotamaphimeis machikanensis* (Diapsida, Crocodylia) from the middle Pleistocene of central Japan: Historical Biology, v. 16, p. 93-97.

Kaufman, L., 1981, There are biological disturbances on Pleistocene coral reefs: Paleobiology, v. 7, p. 527-532.

Kauffman, E.G., 1972, *Ptychodus* predation upon a Cretaceous *Inoceramus*: Palaeontology, v. 15, p. 439-444.

Kauffman, E.G., 1990a, Cretaceous fish predation on a large squid; *in* Boucot, A. J., 1990, ed., Evolutionary paleobiology of behavior and coevolution. Elsevier, Amsterdam, p. 195-196.

Kauffman, E.G. 1990b, Mosasaur predation on ammonites during the Cretaceous – an evolutionary history; *in* Boucot, A. J., 1990, ed., Evolutionary paleobiology of behavior and coevolution. Elsevier, Amsterdam, p. 184–189.

Kauffman, E.G. 2004, Mosasaur predation on Upper Cretaceous nautiloids and ammonites from the United States Pacific coast: Palaios, v. 19, p. 96-100.

Kauffman, E.G. and Kesling, R.V., 1960, An Upper Cretaceous ammonite bitten by a mosasaur: Contributions from the Museum of Paleontology, University of Michigan, v. 15, p. 193–248.

Kauffman, E.G. and Sawdo, J.K., 2013, Mosasaur predation on a nautiloid from the Maastrichtian Pierre Shale, central Colorado, Western Interior Basin, United States: Lethaia, v. 46, p. 180-187.

Kaup, J.J., 1835, Über Thierfährten bei Hildburghausen: Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, v. 1835, p. 327–328.

Kay, R.F. and Covert, H.H., 1983, True grit: A microwear experiment: American Journal of Physical Anthropology, v. 61, p. 33-38.

Kear, B.P., 2005, A new elasmosaurid plesiosaur from the Lower Cretaceous of Queensland, Australia: Journal of Vertebrate Paleontology, v. 25, p. 792-805.

Kear, B.P., 2006, First gut contents in a Cretaceous sea turtle: Biology Letters, v. 2, p. 113-115.

Kear, B.P., 2016, Cretaceous marine amniotes of Australia: Perspectives on a decade of new research: Memoirs of the Museum of Victoria, v. 74, p. 17-28.

Kear, B.P. and Godthelp, H., 2008, Inferred vertebrate bite marks on an Early Cretaceous unionoid bivalve from Lightning Ridge, New South Wales, Australia: Alcheringa, v. 32, p. 65-71.

Kear, B.P., Boles, W.E. and Smith, E.T., 2003, Unusual gut contents in a Cretaceous ichthyosaur: Proceedings of the Royal Society of London, Series B, Biological Sciences, v. 270 (supplement 2), p. S206-S208.

Keighley, D.G. and Pickerill, R.K., 1997, Systematic ichnology of the Mabou and Cumberland groups (Carboniferous) of western Cape Breton Island, eastern Canada, 1: Burrows, pits, trails, and coprolites: Atlantic Geology, v. 33, p. 181-215.

Keller, T., 1976, Magen- und Darminhalte von Ichthyosaurien des süddeutschen Posidonienschiefers: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 5, p. 266-283.

Keller, T., 1977, Frassreste im süddeutschen Posidonienschiefer: Jahrshefte der Gesellschaft für Naturkunde in Württemberg, v. 132. 117-134.

Keller, T. and Schaal, S., 1992, Crocodiles: Large ancient reptiles; *in* Schaal, S. and Ziegler, W., eds., Messel: An insight into the history of life and of the Earth: London, Clarendon Press, p. 109-118.

Kellner, A.W.A., 2004, On a pterosaur neck with a dinosaur tooth: Scavenging or predation: Natura Nascosta, v. 29, p. 41-43.

Kellner, A.W.A., 2006, Pterosauros - os Senhores do céu do Brasil. Rio de Janeiro, Vieira and Lent, 176 p.

Kellner, A.W.A. and Langston, W., Jr., 1996, Cranial remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from Late Cretaceous sediments of Big Bend National Park: Journal of Vertebrate Paleontology, v. 16, p. 222–231.

Kellner, A.W.A., Rich, T.H., Costa, F.R., Vickers-Rich, P., Kear, B.P., Walters, M. and Kool, L. 2010, New isolated pterodactyloid bones from the Albian Toolebuc Formation (western Queensland, Australia) with comments on the Australian pterosaur fauna: Alcheringa, v. 34, p. 219–230.

Kemp, A. H., 1936, An exhibit of gastroliths from Wyoming: Texas Academy of Science Proceedings, v. 19, p. 29-30.

Kemp, R.A. and Trueman, C.N., 2003, Rare earth elements in Solnhofen biogenic apatite: Geochemical clues to the palaeoenvironment: Sedimentary Geology, v. 155, p.109-127.

Kerber, L. and Oliveira, E.V., 2008, Fósseis de vertebrados da Formação Passo del Touro (Pleistoceno Superior), Rio Grande do Sul, Brasil: atualização dos dados e novas contribuições: Gea, Journal of Geoscience, v. 4, p. 49-64.

Keupp, H., 2006, Sublethal punctures in body chambers of Mesozoic ammonites (forma aegrafenestra nf), a tool to interpret synecological relationships, particularly predator-prey interactions: Paläontologische Zeitschrift, v. 80, p. 112-123.

Keupp, H. and Kohring, R., 1993, Ein Magensteinfund aus dem Lias epsilon von Altdorf (Mittelfranken): Geologische Blätter für Nordost-Bayern, v. 43, p. 95-104.

Khosla, A., Chin, K., Alimohammadin, H. and Dutta, D. 2015, Ostracods, plant tissues, and other inclusions in coprolites from the Late Cretaceous Lameta Formation at Pisdura, India: Taphonomical and palaeoecological implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 418, p. 90-100.

Khosla, A., Chin, K., Verma, O., Kaur, J., Alimohammadin, H., Pal, S., Dutta, D., Rashid, M., and Sharma, S., 2016, Systematics and paleobiogeographical implications of the fresh water Late Cretaceous ostracods, charophyte and distinctive residues from coprolites of the Lameta Formation at Pisdura, Chandrapur District (Maharashtra), Central India: New Mexico Museum of Natural History and Science, Bulletin 71, p. 173-183.

Kielan-Jaworowska, Z. and Barsbold, R., 1972, Narrative of the Polish–Mongolian palaeontological expeditions 1967–1971: Palaeontologia Polonica, v. 27, p. 5-13.

Kimmig, J. and Pratt, B.R., 2018, Coprolites in the Ravens Throat River Lagerstätte of northwestern Canada: Implications for the middle Cambrian food web: Palaios, v. 33, p. 125-140.

Kimmig, J. and Strotz, L.C., 2017, Coprolites in mid-Cambrian (Series 2-3) Burgess Shale-type deposits of Nevada and Utah and their ecological implications: Bulletin of Geosciences, v. 92, p. 297-309.

King, S.D., 2009, The ability of mosasaurs to produce unique puncture marks on ammonite shells [M.S. thesis]: Bowling Green, Bowling Green State University, 144 p.

Kirkland, J.I., Scheetz, R.D., and Foster, J.R. 2005, Jurassic and Lower Cretaceous dinosaur quarries of western Colorado and eastern Utah; *in* Gigi, R., compiler, 2005 Rocky Mountain Section of the Geological Society of America Field Trip Guidebook, Grand Junction Geological Society, Field Trip 402, p. 1-26.

Klemme, H.D., 1985, Regional geology of Circum-Mediterranean region: American Association of Petroleum Geologists Bulletin, v. 42, p. 477-512.

Klompmaker, A.A. Herngreen, G.F.W. and Oosterink, H.W., 2010, Biostratigraphic correlation, paleoenvironment stress, and subrosion pipe collapse: Dutch Rhaetian shales uncover their secrets: Facies, v. 56, p. 597-613.

Klompmaker, A.A., Waljaard, N.A. and Fraaije, R.H., 2009, Ventral bite marks in Mesozoic ammonoids: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 280, p. 245-257.

Klompmaker, A.A., Kelley, P.H., Chattopadhyay, D., Clements, J.C., Huntley, J.W. and Kowalewski, M., 2019, Predation in the marine fossil record: Studies, data, recognition, environmental factors, and behavior: Earth Science Reviews, v. 194, p. 472-520.

Klug, C., 2007, Sublethal injuries in Early Devonian cephalopod shells from Morocco: Acta Palaeontologica Polonica, v. 52, p. 749–759.

Klug, C. and Vallon, L.H. 2018, Regurgitated ammonoid remains from the latest Devonian of Morocco: Swiss Journal of Palaeontology, v. 138, p. 87-97.

Klug, C., Schweigert, G., Hofmann, R., Weis, R. and De Baets, K., 2021a, Fossilized leftover falls as sources of palaeoecological data: A 'pabulite' comprising a crustacean, a belemnite and a vertebrate from the Early Jurassic Posidonia Shale: Swiss Journal of Paleontology, 140, 10, doi.org/10.1186/s13358-021-00225-z.

Klug, C., Pohle, A., Roth, R., Hofmann, R., Wani, R. and Tajika, A., 2021b, Preservation of nautilid soft parts inside and outside the conch interpreted as central nervous system, eyes, and renal concrements from the Lebanese Cenomanian: Swiss Journal of Palaeontology, v. 140:15, doi.org/10.1186/s13358-021-00229-9.

Klug, C., Kröger, B., Kiessling, W., Mullins, G. L., Servais, T., Frýda, J., Korn, D. and Turner, S., 2011, The Devonian nekton revolution: Lethaia, v. 43, p. 465–477.

Knaust, D., 2020, Invertebrate coprolites and cololites revised: Papers in Palaeontology, v. 6, p. 385-423.

Knaust, D. and Hoffmann, R., 2021, The ichnogenus *Lumbricaria* Münster from the Upper Jurassic of Germany interpreted as faecal strings of ammonites: Papers in Palaeontology, v. 7, p. 807-823.

Kner, R., 1868, Über *Conchopoma gadiforme* nov. gen. et spec. und *Acanthodes* aus dem Rothliegenden (der untern Dyas) von Lebach bei Saarbriicken in Rheinprcussen: Wiener Akademie Wissenschaften Sitzungberichte, v. 57, p. 278-305.

Kneuper, G. and Schönenberg, R., 1962, Das Stefan A (Untere Ottweiler Gruppe) auf der Nordwestflanke des Saarbrücker Haupsattels: Bergfreiheit, v. 12, p. 1-12.

Knoll, F., Chiappe, L.M., Sanchez, S., Garwood, R.J., Edwards, N.P., Wogelius, R.A., Sellers, W.I., Manning, P.L., Ortega, F., Serrano, F.J., Marugán-Lobón, J., Cuesta, E., Escaso, F. and Sanz, J.L., 2018, A diminutive perinate European Enantiornithes reveals an asynchronous ossification pattern in early birds: Nature Communications, v. 9, p. 1-9, doi: 10.1038/s41467-018-03295-9.

Knsc, T., Shigeta, Y. and Futakami, M., 1994, Limpet home depressions in Cretaceous ammonites: Lethaia, v. 27, p. 49-58.

Kobatake, N. and Kamei, T., 1966, The first discovery of fossil crocodile from central Honshu, Japan: Proceedings of the Japanese Academy, v. 42, p. 264-269.

Kobayashi, Y. and Lü, J., 2003, A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China: Acta Palaeontologica Polonica, v. 48, p. 235-259.

Kobayashi, Y., Lü, J., Dong, Z., Barsbold, R., Azuma, Y. and Tomida, Y., 1999, Herbivorous diet in an ornithomimid dinosaur: Nature, v. 402, p. 480-481.

Kodaira, R., 1921, Fossil nut-shells of *Juglans sieboldiana*, Maximovicz in the Lignite of Asahiyama, near Nagano City, Province of Shinano: The Journal of the Geological Society of Japan, v. 28, p. 1-5.

Koerner, H. E., 1930, Jurassic fishes from New Mexico: American Journal of Science, series 5, v. 19, p. 463.

Kogan, I. and Licht, M., 2013, A *Belonostomus tenuirostris* (Actinopterygii: Aspidorhynchidae) from the Late Jurassic of Kelheim (southern Germany) preserved with its last meal: Paläontologische Zeitschrift, v. 87, p. 543-548.

Konishi, T., Newbrey, M.G. and Caldwell, M.W., 2014, A small, exquisitely preserved specimen of *Mosasaurus missouriensis* (Squamata, Mosasauridae) from the upper Campanian of the Bearpaw Formation, western Canada, and the first stomach contents for the genus: Journal of Vertebrate Paleontology, v. 34, p. 802-819.

Konishi, T., Brinkman, D., Massare, J.A. and Caldwell, M.W., 2011, New exceptional specimens of *Prognathodon overtoni* (Squamata, Mosasauridae) from the upper Campanian of Alberta, Canada, and the systematics and ecology of the genus: Journal of Vertebrate Paleontology, v. 31, p. 1026-1046.

Konuki, R., 2008, Biostratigraphy of sea turtles and possible bite marks on a *Toxochelys* (Testudine, Chelonioidea) from the Niobrara Formation (Late Santonian), Logan County, Kansas, and paleoecological implications for predator–prey relationships among large marine vertebrates [M.S. thesis]: Fort Hays, Fort Hays State University, 169 p.

Korth, W., 1979, Taphonomy of microvertebrate fossil assemblages: Annals of Carnegie Museum, v. 48, p. 235–285.

Korth, W.W. and Emry, R.J., 1991, The skull of *Cedromus* and a review of the Cedromurinae (Rodentia, Sciuridae): Journal of Paleontology, v. 65, p. 984-994.

Kosintsev, P.A., Lapteva, E.G., Trofimova, S.S., Zanina, O.G., Tikhonov, A.N. and Van der Plicht, J., 2012, Environmental reconstruction inferred from the intestinal contents of the Yamal baby mammoth Lyuba (*Mammuthus primigenius* Blumenbach, 1799): Quaternary International, v. 255, p. 231-238.

Kowalewski, M. and and Nebelsick, J. H., 2003, Predation on Recent and fossil echinoids; *in* Kelley, P. H., Kowalewski, M. and Hansen, T. A., eds., Predator-prey interactions in the fossil record. New York, Kluwer Academic/Plenum Publishers, p. 279-324.

Kowal-Linka, M. and Bodzioch, A., 2012, Warstwy kooecionooene z *Dactylosaurus* (Reptilia, Sauropterygia) z retu (trias dolny, olenek) Opolszczyzny: Przeglad Geologiczny, v. 60, p. 646-649.

Kowalski, K., 1960, Cricetidae and Microtidae (Rodentia) from the Pliocene of Weze (Poland): Acta Zoologica Cracow, v. 5, p. 447-505.

Kramer, J.M., Erickson, B.R., Lockley, M.G., Hunt, A.P., Braddy, S.J., Lucas, S.G. and Heckert, A.B., 1995, Pelycosaur predation in the Permian: Evidence from *Laoporus* trackways from the Coconino Sandstone with description of a new species of *Permichnium*: New Mexico Museum of Natural History and Science, Bulletin 6, p. 245-249.

Krause, J.M. and Piña, C.I., 2012, Reptilian coprolites in the Eocene of central Patagonia: Argentina: Journal of Paleontology, v. 86, p. 527-538.

Krause, J.M., Verde, M. and Diz, R., 2007, Coprolitos del Grupo Rio Chico (Paleoceno Médio) en el sudeste de Chubut: Congresso Argentino de Paleontologia y Bioestratigrafia, 9, Resúmenes, p. 287.

Kräusel, R., 1922, Die Nahrung von *Trachodon*: Paläontologische Zeitschrift, v. 4, p. 80.

Krishnamani, R. and Mahaney, W.C., 2000, Geophagy among primates: Adaptive significance and ecological consequences: Animal Behaviour, v. 59, p. 899-915.

Kriwet, J., Witzmann, F., Klug, S. and Heidtke, U.H., 2008, First direct evidence of a vertebrate three-level trophic chain in the fossil record: Proceedings of the Royal Society, Series B, Biological Sciences, v. 275, p. 181-186.

Kriwet, Ü., 2001, Feeding mechanisms and ecology of pycnodont fishes (Neopterygii, Pycnodontiformes): Mitteilungen Museum Naturkunde Berlin Geowissenschaften Reihe, v. 4, p. 139-165.

Krüger, F.J., 2003, Bergung von Magensteinen und *Actinocamax primus* (Belemnoidea) aus dem Mittelcenoman von Baddeckenstedt: Arbeitskreis Paläontologie Hannover, v. 31, p. 61-75.

Krzykawski, T., Szopa, K., Brachaniec, T. and Salamon, M.A., 2014, Carboniferous coprolite in the siderite concretion from Sosnowiec-Zagórze Lagerstätte, Poland–preliminary data: Freiberger Forschungshefte, C, v. 548, p. 101–107.

Kubo, T., Mitchell, M.T. and Henderson, D.M., 2012, *Albertonectes vanderveldei*, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta: Journal of Vertebrate Paleontology, v. 32, p. 557-572.

Kühl, G., Bartels, C., Briggs, D. E. G. and Rust, J., 2012, Visions of a vanished world: The extraordinary fossils of the Hunsrück Slate. New Haven, Yale University Press, 128 p.

Kusmer, K.D., 1990, Taphonomy of owl pellet deposition: Journal of Paleontology, v. 64, p. 629-637.

Labandeira, C.C., 1998, Early history of arthropod and vascular plant associations: Annual Review of Earth and Planetary Sciences, v. 26, p. 329-377.

Labarca, R., Recabarren, O.P., Canales-Brellenthin, P. and Pino, M., 2014, The gomphotheres (Proboscidea: Gomphotheriidae) from Pilauco site: Scavenging evidence in the Late Pleistocene of the Chilean Patagonia: Quaternary International, v. 352, p. 75-84.

Lach, R., Brom, K. and Leśko, K., 2015, Bite marks and overgrowths on crinoids from the Štramberk-type limestones in Poland: Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, v. 276, p. 151-154.

LaGarry, H.E., 1997, Geology of the Toadstool Park region of northwestern Nebraska, with the lithostratigraphic revision and redescription of the Brule Formation and remarks on Oligocene bone processing [Ph.D. dissertation]: Lincoln, University of Nebraska, 350 p.

LaGarry, H.E., 2004, Taphonomic evidence of bone processing from the Oligocene of northwestern Nebraska: School of Natural Resources, Institute of Agriculture and Natural Resources, University of Nebraska-Lincoln, Professional Paper, v. 2, p. 1–35.

Lambert, O. and Bianucci, G., 2019, How to break a sperm whale's teeth: Dental damage in a large Miocene physeteroid from the North Sea basin: Journal of Vertebrate Paleontology, v. 39, e1660987, doi:10.1080/ 02724634.2019.1660987.

Lambert, O. and Gigase, P., 2007, A monodontid cetacean from the early Pliocene of the North Sea: Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Sciences de la Terre, v. 77, p. 197–210.

Lambert, O., de Muizon, C., Malinverno, E., Celma, C.D., Urbina, M. and Bianucci, G., 2018, A new odontocete (toothed cetacean) from the early Miocene of Peru expands the morphological disparity of extinct heterodont dolphins: Journal of Systematic Palaeontology, v. 16, p. 981-1016.

Lambert, O., Collareta, A., Landini, W., Post, K., Ramassamy, B., Di Celma, C., Urbina, M. and Bianucci, G., 2015, No deep diving: Evidence of predation on epipelagic fish for a stem beaked whale from the late Miocene of Peru: Proceedings of the Royal Society, Series B, v. 282: 20151530. http://dx.doi.org/10.1098/rspb.2015.1530.

Lambrecht, K., 1931, *Protoplotus beauforti* ein Schlangenhalsvogel aus dem Tertiär von W. Sumatra: Dienst van den Mijnbouw in Nedferlandiisch-Indie Wettenschappelijke Mededeelingen, v. 17, p. 15-24.

Lamsdell, J.C. and Braddy, S.J., 2009, Cope's Rule and Romer's theory: Patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates: Biology Letters, v. 6, p. 265-269.

Lange, S.P., 1968, Zur Morphologie und Taxonomie der Fischgattung *Urocles* aus der Jura und Kreide Europas: Palaeontographica Abteilung A, v. 131, p. 1-78.

Langer, M.C., 2005, Studies on continental Late Triassic tetrapod biochronology. I. The type locality of *Saturnalia tupiniquim* and the faunal succession in south Brazil: Journal of South American Earth Sciences, v. 19, p. 205-218.

Langston, W.J., 1963, Fossil vertebrates and the late Palaeozoic redbeds of Prince Edward Island: National Museum of Canada Bulletin, v. 187 p. 1–36.

Lanzirotti, A., Becker, M., Hanson, G.N. and Sutton, S.R., 2000, Uranium behavior in Jurassic fish coprolites: Combined Microbeam Synchrotron X-Ray Fluorescence, Diffraction, and XANES Analysis: NSLS Activity Report 2, p. 48-52.

Laojumpon, C., Matkhammee, T., Wathanapitaksakul, A., Suteethorn, V., Suteethorn, S., Lauprasert, K., Srisuk, P. and Le Loeuff, J., 2012, Preliminary report on coprolites from the Late Triassic of Thailand: New Mexico Museum of Natural History and Science, Bulletin 57, p. 207-213.

LaRock, J.W., 2000, Sedimentology and taphonomy of a dinosaur bonebed from the Upper Cretaceous (Campanian) Judith River Formation of north central Montana [Ph.D. dissertation]: Bozeman, Montana State University, 61 p.

Larson, P., 2001, Paleopathologies in *Tyrannosaurus rex*: Dinopress, v. 5, p. 26-37 [In Japanese].

Larsson, H.C.E., Hone, D.W., Dececchi, T.A., Sullivan, C. and Xu, X., 2010. The winged non-avian dinosaur *Microraptor* fed on mammals: Implications for the Jehol Biota ecosystem: Journal of

Vertebrate Paleontology, 30 (supplement to no. 3), p.114A.

Laudet, F. and Fosse, P., 2001, Un assemblage d'os grignote par les rongeurs au Paleogene (Oligocene superieur, phosphorites du Quercy): Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science, v. 333, p. 195-200.

Lauters, P., Bolotsky, Y.L., Van Itterbeeck, J. and Godefroit, P., 2008, Taphonomy and age profile of a latest Cretaceous dinosaur bone bed in far eastern Russia: Palaios, v. 23, p. 153-162.

Leahey, L.G., Molnar, R.E., Carpenter, K., Witmer, L. M. and Steven W. Salisbury, S. W., 2015, Cranial osteology of the ankylosaurian dinosaur formerly known as *Minmi* sp. (Ornithischia: Thyreophora) from the Lower Cretaceous Allaru Mudstone of Richmond, Queensland, Australia: PeerJ, v. 3: e1475, doi: 10.7717/peerj.1475.

Leal, M.E.C. and Martill, D., 2007, Anurans of the Crato Formation; *in* Martill, D., Bechly, G. and Loveridge, R.F., eds., The Crato fossil beds of Brazil: Window into an ancient world. Cambridge, Cambridge University Press, p. 444–451.

Lebedev, O.A., Mark-Kurik, E., Karatajūtė-Talimaa, V.N., Lukševičs, E. and Ivanov, A., 2009, Bite marks as evidence of predation in early vertebrates: Acta Zoologica, v. 90 (supplement 1), p. 344-356.

Lee, D.E., Kaulfuss, U., Conran, J.G., Bannister, J.M. and Lindqvist, J.K., 2016, Biodiversity and palaeoecology of Foulden Maar: An early Miocene Konservat-Lagerstätte deposit in southern New Zealand: Alcheringa, v. 40, p. 525-541.

Lee, S., Lee, Y.-N., Chinsamy, A., Lü, J., Barsbold, R. and Tsogtbaatar, K., 2019, A new baby oviraptorid dinosaur (Dinosauria: Theropoda) from the Upper Cretaceous Nemegt Formation of Mongolia: PLoS ONE, v. 14(2): e0210867, doi: org/10.1371/journal.pone.0210867.

Lee, Y.N., Barsbold, R., Currie, P.J., Kobayashi, Y., Lee, H.J., Godefroit, P., Escuillié, F. and Chinzorig, T., 2014, Resolving the long-standing enigmas of a giant ornithomimosaur *Deinocheirus mirificus*: Nature, v. 515, p. 257-260.

Lehmann, T. and Ruf, I., 2018, The advent of even-toed hoofed mammals; *in* Smith, K.T., Schaal, S.F.K. and Habersetzer, J., eds., Messel – ancient greenhouse ecosystem. Frankfurt am Main, Senckenberg Gesellschaft für Naturforschung, p. 285-291.

Lehmann, U., 1975, Über Biologie und Gehäusebau bei *Dactylioceras* (Ammonoidea) aufgrund einer Fraktur-Analyse: Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, v. 44, p. 195–206.

Leigh, S.C., Summers, A.P., Hoffmann, S.L. and German, D.P., 2021, Shark spiral intestines may operate as Tesla valves: Proceedings of the Royal Society, Series B, v. 288: 20211359, doi.org/10.1098/rspb.2021.1359.

Leighton, L.R., 2011, Analyzing predation from the dawn of the Phanerozoic; *in* Laflamme, M., Schiffbauer, J. D. and Dornbos, S. Q., eds., Quantifying the evolution of early life. Amsterdam, Springer, p. 230–257.

Lemke, E. and Weiler, W., 1942, Die Fischreste ause den permischen Brandschiefern am Fusse des Reisengebirges (Sudetengau): Mitteilungen des Reichsamtes für Bodenforschung Zweigstelle, v. 22, 24 p.

Lemley, R.E., 1971, Notice of new finds in the Badlands: Proceedings of the South Dakota Academy of Sciences, v. 50, p. 70-74.

Lequat, F., 1708, Voyages et avantures de Francois Lequat et de ses compagnons en duex isles desertes des Indes Orientales. London, David Mortier, 180 p.

Levey, D.J. and del Rio, C.M., 2001, It takes guts (and more) to eat fruit: Lessons from avian nutritional ecology: The Auk: Ornithological Advances, v. 118, p. 819–831.

Lewis, C., 2011, Evidence of dinosaur herbivory in the Upper Cretaceous Aguja Formation, Big Bend National Park, [M.S. thesis]: Lubbock, Texas Tech University, 144 p.

Liggett, G.A., 2005, A review of the dinosaurs from Kansas: Transactions of the Kansas Academy of Science, v. 108, p. 1-5.

Lillegraven, J. A., McKenna, M. C. and Krishtalka, L., 1981, Evolutionary relationships of middle Eocene and younger species of *Centetodon* (Mammalia, Insectivora, Geolabidae) with a description of the dentition of *Ankylodon* (Adapisoricidae): University of Wyoming Publication, v. 45, 115 p.

Lin, J.-P., Zhao, Y.-L., Rahman, I.A., Xiao, S., and Wang, Y., 2010, Bioturbation in Burgess Shale-type Lagerstätten—case study of trace fossil-body fossil association from the Kaili Biota (Cambrian Series 3), Guizhou, China: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 292, p. 245-256.

Lingham-Soliar, T., 2000, Plesiosaur locomotion: Is the four-wing problem real or merely a theoretical exercise: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 217, p. 45-87.

Lingham-Soliar, T., 2004, Palaeopathology and injury in extinct mosasaurs (Lepidosauromorpha, Squamata) and implications for modern reptiles: Lethaia, v. 37, p. 255-262.

Lingham-Soliar, T., 2008, A unique cross section through the skin of the dinosaur *Psittacosaursus* from China showing a complex fibre architecture: Proceedings of the Royal Society, Series B, v. 275, p. 775-780.

Lindgren, J., Caldwell, M.W., Konishi, T. and Chiappe, L.M., 2010, Convergent evolution in aquatic tetrapods: Insights from an exceptional fossil mosasaur: PLoS ONE, v. 5(8): e11998, doi:10.1371/journal.pone.0011998.

Lindqvist, J.K. and Lee, D.E., 2009, High-frequency paleoclimate signals from Foulden Maar, Waipiata Volcanic Field, southern New Zealand: an early Miocene varved lacustrine diatomite deposit: Sedimentary Geology, v. 222, p. 98-110.

Liu, H.P., Bergström, S.M., Witzke, B.J., Briggs, D.E.G., Mckay, R.M., and Ferretti, A., 2017, Exceptionally preserved conodont apparatuses with giant elements from the Middle Ordovician Winneshiek Konservat-Lagerstätte, Iowa, USA: Journal of Paleontology, v. 91, p. 493–511.

Liu, S., Li, Z., Bailleul, A. M. and O'Connor, J., 2021, Investigating possible gastroliths in a referred specimen of *Bohaiornis guoi* (Aves: Enantiornithes): Frontiers in Earth Science, v. 9, p. 1-13.

Llona Pinto, A.C., and Andrews, P.J., 2004, Taphonomy and palaeoecology of *Ursus spelaeus* from northern Spain; *in* Philippe, M., Argant, A., and Argant, J., eds., 9th International Cave Bear Symposium, Cahiers scientifiques, hors serie No. 2, Lyons, France, Publications du musée des Confluences Année 2004, p. 163-170.

Lloyd, G.T., Davis, K.E., Pisani, D., Tarver, J.E., Ruta, M., Sakamoto, M., Hone, D.W., Jennings, R. and Benton, M.J., 2008, Dinosaurs and the Cretaceous terrestrial revolution: Proceedings of the Royal Society B, Biological Sciences, v. 275, p. 2483-2490.

Lockley, M.G., 2007, A tale of two ichnologies: The different goals and missions of invertebrate and vertebrate ichnotaxonomy and how they relate in ichnofacies analysis: Ichnos, v. 14, p. 39–57.

Lockley, M.G. and Hunt, A.P., 1995, Dinosaur tracks and other fossil footprints of the western United States. New York, Columbia University Press, 338 p.

Lockley, M.G. and Madsen Jr., J.H., 1993, Early Permian vertebrate trackways from the Cedar Mesa Sandstone of eastern Utah: Evidence of predator-prey interaction: Ichnos, v. 2, p. 147-153.

Lockley, M.G. and Wright, J.L., 2003, Pterosaur swimtracks and other ichnological evidence of behaviour and ecology; *in* Buffetaut, E. and Mazin, J.M., eds., Evolution and palaeobiology of pterosaurs. Geological Society of London, Special Publications, v. 217, p. 297–313.

Lockley, M.G., Meyer, C., Siber, H.-J. and Pabst, B., 1998, Theropod tracks from the Howe Quarry, Morrison Formation, Wyoming: Modern Geology, v. 23, p. 309–316.

Lohmann, U. and Sachs, S., 2001, Observations on the postcranial morphology, ontogeny and palaeobiology of *Sclerocephalus haeuseri* (Amphibia: Actinodontidae) from the lower Permian of southwest Germany: Memoirs of the Queensland Museum, v. 46, p. p.771-782.

Loinaze, V.S.P., Vera, E.I., Fiorelli, L.E. and Desojo, J.B., 2018, Palaeobotany and palynology of coprolites from the Late Triassic Chañares Formation of Argentina: Implications for vegetation provinces and the diet of dicynodonts: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 502, p. 31-51.

Lomax, D.R., 2010, An *Ichthyosaurus* (Reptilia, Ichthyosauria) with gastric contents from Charmouth, England: First report of the genus from the Pliensbachian: Paludicola, v. 8, p. 22-36.

Lomax, D.R., Larkin, N.R., Boomer, I., Dey, S. and Copestake, P., 2019, The first known neonate skeleton: A rediscovered specimen from the Lower Jurassic, UK: Historical Biology, v. 31, p. 600-609.

Lomax, D.R., Robinson, P., Cleal, C.J., Bowden, A. and Larkin, N.R., 2016, Exceptional preservation of upper Carboniferous (lower Westphalian) fossils from Edlington, Doncaster, South Yorkshire, UK: Geological Journal, v. 51, p. 42-50.

Long, C., Wings, O., Ciaohong, C. and Sander, P.M., 2006, Gastroliths in the Triassic ichthyosaur *Panjiangsaurus* from China: Journal of Paleontology, v. 80, p. 583-588.

Long, C.T., Page, R.B., Howard, A.M., McKeon, G.P. and Felt, S.A., 2010, Comparison of gastrografin to barium sulphate as a gastrointestinal contrast agent in red-eared slider turtles (*Trachemys scripta elegans*): Veterinary Radiology and Ultrasound, v. 51, p. 42 –47.

Long, J.A., 1991, Arthrodire predation by *Onychodus* (Pisces, Crossopterygii) from the Late Devonian Gogo Formation, Western Australia: Western Australian Museum: Records, v. 15, p. 503-516.

Long, J.A., 1992, *Gogodipterus paddyensis* gen. nov., a new chirodipterid lungfish from the Late Devonian Gogo Formation, Western Australia: The Beagle: Records of the Museums and Art Galleries of the Northern Territory, v. 9, p. 11–20.

Long, J. A., 1995, The rise of fishes. Baltimore, The Johns Hopkins University Press, 223 p.

Long, J.A. and Trinajstic, K., 2010, The Late Devonian Gogo Formation Lägerstatte of western Australia: Exceptional early vertebrate preservation and diversity: Annual Review of Earth and Planetary Sciences, v. 38, p 255-279.

Long, R.A. and Murry, P.A., 1995, Late Triassic (Carnian and Norian) tetrapods from the southwestern United States: New Mexico Museum of Natural History and Science, Bulletin 4, p. 1-254.

Longbottom, A.E. and Patterson, C., 2002, Fishes; *in* Smith, A. B. and Batten, D. J., eds., Fossils of the Chalk (Second Edition): The Palaeontological Association Field Guides to Fossil, v. 2. London, The Palaeontological Association, p. 296-324.

Longrich, N.R. and Ryan, M.J., 2010, Mammalian tooth marks on the bones of dinosaurs and other Late Cretaceous vertebrates: Palaeontology, v. 53, p. 703-709.

Longrich, N.R., Horner, J.R., Erickson, G.M. and Currie, P.J., 2010. Cannibalism in *Tyrannosaurus rex*: PLoS ONE, v. 5(10): e13419, doi:10.1371/journal.pone.0013419.

Loop, M.S. 1974, The effect of relative prey size on the ingestion behavior of the Bengal monitor, *Varanus bengalensis* (Sauria: Varanidae): Herpetologica, v. 30, p. 123-127.

Loop, M.S. and L. G. Bailey, L.G., 1972, The effect of relative prey size on the ingestion behavior of rodent-eating snakes: Psychonomic Science, v. 28, p. 167-169.

López-Villalta, J.S., 2016, Testing the predation-diversification hypothesis for the Cambrian-Ordovician radiation: Paleontological Research, v. 20, p. 312-321.

Louchart, A. and Virot, L., 2011, From snout to beak: The loss of teeth in birds: Trends in Ecology and Evolution, v. 26, p. 663-673.

Lucas, S.G., 2000, The gastromyths of *"Seismosaurus,"* a Late Jurassic dinosaur from New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 61-67.

Lucas, S.G., 2005, Tetrapod ichnofacies and Ichnotaxonomy: quo vadis?: Ichnos, v. 12, p. 157–162.

Lucas, S.G., 2006, Global Permian tetrapod biostratigraphy and biochronology; *in* Lucas, S.G., Cassinis, G. and Schneider, J.W., eds., Non-marine Permian biostratigraphy and biochronology: Geological Society of London, Special Publications, v. 265, p. 65-93.

Lucas, S.G., 2007, Tetrapod footprint biostratigraphy and biochronology: Ichnos, v. 14, p. 5–38.

Lucas, S.G., 2009, Timing and magnitude of tetrapod extinctions across the Permo-Triassic boundary: Journal of Asian Earth Sciences, v. 36, p. 491-502.

Lucas, S.G., 2013, Vertebrate biostratigraphy and biochronology of the upper Paleozoic Dunkard Group, Pennsylvania–West Virginia–Ohio, USA: International Journal of Coal Geology, v. 119, p. 79–87.

Lucas, S.G., 2016, Two new, substrate-controlled nonmarine ichnofacies: Ichnos, v. 23, p. 248–261.

Lucas, S.G., 2017, Permian tetrapod extinction events: Earth-Science Reviews, v. 170, p. 31-60.

Lucas, S.G., 2019, An ichnological perspective on some major events of Paleozoic tetrapod evolution: Bollettino della Società Paleontologica Italiana, v. 58, p. 223-266.

Lucas, S.G., 2021, Tetrapod origins; *in* Alderton, D. and Elias, S., eds., Encyclopedia of geology (Second Edition), volume 3. London, Elsevier, p 138-146.

Lucas, S.G. and Hunt, A.P., 1993, A dicynodont from the Upper Triassic of New Mexico and its biochronological significance: New Mexico Museum of Natural History and Science, Bulletin 3, p. 321-325.

Lucas, S.G. and Hunt, A.P., 2006, Reappraisal of "reptile nests" from the Upper Triassic Chinle Group, Petrified Forest National Park, Arizona: New Mexico Museum of Natural History and Science, Bulletin 37, p. 155-159.

Sucas, S.G. and Hunt, A.P., 2021, Gastroliths in archaeology: A note of caution: International Journal of Osteoarchaeology, 1-3, doi: 10.1002/00.3042.

Lucas, S.G. and Schoch, R.M., 1987, Paleopathology of early Cenozoic *Coryphodon* (Mammalia; Pantodonta): Journal of Vertebrate Paleontology, v. 7, p. 145-154.

Lucas, S.G. and Tanner, L.H., 2015, End Triassic nonmarine biotic events: Journal of Palaeogeography, v. 4, p. 331–340.

Lucas, S.G. and Tanner, L.H., 2018, The missing mass extinction at the Triassic-Jurassic boundary; *in* Tanner, L., ed., The Late Triassic world. New York, Springer, p. 721-785.

Lucas, S.G., Hunt, A.P. and Bennett, S.C., 1985a, Triassic vertebrates from east-central New Mexico in the Yale Peabody Museum: New Mexico Geological Society, Guidebook 36, p. 199-204.

Lucas, S.G., Kietzke, K. and Hunt, A.P., 1985b, The Jurassic System in east-central New Mexico: New Mexico Geological Society, Guidebook 36, p. 213-242.

Lucas, S.G., Rinehart, L.F. and Celeskey, M.D., 2018, The oldest specialized tetrapod herbivore: A new eupelycosaur from the Permian of New Mexico, USA: Palaeontologia Electronica, v. 21.3.39A 1-42, doi.org/10.26879/899 palaeo-electronica.org/content/2018/2343-new-eupelycosaur.

Lucas, S.G., Emry, R.J., Krainer, K., Hunt, A.P. and Spielmann, J.A., 2012, Strigilites (fossilized owl pellets) from the Oligocene of Wyoming: New Mexico Museum of Natural History and Science, Bulletin 57, p. 325-335.

Lucas, S.G., Spielmann, J.A., Rinehart, L.F., Heckert, A.B., Herne, M.C., Hunt, A.P., Foster J. R. and Sullivan, R.M., 2006, Taxonomic status of *Seismosaurus hallorum*, a Late Jurassic sauropod dinosaur from New Mexico: New Mexico Museum of Natural History and Science, Bulletin 36, p. 149-161.

Ludvigsen, R. and Beard, G., 1994, West-coast fossils. Whitecap Books, Toronto, 199 p.

Ludvigsen, R. and Beard, G., 1997, West-coast fossils (Revised Edition). Madeira Park, Harbour Publishing, 216 p.

Lukeneder, A. and Lukeneder, P., 2021, The Upper Triassic Polzberg palaeobiota from a marine Konservat-Lagerstätte deposited during the Carnian Pluvial Episode in Austria: Scientific Reports, v. 11, 16644, doi.org/10.1038/s41598-021-96052-w.

Lukeneder, A., Surmik, D., Gorzelak, P., Niedźwiedzki, R., Brachaniec, T. and Salamon, M. A., 2020, Bromalites from the Upper Triassic

Polzberg section (Austria); insights into trophic interactions and food chains of the Polzberg palaeobiota: Scientific Reports, v. 10**,** 20545, doi.org/10.1038/s41598-020-77017-x.

Lund, R. and Janvier, P., 1986, A second lamprey from the lower Carboniferous (Namurian) of Bear Gulch, Montana (USA): Geobios, v. 19, p. 647-652.

Lund, R. and Lund, W., 1984, New genera and species of coelacanths from the Bear Gulch Limestone (lower Carboniferous) of Montana (USA): Geobios, v. 17, p. 237-244.

Lund, R. and Lund W., 1985, The coelacanths from the Bear Gulch Limestone (Namurian) of Montana and the evolution of the Coelacanthiformes: Bulletin of the Carnegie Museum of Natural History, v. 25, p. 1-74.

Lund, W., Lund, R. and Klein G.A., 1985, Coelacanth feeding mechanisms and ecology of the Bear Gulch coelacanths: Compte Rendu, Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère*,* v. 5, p. 492-500.

Luo, M., Hu, S., Benton, M.J., Shi, G.R., Zhao, L., Huang, J., Song, H., Wen, W., Zhang, Q., Fang, Y. and Huang, Y., 2017, Taphonomy and palaeobiology of early Middle Triassic coprolites from the Luoping biota, southwest China: Implications for reconstruction of fossil food webs: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 474, p. 232-246.

Luppa, H., 1978, Histology of the digestive tract; *in* Gans, C., and Parsons, T. S., eds., Biology of the Reptilia. Volume 6. Morphology E. London, Academic Press, p. 225-313.

Lyell, C., 1863, Principles of geology. London, John Murray, 398 p.

Lyman, R.L., 1994, Vertebrate taphonomy. Cambridge manuals in archaeology. Cambridge, Cambridge University Press, 552 p.

Machado, E.B., Avilla, L.S., Nava, W.R., Campos, D.A. and Kellner, A.W., 2013, A new titanosaur sauropod from the Late Cretaceous of Brazil: Zootaxa, v. 3701, p. 301-321.

Mackness, B.S., Cooper, J.E., Wilkinson, C.E.C. and Wilkinson, D., 2010, Palaeopathology of a crocodile femur from the Pliocene of eastern Australia: Alcheringa, v. 34, p. 515-521.

Madurell-Malapeira, J., Alba, D.M., Aurell-Garrido, P. and Moyà-Solà, S., 2011, Taphonomic approach to the last Villafranchian faunas of Europe: The layer 7 of the Vallparadís Estació local section (Vallès-Penedès Basin, NE Iberian Peninsula): IX Encuentro de Jóvenes Investigadores en Paleontología, Morella (Castellón), Proceedings Volume, p. 203-210.

Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S. and Berástegui, X., 2010, The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe: Quaternary Science Reviews, v. 29, p. 3972-3982.

Mahaney, W.C., Barendregt, R.W., Allen, C.C.R., Milner, M.W. and Bay, D., 2013, Coprolites from the Cretaceous Bearpaw Formation of Saskatchewan: Cretaceous Research, v. 14, p. 31-38.

Mahaney, W. C., Hancock, R. G. V., Aufreiter, S., and Huffman, M. A. 1996, Geochemistry and clay mineralogy of termite mound soil and the role of geophagy in chimpanzees of the Manhale Mountains, Tanzania: Primates, v. 37, p. 121-134.

Maier, W., Richter, R. and Storch, G., 1986*, Leptictidium nasutum* – ein archisches Saugetier aus Messel mit aussergewohnlichen Anpassungen: Natur und Museum, v. 116, p. 1-19.

Maisch, M.W., 2009, The small dicynodont *Katumbia parringtoni* (von Huene 1942) (Therapsida: Dicynodontia) from the upper Permian Kawinga Formation of Tanzania as gorgonopsian prey: Palaeodiversity, v. 2, p. 279-282.

Maisch, M.W. and Matzke, A.T., 2003, The cranial osteology of the ichthyosaur *Leptonectes* cf. *tenuirostris* from the Lower Jurassic of England: Journal of Vertebrate Paleontology, v. 23, p. 116–127.

Maisey, J.G., 1994, Predator relationships and trophic level reconstruction in a fossil fish community: Environmental Biology of Fishes, v. 40, p. 1-22.

Maisey, J.G., 1996, Discovering fossil fishes. New York, Henry Holt and Company, 223 p.

Maisey, J.G. and Melo, J.H.G., 2005, Some Middle Devonian (Eifelian–Givetian) fossil fish remains from the Pimenteira Formation of the Parnaíba Basin, northeast Brazil: Arquivos do Museu Nacional, v. 63, p. p. 495-505.

Malkani, M.S., 2006, First rostrum of carnivorous Vitakridrinda (abelisaurid theropod dinosaur) found from the Latest Cretaceous Dinosaur Beds (Vitakri) Member of Pab Formation, Alam Kali Kakor Locality of Vitakri area, Barkhan District, Balochistan, Pakistan: Sindh University Research Journal (Science Series), v. 38 p. 5-24.

Malkani, M.S., 2009, New *Balochisaurus* (Balochisauridae, Titanosauria, Sauropoda) and Vitakridrinda (Theropoda) remains from Pakistan: Sindh University Research Journal (Science Series), v. 41, p. 65-92.

Malkani, M.S., 2010, *Vitakridrinda* (Vitakrisauridae, Theropoda) from the Latest Cretaceous of Pakistan: Journal of Earth Science, v. 21, p. 204-212.

Malone, J.R., Malone, D.H., Kowallis, B., Straesser, J.C., 2019, Detrital zircon geochronology of quartzite gastroliths in the Jurassic Morrison Formation, northeast Utah: Geological Society of America, Abstracts with Programs, v. 51(5), doi: 10.1130/abs/2019AM-337559.

Malone, J.R., Strasser, J.C., Malone, D.H., D'Emic, M.D., Brown, L., and Craddock, J.P., 2021, Jurassic dinosaurs on the move: Gastrolith provenance and long-distance migration: Terra Nova*.* 2021;00:1–8, doi: 10.1111/ter.12522.

Malzahn, E., 1968, Uber neue Funde von *Janassa bitminosa* (Schloth.) im niederrheinischen Zechstein: Geologidches Jahrbuch, v. 85, p. 67-96.

Malzahn, E., 1972, Zur Kenntnis der Kopfskeletts von *Janassa bituminosa* (Schloth.) aus dem hessischen Kupferschiefer: Geologische Jahrbuch, v. 90, p. 431-440.

Manchester, S.R., Lehman, T.M. and Wheeler, E.A., 2010, Fossil palms (Arecaceae, Coryphoideae) associated with juvenile herbivorous dinosaurs in the Upper Cretaceous Aguja Formation, Big Bend National Park, Texas: International Journal of Plant Sciences, v. 171, p. .679-689.

Mancuso, A. C., Marsicano, C. and Palma, R., 2004, Vertebrate coprolites from the Triassic of Argentina (Cuyana Basin): Ameghiniana, v. 41, p. 347-354.

Mancuso, A.C., Benavente, C.A., Previtera, E., Arcucci, A.B. and Irmis, R.B., 2018, Carnivore coprolites from the lower Carnian (Upper Triassic) Chañares Formation, northwestern Argentina: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 489, p. 15-28.

Mángano, M.G. and Buatois, L.A., 2016a, The Cambrian explosion; *in* Mángano, M.G. and Buatois, L.A., eds., The trace-fossil record of major evolutionary events. Volume 1. Precambrian and Paleozoic. Topics in Geobiology 40. Dordrecht, Springer, p. 73-126.

Mángano, M.G. and Buatois, L.A., eds., 2016b, The trace-fossil record of major evolutionary events. Volume 1. Precambrian and Paleozoic. Topics in Geobiology 40. Dordrecht, Springer, 358 p.

Mángano, M.G. and Buatois, L.A., eds., 2016c, The trace-fossil record of major evolutionary events. Volume 2. Mesozoic and Cenozoic. Topics in Geobiology 40. Dordrecht, Springer, 473 p.

Mángano, M.G. and Buatois, L.A., 2021, The Cambrian explosion; *in*, Alderton, D. and Elias, S., eds*.*, Encyclopedia of geology (Second Edition), Volume 3. London, Elsevier, p. 583-600.

Manley, K., 1989, Technique for distinguishing *bona fide* and suspected gastroliths: Abstracts of the Symposium on Southwestern Geology and Paleontology 1989, Museum of Northern Arizona, Flagstaff, p. 18.

Manley, K., 1991a, Gastrolith identification and sauropod migration: Geological Society of America, Abstracts with Programs, v. 23, no. 4, p. 45.

Manley, K., 1991b, Two techniques for measuring surface polish as applied to gastroliths: Ichnos, v. 1, p. 313-316.

Manley, K., 1993, Surface polish measurements from *bona fide* and suspected dinosaur gastroliths, wave and stream supported clasts: Ichnos, v. 2, p. 167-169.

Mansky, C., Lucas, S.G. and Hunt, A.P., 2012, Mississippian bromalites from Blue Beach, Nova Scotia, Canada: New Mexico Museum of Natural History and Science, Bulletin 57, p. 161-170.

Mantell, G.A., 1822, The fossils of the South Downs: Or illustrations of the geology of Sussex. London, Lupton Relfe, 305 p.

Mapes, R. and Chaffin, D.T., 2003, Predation on cephalopods: A general overview with a case study from the upper Carboniferous of Texas; *in* Kelley, P. H., Kowalewski, M. and Hansen, T. A., eds., Predator-prey interactions in the fossil record. New York, Kluwer Academic/Plenum Publishers, p. 177-213.

Mapes, R.H. and Hansen, M.C., 1983, Pennsylvanian shark-cephalopod predation: A case study: Lethaia, v. 17, p. 175-183.

Mapes, R.H., Fahrer, T.R. and Babcock, L.E., 1989, Sublethal and lethal injuries of Pennsylvanian conulariids from Oklahoma: Journal of Paleontology, v. 63, p. 34-37.

Mapes, R.H., Sims, M.S. and Boardman, D.R., 1995, Predation on the Pennsylvanian ammonoid *Gonioloboceras* and its implications for allochthonous vs. autochthonous accumulations of *Goniatites* and other ammonoids: Journal of Paleontology, v. 69, p. 441-446.

Markwick, P.J., 1998, Crocodilian diversity in space and time: The role of climate in paleoecology and its implication for understanding K/T extinctions: Paleobiology, v. 24, p. 470-497.

Marra, A.C., Villa, P., Beauval, C., Bonfiglio, L. and Goldberg, P., 2004, Same predator, variable prey: Taphonomy of two Upper Pleistocene hyena dens in Sicily and SW France: Revue de Paléobiologie, v. 23, p. 787-801.

Marron, A.O. and Moore, J.R., 2013, Evidence of frugivory and seed dispersal in Oligocene tortoises from South Dakota: Geological Magazine, v. 150, p. 1143-1149.

Marsh, O.C., 1869, Notice of some new reptilian remains from the Cretaceous of Brazil: American Journal of Science, v. 47, p. 390-392.

Marsh, O.C., 1877, Introduction and succession of vertebrate life in America. New Haven, Tuttle, Morehouse and Taylor, 57 p.

Marshall, C.R., 2006, Explaining the Cambrian "explosion" of animals: Annual Review of Earth and Planetary Sciences, v. 34, p. 355–384.

Martill, D.M., 1985a, The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England: Philosophical Transactions, Royal Society London, Series B, v. 311, p. 155-165.

Martill, D.M., 1985b, The world's largest fish: Geology Today, v. 2, p. 61-63.

Martill, D.M., 1986, The diet of *Metriorhynchus*, a Mesozoic marine crocodile: Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 1986, p. 621-625.

Martill, D.M., 1990, Predation on *Kosmoceras* by semionotid fish in the Middle Jurassic Oxford Clay of England: Palaeontology, v. 33, p. 739-742.

Martill, D.M., 1992, Pliosaur stomach contents from the Oxford Clay: Mercian Geologist, v. 13, p. 37–42.

Martill, D.M., 1996, Fossils explained 17: Ichthyosaurs: Geology Today, v. 12, p. 194-196.

Martill, D.M. and Barker, M. J., 2000, An ammonite steinkern gastrolith from the Lower Cretaceous of the Isle of Wight, England: Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 2000, p. 186-192.

Martill, D.M. and Naish, D., 2001, Dinosaur trace fossils: Footprints, coprolites and gastroliths; *in* Martill, D.M. and Naish, D., eds., Dinosaurs of the Isle of Wight: Palaeontological Association, Field Guides to Fossils, no. 10, p. 310-323.

Martill, D.M., Taylor, M.A., Duff, K.L., Riding, J.B. and Bown, P.R., 1994, The trophic structure of the biota of the Peterborough Member, Oxford Clay Formation (Jurassic), UK: Journal of the Geological Society of London, v. 151, p. 173-194.

Martin, A.J., Vazquez-Prokopec, G.M. and Page, M., 2010, First known feeding trace of the Eocene bottom-dwelling fish *Notogoneus osculus* and its paleontological significance: PLoS ONE, v. 5(5): e10420, doi:10.1371/journal.pone.0010420.

Martin, J.E., 1981, Contents of coprolites from Hemphillian sediments in northern Oregon and their importance in paleoecological interpretations: Proceedings of South Dakota Academy of Sciences, v. 60, p. 105-115.

Martin, J. E., 1994, Gastric residues in marine reptiles from the Late Cretaceous Pierre Shale in South Dakota: Their bearing on extinction: Journal of Vertebrate Paleontology, v. 14 (supplement to no. 3), p. 36A.

Martin, J. E., 2013, Surviving a potentially lethal injury? Bite mark and associated trauma in the vertebra of a dyrosaurid crocodilian: Palaios, v. 28, p. 6-8.

Martin, J. E. and Bjork, P. R., 1987, Gastric residues associated with a mosasaur from the Late Cretaceous (Campanian) Pierre Shale in South Dakota: Dakoterra, v. 3, p. 68–72.

Martin, J. E. and Fox, J.E., 2004, Molluscs in the stomach contents of *Globidens*, a shell crushing mosasaur, from the Late Cretaceous Pierre Shale, Big Bend area of the Missouri River, central South Dakota: Geological Society of America, Abstracts with Programs, v. 36, p. 80.

Martin, J.E. and Fox, J.E., 2007, Stomach contents of *Globidens*, a shell-crushing mosasaur (Squamata), from the Late Cretaceous Pierre Shale Group, Big Bend area of the Missouri River, central South Dakota; *in* Martin, J.E. and Parris, D.C., eds., The geology and paleontology of the Late Cretaceous marine deposits of the Dakotas: Geological Society of America, Special Paper, v. 427, p. 167-176.

Martin, J. E. and Kennedy, L. E., 1988, A plesiosaur with stomach contents from the Late Cretaceous (Campanian) Pierre Shale of South Dakota: A preliminary report: Proceedings of the South Dakota Academy of Science, v. 67, p. 76-79.

Martin, L. D. and Bennett, D. K., 1977, The burrows of the Miocene beaver *Palaeocastor*, western Nebraska, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173-193.

Martin, L. D. and Rothschild, B. M., 1989, Paleopathology and diving mosasaurs: American Scientist, v. 77, p. 460-467.

Martin, L. D. and Tate, J., 1976, The skeleton of *Baptornis advenus* (Aves: Hesperornithformes): Smithsonian Contributions to Paleobiology, v. 27, p. 35–66.

Martin, L. D., Rothschild, B. M. and Burnham, D. A., 2016, *Hesperornis* escapes plesiosaur attack: Cretaceous Research, v. 63, p. 23-27.

Martin, P. S., 2005, Twilight of the mammoths: Ice Age extinctions and the rewilding of America. Berkeley, University of California Press, 250 p.

Martin, P.S., Sabela, B.E. and Shutler, D., 1961, Rampart Cave coprolites and ecology of the Shasta ground sloth: American Journal of Science, v. 259, p. 102-127.

Martin, P.S., Thompson, R.S. and Long, A., 1985, Shasta ground sloth extinction: A test of the blitzkrieg model; *in* Mead, J.I. and Meltzer, D.J., eds., Environments and extinction: Man in late glacial North America: Orono, University of Maine, p. 5-14.

Martinelli, J., De Gibert, J.M., Domènech, R., Ekdale, A.A. and Steen, P.P., 2001, Cretaceous ray traces?: An alternative interpretation for the alleged dinosaur tracks of La Posa, Isona, NE Spain: Palaios, v. 16, p. 409-416.

Martínez-Cáceres, M., Lambert, O. and de Muizon, C., 2017, The anatomy and phylogenetic affinities of *Cynthiacetus peruvianus*, a large *Dorudon*-like basilosaurid (Cetacea, Mammalia) from the late Eocene of Peru: Geodiversitas, v. 39, p. 7-163.

Martini, E., 1965, Die Fischfauna von Sieblos/Rhön (Oligozän): 2. Fischreste aus Koprolithen: Senckenbergia, v. 46, p. 307-314.

Massare, J.A., 1987, Tooth morphology and prey preference of Mesozoic marine reptiles: Journal of Vertebrate Paleontology, v. 7, p. 121-137.

Massare, J.A. and Young, H.A., 2005, Gastric contents of an ichthyosaur from the Sundance Formation (Jurassic) of central Wyoming: Paludicola, v. 5, p. 20-27.

Mateer, N. J. 1974, Three Mesozoic crocodiles in the collections of the Palaeontological Museum, Uppsala: Bulletin of the Geological Institutions of the University of Uppsala, New Series, v. 4, p. 53–72.

Mateus, O., 1998, *Lourinhosaurus antunesi*, a new Upper Jurassic allosaurid (Dinosauria: Theropoda) from Lourinha, Portugal: Memórias da Academia de Ciências de Lisboa, v. 37, p. 111-124.

Mateus, O., Polcyn, M.J., Jacobs, L.L., Araújo, R., Schulp, A.S., Marinheiro, J., Pereira, B. and Vineyard, D., 2012, Cretaceous amniotes from Angola: Dinosaurs, pterosaurs, mosasaurs, plesiosaurs, and turtles; *in* Hurtado, P. H., Fernández-Baldor, F. T. and Sanagustín, J. I. C., eds., Actas de V Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, p. 71-105.

Matley, C., 1939a, On some coprolites from the Maleri Beds of India: Records of the Geological Survey of India, v. 74, p. 535-547.

Matley, C., 1939b, The coprolites of Pijdura, Central Province: Records of the Geological Survey of India, v. 74, p. 530-534.

Matsumoto, T., Obata, I., Okazaki, Y., Kani, Y., 1982, An interesting occurrence of a fossil reptile in the Cretaceous of the Obira area, Hokkaido: Proceedings of the Japanese Academy, Series B, v. 58, p. 109-113.

Matthew, W., 1908, *Allosaurus,* a carnivorous dinosaur, and its prey: American Museum Journal, v. 8, p. 3–5.

Maus, M. and Wuttke, M., 2002, Comparative anatomical and taphonomical examination of the larvae of *Pelobates decheni* Troschel 1861 and *Eopelobates anthracinus* Parker 1929 (Anura: Pelobatidae) found at the Upper Oligocene sites at Enspel (Westerwald⁄Germany) and Rott (Siebengebirge⁄Germany): Courier Forschungsinstitut Senckenberg, v. 237, p. 129–138.

Mayhew, D.F., 1977, Avian predators as accumulators of fossil mammal material: Boreas, v. 6, p. 25–31

Mayne, R. G., 1854, An expository lexicon of the terms, ancient and modern, in medical and general science. London, J. Churchill, 456 p.

Mayr, G., 2002, A new specimen of *Salmila robusta* (Aves: Gruiformes: Salmilidae n. fam.) from the middle Eocene of Messel: Paläontologische Zeitschrift, v. 76, p. 305–316.

Mayr, G., 2004, A partial skeleton of a new fossil loon (Aves, Gaviiformes) from the early Oligocene of Germany with preserved stomach content: Journal of Ornithology, v. 145, p. 281-286.

Mayr, G., 2009, Paleogene fossil birds. Berlin, Springer, 262 p.

Mayr, G., 2013, Late Oligocene mousebird converges on parrots in skull morphology: Ibis, v. 155, p. 384–396.

Mayr, G., 2015, A new specimen of the early Eocene *Masillacolius brevidactylus* and its implications for the evolution of feeding specializations in mousebirds (Coliiformes): Comptes Rendus Palevol, v. 14, p. 363-370.

Mayr, G. and Mourer-Chauviré, C., 2000, Rollers (Aves. Coraciiformes s.s.) from the middle Eocene of Messel (Germany) and the Upper Eocene of the Quercy (France): Journal of Vertebrate Paleontology, v. 20, p. 533–546.

Mayr, G. and Peters, D.S., 1998, The mousebirds (Aves: Coliiformes) from the middle Eocene of Grube Messel (Hessen, Germany): Senckenberg Lethaea, v. 78, p. 179–197.

Mayr, G. and Richter, G., 2011, Exceptionally preserved plant parenchyma in the digestive tract indicates a herbivorous diet in the middle Eocene bird *Strigogyps sapea* (Ameghinornithidae): Paläontologische Zeitschrift, v. 85, p. 303–307.

Mayr, G. and Schaal, S.F.K., 2016, Gastric pellets with bird remains from the early Eocene of Messel: Palaios, v. 31, p. 447–451.

Mayr, G., and Wilde, V., 2014, Eocene fossil is earliest evidence of flower-visiting by birds: Biology Letters, v. 10(5), 20140223, dx.doi.org/10.1098/rsbl.2014.0223

Mayr, G., Mourer-Chauviré, C. and Weidig, I., 2004, Osteology and systematic position of the Eocene Primobucconidae (Aves, Coraciiformes sensu stricto), with first records from Europe: Journal of Systematic Paleontology, v. 2, p. 1–12.

Mayr, G., Poschmann, M. and Wuttke, M., 2006, A nearly complete skeleton of the fossil galliform bird *Palaeortyx* from the late Oligocene of Germany: Acta Ornithologica, v. 41, p. 129–135.

Mayr, G., Kaye, T.G., Pittman, M., Saitta, E.T. and Pott, C., 2020, Reanalysis of putative ovarian follicles suggests that Early Cretaceous birds were feeding not breeding: Scientific Reports, v. 10, p. 1-10, doi.org/10.1038/s41598-020-76078-2.

Mazin, J., Billon-Bruyat, J., Hantzepergue, P. and Larauire, G., 2003, Ichnological evidence for quadrupedal locomotion in pterodactyloid pterosaurs: Trackways from the Late Jurassic of Crayssac; *in* Buffetaut, E. and Mazin, J.M., ed., Evolution and palaeobiology of pterosaurs. Geological Society of London, Special Publications, v. 217, p. 283–296,

Mazza, P.P., 2006, Poggio Rosso (Upper Valdarno, central Italy), a window on latest Pliocene wildlife: Palaios, v. 21, p. 493-498.

Mazza, P.P., Bertini, A. and Magi, M., 2004, The late Pliocene site of Poggio Rosso (central Italy): Taphonomy and paleoenvironment: Palaios, v. 19, p. 227-248.

McAllister, J.A., 1985, Reevaluation of the origin of spiral coprolites: University of Kansas Palaeontological Contributions, v. 114, p. 1-12.

McAllister, J.A., 1987, Phylogenetic distribution and morphological reassessment of the intestines of fossil and modern fishes: Zoologische Jahrbücher Abtheilung für Anatomie und Ontogenie der Thiere, v. 115, p. 281-294.

McAllister, J.A., 1988, Preliminary description of the coprolitic remains from Hamilton Quarry, Kansas; *in* Mapes, G. and Mapes, R. H., eds., Regional geology and paleontology of Upper Paleozoic Hamilton Quarry area: Kansas Geological Survey, Guidebook 6, p. 195-202.

McAllister, J.A., 1996, Coprolites; *in* Schultze, H.-P. and Cloutier, R., eds., Devonian fishes and plants of Miguasha, Quebec, Canada: München, Verlag Dr Friedrich Pfeil, p. 328-347.

McCarville, K. and Bishop, G.A., 2002, To pee or not to pee: Evidence for liquid urination in sauropod dinosaurs: Journal of Vertebrate Paleontology, v. 22 (supplement to no. 3), p. 85.

McCoy, M.R., Karl, H.V., Tichy, G., Steinbacher, J., Aigner, G. and Cemper-Kisslich, J., 2012, Radiological evaluation of a fossil turtle trauma from the Upper Jurassic of Eichstätt (Testudines: Cryptodira): Studia Geologica Salmanticensia, v. 48, p. 37-44.

McCune, A.R. and Schaeffer, B., 1986, Triassic and Jurassic fishes: Patterns of diversity; *in* Padian, K., ed., The beginning of the age of dinosaurs: Faunal change across the Triassic-Jurassic boundary. Cambridge, Cambridge University Press, p. 171-181.

McGraw, W. S., Cooke, C. and Shultz, S., 2006, Primate remains from African crowned eagle (*Stephanoaetus coronatus*) nests in Ivory Coast's Tai Forest: Implications for primate predation and early hominid taphonomy in South Africa: American Journal of Physical Anthropology, v. 131, p. 151-165.

McHenry, C.R., 2009, 'Devourer of Gods' - The palaeoecology of the Cretaceous pliosaur *Kronosaurus queenslandicus* [Ph.D. dissertation]: Newcastle, University of Newcastle, 616 p.

McHenry, C.R., Cook, A.G. and Wroe, S., 2005, Bottom-feeding plesiosaurs: Science, v. 310, p. 75.

McHenry, C.R., Clausen, P.D., Daniel, W.J.T., Meers, M.B. and Pendharkar, A., 2006, Biomechanics of the rostrum in crocodilians: A comparative analysis using finite element modeling: The Anatomical Record, v. 288A, p. 827–849.

McKee, J.W.A., 1987, The occurrence of the Pliocene penguin *Tereingaomis moisleyi* (Sphenisciformes: Spheniscidae) at Hawera, Taranaki, New Zealand: New Zealand Journal of Zoology, v. 14, 557-561.

McKean, R.L.S. and Gillette, D.D., 2015, Taphonomy of large marine vertebrates in the Upper Cretaceous (Cenomanian-Turonian) Tropic Shale of southern Utah: Cretaceous Research, v. 56, p. 278-292.

McLain, M.A., 2016, Taphonomy of a Lance Formation (Maastrichtian, WY) dinosaur bonebed with a focus on tooth traces [Ph.D. dissertation]: Loma Linda, Loma Linda University, 149 p.

McLain, M.A., Nelsen, D., Snyder, K., Griffin, C.T., Siviero, B., Brand, L.R. and Chadwick, A.V., 2018, Tyrannosaur cannibalism: A case of a tooth-traced tyrannosaurid bone in the Lance Formation (Maastrichtian), Wyoming: Palaios, v. 33, p. 164-173.

McLennan, L.J. and Purnell, M.A., 2021, Dental microwear texture analysis as a tool for dietary discrimination in elasmobranchs: Scientific Reports, v. 11, 2444, doi.org/10.1038/s41598-021-81258-9.

McMenamin, M.A.S., 2003, Origin and early evolution of predators; *in* Kelley, P. H., Kowalewski, M. and Hansen, T. A., eds., Predator-prey interactions in the fossil record. New York, Kluwer Academic/Plenum Publishers, p. 379-400.

McMenamin, M.A.S., ed. 2001, Paleontology Sonora: Lipalian and Cambrian. South Hadley, Meanma Press, 192 p.

McNamara, M. E., Orr, P.J., Kearns, S.L., Alcalá, L., Anadon, P. and Peñalver-Mollá, E., 2009, Soft-tissue preservation in Miocene frogs from Libros, Spain: Insights into the genesis of decay microenvironments: Palaios, v. 24, p. 104–117.

McNamara, M.E., Orr, P.J., Kearns, S.L., Alcalá, L., Anadón, P. and Peñalver-Mollá, E., 2010, Exceptionally preserved tadpoles from the Miocene of Libros, Spain: Ecomorphological reconstruction and the impact of ontogeny upon taphonomy: Lethaia, v. 43, p. 290–306.

McWhorter, T.J. and Martínez del Rio, C., 2000, Does gut function limit hummingbird food intake?: Physiological and Biochemical Zoology, v. 73, p. 313–324.

McWilliams, S.R., Caviedes-Vidal, E. and Karasov, W.H., 1999, Digestive adjustments in cedar waxwings to high feeding rate: Journal of Experimental Zoology, v. 283, p. 394–407.

Mead, J.I. and Agenbroad, L.D., 1989, Pleistocene dung and the extinct herbivores of the Colorado Plateau, southwestern USA: Cranium, v. 6, p. 29-44.

Mead, J.I. and Agenbroad, L.D., 1992, Isotope dating of Pleistocene dung deposits from the Colorado Plateau, Arizona and Utah: Radiocarbon, v. 34, p. 1-19.

Mead, J.I. and Swift, S.L., 2012, Late Pleistocene (Rancholabrean) dung deposits of the Colorado Plateau, western North America: New Mexico Museum of Natural History and Science, Bulletin 57, p. 337-342.

Mead, J.I, Agenbroad, L.D. and Stuart, A., 1993, Late Pleistocene vertebrates from Bechan Cave, Colorado Plateau, Utah; *in* Santucci, V.L. and McClelland, L., eds., National Park Service Paleontological Research Abstract Volume. Technical Report NPS/NRPEFO/NRTR-93/11, p. 69.

Mead, J.I., Agenbroad, L. D., Davis, O.K. and Martin, P.S., 1986a, Dung of *Mammuthus* in the arid Southwest, North America: Quaternary Research, v. 25, p. 121-127.

Mead, J.I., Agenbroad, L. D., Martin, P. S. and Davis, O. K., 1984, The mammoth and sloth dung from Bechan Cave in southern Utah: Current Research in the Pleistocene, v. 1, p. 79-80.

Mead, J.I., Tweet, J.S., Santucci, V.L., Tobin, B., Chambers, C.L., Thomas, S.C. and Carpenter, M.C., 2020, Pleistocene/Holocene cave fossils from Grand Canyon National Park: Ice Age (Pleistocene) flora, fauna, environments, and climate of the Grand Canyon, Arizona; *in* Santucci, V. L., and J. S. Tweet, eds., Grand Canyon National Park: Centennial paleontological resource inventory. Natural Resource Report NPS/GRCA/NRR–2020/2103. Fort Collins, National Park Service, p. 403-463.

Mead, J.I., Martin, P.S., Euler, R.C., Long, A., Jull, A.T., Toolin, L.T., Donahue, D.J. and Linick, T.W., 1986b, Extinction of Harrington's Mountain Goat: Proceedings of the National Academy of Science, v. 83, p. 836-839.

Meador, L., 2017, Who ate the subfossil lemurs? A taphonomic and community study of raptor, crocodylian and carnivoran predation of the extinct Quaternary lemurs of Madagascar [Ph.D. dissertation]: Amherst, University of Massachusetts, 388 p.

Meehan, T.J., 2007, Hair traces in carnivorous coprolites: Geological Society of America, Abstracts with Programs, v. 39(3), p. 18.

Megirian, D., Murray, P. and Wells, R., 1996, The late Miocene Ongeva local fauna of central Australia: Beagle: Records of the Museums and Art Galleries of the Northern Territory, v. 13, p. 9-37.

Mehl, J., 1978, Ein Koprolith mit Ammoniten-Aptychen aus den Solnhofener Plattenkalken: Jahresberichte der Wetterausischen Gesellschaft für Naturkunde, v. 1978, p. 85-89.

Meillet, A., 1842, Minéralogie de basin de Paris: Analyse de l'Apatélite et des coprolithes du Calcaire grossier et de la craie: Revue de science et industrie, Paris, v. 11, p. 254-257

Meinertzhagen, R., 1954, Grit: Bulletin of the British Ornithological Club, v. 74, p. 97-102.

Melchor, R.N. and Genise, J.F. 2004, Critical appraisal of vertebrate ichnotaxonomy. 32nd International Geological Congress, Italia 2004, Abstracts Part 1. International Union of Geological Sciences, p. 597.

Mellett, J.S., 1975, Scatological origins of microvertebrate fossils: Science, v. 185, p. 349- 350.

Melton, W.G., 1972, The Bear Gulch Limestone and the first conodont-bearing animals: Montana Geological Society, 21st Annual Field Conference. Billings, Montana Geological Society, p. 65–68.

Meng, J., and Wyss, A.R., 1997, Multituberculate and other mammal hair recovered from Palaeogene excreta: Nature, v. 385, p. 712–714.

Merceron, G., de Bonis, L., Viriot, L. and Blondel, C., 2005, Dental microwear of fossil bovids from northern Greece: Paleoenvironmental conditions in the eastern Mediterranean during the Messinian: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 217, p. 173-185.

Meso, J.G., Hendrickx, C., Baiano, M.A., Canale, J.I., Salgado, L., and Diaz Martinez, I., 2021, Isolated theropod teeth associated with a sauropod skeleton from the Late Cretaceous Allen Formation of Río Negro, Patagonia, Argentina: Acta Palaeontologica Polonica, v. 66, p. 409-423.

Meunier, F.J., Cupello, C., Yabumoto, Y. and Brito, P.M., 2018, The diet of the Early Cretaceous coelacanth †*Axelrodichthys araripensis* Maisey, 1986 (Actinistia: Mawsoniidae): Cybium, v. 42, p. 105-111.

Meyer C. A., 1991, Burial experiments with marine turtle carcasses and their paleoecological significance: Palaios, v. 6, p. 89–96.

Meyer, C.A. and Thüring, B., 2003, Dinosaurs of Switzerland: Comptes Rendus Palevol, v. 2, p. 103–117.

Mierzwiak, J.S. and Godfrey, S.J., 2019, *Megalodon*-bitten whale rib from South Carolina: The Ecphora, v. 34(2), p. 15–20.

Mikuláš, R., 1995, Trace fossils from the Paseky Shale (early Cambrian, Czech Republic): Journal of the Czech Geological Society, v. 40, p. 37–54.

Mikuláš, R. and Dvorák, Z., 2010, Possible crocodylian bite traces, Miocene of the Most Basin (Czech Republic): New Mexico Museum of Natural History and Science, Bulletin 51, p. 191-194.

Mikuláš, R., Kadlecová, E., Fejfar, O. and Dvořák, Z., 2006, Three new ichnogenera of biting and gnawing traces on reptilian and mammalian bones: A case study from the Miocene of the Czech Republic: Ichnos, v. 13, p. 113-127.

Milàn, J., 2010, Coprolites from the Danian Limestone (lower Paleocene) of Faxe Quarry, Denmark: New Mexico Museum of Natural History and Science, Bulletin 51, p. 215-218.

Milàn, J., 2012, Crocodylian scatology – a look into morphology, internal architecture, inter- and intraspecific variation and prey remains in extant crocodylian feces: New Mexico Museum of Natural History and Science, Bulletin 57, p. 65-71.

Milàn, J., 2018, First find of the coprolite ichnotaxon *Daniacopros hofstedtae*, from the Middle Danian Faxe Formation of Faxe Quarry, Denmark: New Mexico Museum of Natural History and Science, Bulletin 79, p. 499-501.

Milàn, J. and Hedegaard, R., 2010, Interspecific variation in tracks and trackways from extant crocodylians: New Mexico Museum of Natural History and Science, Bulletin 51, p. 15-29.

Milàn, J. and Hunt, A.P., 2016, *Daniacopros hofstedtae*, ichnogen. et ichnosp. nov., a new vertebrate coprolite ichnotaxon from the

Lower Danian Stevns Klint Formation of the Hammelev limestone quarry, Denmark: New Mexico Museum of Natural History and Science, Bulletin 74, p. 159-161.

Milàn, J., Lindow, B.E. and Lauridsen, B.W., 2011, Bite traces in a turtle carapace fragment from the middle Danian (Lower Paleocene) bryozoan limestone, Faxe, Denmark: Bulletin of the Geological Society of Denmark, v. 59, p. 61-67.

Milàn, J., Rasmussen, E.S. and Dybkjær, K., 2018, A crocodilian coprolite from the lower Oligocene Viborg Formation of Sofienlund Lergrav, Denmark: Bulletin of the Geological Society of Denmark, v. 66, p. 181-187.

Milàn, J., Rasmussen, B.W. and Lynnerup, N., 2012a, A coprolite in the MDCT-scanner – internal architecture and bone contents revealed: New Mexico Museum of Natural History and Science, Bulletin 57, p. 99–103.

Milàn, J., Hunt, A.P., Adolfssen, J.S., Rasmussen, B.W. and Bjerager, M., 2015, First record of a vertebrate coprolite from the Upper Cretaceous (Maastrichtian) Chalk of Stevns Klint, Denmark: New Mexico Museum of Natural History and Science, Bulletin 67, p. 227-229.

Milàn, J., Mateus, O., Mau, M., Rudra, A., Sanei, H. and Clemmensen, L. B., 2021, A possible phytosaurian (Archosauria, Pseudosuchia) coprolite from the Late Triassic Fleming Fjord Group of Jameson Land, central East Greenland: Bulletin of the Geological Society of Denmark, v. 69, p. 71-80.

Milàn, J., Clemmensen, L.B., Adolfssen, J.S., Estrup, E.J., Frobøse, N., Klein, N., Mateus, O. and Wings, O., 2012b, A preliminary report on coprolites from the Late Triassic part of the Kap Stewart Formation, Jameson Land, East Greenland: New Mexico Museum of Natural History and Science, Bulletin 57, p. 203-206.

Miles, R.S., 1973, Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder-girdle: Bulletin of the British Museum (Natural History), Geology, v. 24, p. 113–213.

Miles, R.S. and T.S. Westoll, 1968, The placoderm fish *Coccosteus cuspidatus* Miller ex Agassiz from the Middle Old Red Sandstone of Scotland. Part I. Descriptive morphology: Transactions of the Royal Society of Edinburgh, v. 67, p. 373–476.

Miller, C. V. and Pittman, M., 2021, The diet of early birds based on modern and fossil evidence and a new framework for its recognition: Biological Reviews, doi: 10.1111/brv.12743.

Miller, F.W., 1987, Ventifacts: Nature's lapidary work: Rocks and Minerals, v. 62, p. 180-187.

Miller, G.J., 1980, Some new evidence in support of the stabbing hypothesis for *Smilodon californicus* Bovard: Carnivore, v. 3, p. 8-26.

Miller, H.W., 1957, Intestinal casts in *Pachyrhizodus*, an elopid fish, from the Niobrara Formation of Kansas: Kansas Academy of Science Transactions, v. 60, p. 399-401.

Milner, A. and Charig, A., 1997, *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey: Bulletin of the British Museum (Natural History), Geology Series, v. 53, p. 11-70.

Milner, A.R. 1982, Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois: Palaeontology, v. 25, p. 635– 664.

Milner A.R.C. and Kirkland J.I., 2007, The case for fishing dinosaurs at the St. George Dinosaur Discovery Site at Johnson Farm: Utah Geological Survey Notes, v. 39, p. 1–3.

Milton, S.J., Dean, W.H.J. and Siegfried, W.R., 1994, Food selection by ostrich in southern Africa: Journal of Wildlife Management, v. 58, p. 234-248.

Minor, W.C., 1937, Dinosaur gizzard stones: Mineralogist, v. 12, p. 229-231.

Minter, N.J. and Braddy, S.J., 2006, The fish and amphibian swimming traces *Undichna* and *Lunichnium*, with examples from the lower Permian of New Mexico, USA: Palaeontology, v. 49, p. 1123–1142.

Mironenko, A., 2020, A hermit crab preserved inside an ammonite shell from the Upper Jurassic of central Russia: Implications to ammonoid palaeoecology: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 537, doi:org/10.1016/j.palaeo.2019.109397.

Mirsky, A., 1962, Stratigraphy of non-marine Upper Jurassic and Lower Cretaceous rocks, southern Bighorn Mountains, Wyoming: American Association of Petroleum Geologists Bulletin, v. 46, p. 1653-1680.

Mitzopoulos, M.K. and Zapfe, H., 1963, Fossile Hyäniden-Koprolithen au Pikermi: Annales Géologie Pays Hellèniques, Athénes, v. 14, p. 405- 407.

Moberly, R. J., 1960, Morrison, Cloverly and Sykes Mountain formations, northern Bighorn basin, Wyoming and Montana: Geological Society of America Bulletin, v. 71, p. 1137-1176.

Modesto, S.P. and Botha-Brink, J., 2010, A burrow cast with *Lystrosaurus* skeletal remains from the Lower Triassic of South Africa: Palaios, v. 25, p. 274-281.

Modesto, S.P., Scott, D.M. and Reisz, R.R., 2009, Arthropod remains in the oral cavities of fossil reptiles support inference of early insectivory: Biology Letters, v. 5, p. 838-840.

Mohr, E., 1964, Bermerkungen uber Hyänenkot und Koprolithen; *in* Kosswig Festschrift: Hamburg, Hamburger Zoologische Institut und Museum Mittelung, p. 107-111.

Mol, D., Shoshani, J., Tikhonov, A., Van Geel, B., Sano, S.I., Lazarev, P., Boeskorov, G. and Agenbroad, L.D., 2006, The Yukagir Mammoth: Brief history, 14C dates, individual age, gender, size, physical and environmental conditions and storage: Scientific Annals, School of Geology, Aristotle University of Thessaloniki, Special Volume, v. 98, p. 299–314.

Molnar, R.E., 1973, The cranial morphology and mechanics of *Tyrannosaurus rex* (Reptilia: Saurischia) [Ph.D. dissertation]: Los Angeles, University of California, 450 p.

Molnar, R.E., 2008, Reconstruction of the jaw musculature of *Tyrannosaurus rex*; *in* Larson, P. L. and Carpenter, K., eds., *Tyrannosaurus rex,* the tyrant king, Indiana University Press, p. 254-81.

Molnar, R.E. and Clifford, H.T., 2000, Gut contents of a small ankylosaur: Journal of Vertebrate Paleontology, v. 20, p. 194–196.

Molnar, R. E., Clifford, H. T., 2001, An ankylosaurian cololite from the Lower Cretaceous of Queensland, Australia; *in* Carpenter, K., ed., The armored dinosaurs. Bloomington, Indiana University Press, p. 399-412.

Montalvo, C. I. and Fernández, F. J., 2019, Review of the actualistic taphonomy of small mammals ingested by South American predators. Its importance in the interpretation of the fossil record: Publicación Electrónica de la Asociación Paleontológica Argentina, v. 19, p. 18–46.

Montalvo, C.I., Tomassini, R.L. and Sostillo, R., 2016, Leftover prey remains: A new taphonomic mode from the late Miocene Cerro Azul Formation of Central Argentina: Lethaia, v. 49, p. 219-230.

Montalvo, C.I., Tomassini, R.L., Visconti, G. and Tiranti, S., 2012, Análisis tafonómico de micromamíferos del Pleistoceno superior del Quequén Salado, provincia de Buenos Aires, Argentina: Revista Brasileira de Paleontologia, v. 15, p. 345–358.

Montalvo, C.I., Raigemborn, M.S., Tomassini, R.L., Zapata, L., Bargo, M.S., Uncal, M.C.M. and Vizcaíno, S.F., 2019, Floodplain taphonomic mode of early Miocene vertebrates of southern Patagonia, Argentina: Palaios, v. 34, p. 105-120.

Moodie, R. L., 1912, The stomach stones of reptiles: Science, New Series, v. 35, p. 377-378.

Moon, E. L., 1940, Notes on hawk and owl pellet formation and identification: Transactions of the Kansas Academy of Science, v. 43, p. 457-466.

Moore C., 1856, On the skin and food of ichthyosauri and teleosauri: Reports of the British Association for the Advancement of Science, v. 1856, p. 69-70.

Moore, M., 2021, Bitten coprolite: A dentalite: The Ecphora, v. 36(3), p. 10.

Moore, S. J., 1999, Food breakdown in an avian herbivore: Who needs teeth?: Australian Journal of Zoology, v. 47, p. 625-632.

Morales, J., 2016, Systematics of African Amphicyonidae, with descriptions of new material from Napak (Uganda) and Grillental (Namibia): Journal of Iberian Geology, v. 42, p. 131-150.

Morales, J., Senut, B. and Pickford, M., 2011, *Crocuta dietrichi* from Meob, Namibia: Implications for the age of the Tsondab Sandstone in the coastal part of the Namib Desert: Estudios Geologicos, v. 67, p. 207-215.

Morales, M., 1987, Terrestrial fauna and flora from the Triassic Moenkopi Formation of the southwestern United States: Journal of the Arizona-Nevada Academy of Sciences, v. 22, p. 1-20.

Morgan, G.S., 1994, Late Quaternary fossil vertebrates from the Cayman Islands; *in* Brunt, M.A. and Davies, J.E., eds., The Cayman Islands: Natural history and biogeography. Dordrecht, Kluwer Academic Publishers, p. 465-508.

Morgan, G.S. and Albury, N.A., 2013, The Cuban crocodile (*Crocodylus rhombifer*) from late Quaternary fossil deposits in the Bahamas and Cayman Islands: Bulletin of The Florida Museum of Natural History, v. 52, p. 161-236.

Morgan, G.S. and Williamson, T.E., 2000, Middle Miocene (late Barstovian) vertebrates from the Benavidez Ranch local fauna, Albuquerque Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 16, p. 195-208.

Morlo, M., 2004, Diet of *Messelornis* (Aves: Gruiformes), an Eocene bird from Germany: Courier Forschungsinstitut Senckenberg, v. 252, p. 29-33.

Morlo, M., Gunnell, G.F., and Smith, K.T., 2012, Mammalian carnivores from Messel and a comparison of non-volant predator guilds from the middle Eocene of Europe and North America; *in* Lehmann, T. and Schaal, S.K.F., eds., The world at the time of Messel: puzzles in palaeobiology, palaeoenvironment, and the history of early primates. Frankfurt am Main, Senckenberg Gesellschaft für Naturforschung, p. 120-121.

Moy-Thomas, J.A and Miles, R.S. 1971, Palaeozoic fishes. Philadelphia, W. Saunders Co., 259 p.

Mudge, B., 1877, Notes on the Tertiary and Cretaceous periods of Kansas. Part I (Geology): U. S. Geological and Geographical Survey of the Territories [Hayden] for 1875, Ninth Annual Report, p. 277-294.

Muftah, A.M., 2020, Panoramic of paleohabitats of Pliocene Sahabi Formation and Recent As-Sahabi Area, northern Libya: The Iraqi Geological Journal, v. 53, p.1-11.

Muftah, A.M., El-Shawaihdi, M.H., Al Riaydh, M.H. and Boaz, N.T., 2020, Coprolites from the Neogene Sahabi Formation, northeastern Sirt Basin of Libya: Arabian Journal of Geosciences, v. 13, p. 1-10.

Mulder, E.W.A., 2003a, Comparative osteology, palaeoecology and systematics of the Late Cretaceous turtle *Allopleuron hofmanni* (Gray 1831) from the Maastrichtian type area: Publicaties van het Natuurhistorisch Genootschap in Limburg, v. 44, p. 23-92.

Mulder, E.W.A., 2003b, Transatlantic latest Cretaceous mosasaurs (Reptilia: Squamata) from the Maastrichtian type area and New Jersey: Publicaties van het Natuurhistorisch Genootschap in Limburg, v. 44, p. 127-143.

Mulder, E.W.A., 2013, On the piscivorous behaviour of the Early Cretaceous amiiform neopterygian fish *Calamopleurus cylindricus* from the Santana Formation, northeast Brazil: Netherlands Journal of Geosciences - Geologie en Mijnbouw, v. 92, p. 119-122.

Mulder, E.W., Jagt, J.W. and Stroucken, J.W., 2016, New records of latest Cretaceous neosuchian crocodyliforms from the Maastrichtian type area (southern Limburg, the Netherlands): New Mexico Museum of Natural History and Science, Bulletin 73, p. 169-172.

Müller, A.H., 1953, Die isolierten Skelettelemente der Asteroidea (Asterozoa) aus der obersenonen Schreibkreide von Rügen: Beihefte zur Zeitschrift für Geologie, v. 8, p. 1-66.

Müller, A.H., 1969, Zum Lumbricaria-Problem (Miscellanea), mit einigen Bemerkungen über Saccocoma (Crinoidea, Echinodermata): Monatsberichte der deutschen Akademie der Wissenschaften Berlin, v. 11, p. 750-758.

Müller, R.T., de Araújo-Júnior, H.I., Aires, A.S.S., Roberto-da-Silva, L. and Dias-da-Silva, S., 2015, Biogenic control on the origin of a vertebrate monotypic accumulation from the Late Triassic of southern Brazil: Geobios, v. 48, p. 331-340.

Muñiz, F., Toscano, A., Bromley, R. G. and Esperante, R., 2009, Excepcional caso de interacción trófica entre tiburones hexanchiformes y una ballena Balaenoptera en el Plioceno inferior de Huelva (SO de España): Libro de Actas de las XXV Jornadas de la Sociedad Española de Paleontología, Ronda (Málaga), p. 242-244.

Muñiz, F., Belaústegui, Z., Toscano, A., Ramirez-Cruzado, S. and Gámez Vintaned, J.A., 2020, New ichnospecies of *Linichnus* Jacobsen & Bromley, 2009: Ichnos, v. 27, p. 344-351.

Muñiz, F., Toscano, A., Sánchez, A., Esperante, R. and Korestky, I., 2008, Bioerosión producida por necrófagos marinos enrestosóseos del Plioceno Inferior de Huelva (SO España); *in* Ruiz-Omeñaca, J.I., Piñuela, L. and García-Ramos, J.C., eds., Libro de Resúmenes. XXIV Jornadas de la Sociedad Española de Paleontología. Museo del Jurásico de Asturias, Colunga, p. 47–48.

Munk, W. and Sues, H.D., 1993, Gut contents of *Parasaurus* (Pareiasauria) and *Protorosaurus* (Archosauromorpha) from the Kupferschiefer (Upper Permian) of Hessen, Germany: Paläontologische Zeitschrift, v. 67, p. 169-176.

Murchison, R.I., 1839, The Silurian System, founded on geological researches in the Counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford: With descriptions of the coalfields and overlying formations. London, John Murray, 768 p.

Murchison, R.I., 1867, Siluria (Fourth Edition). London, John Murray, 566 p.

Murie, O. J., 1974, Animals tracks (Second Edition). Peterson Field Guide Series. Boston, Houghton Mifflin, 375 p

Murphey, P.C., Torick, L.L., Bray, E.S., Chandler, R. and Evanoff, E., 2001, Taphonomy, fauna, and depositional environment of the *Omomys* Quarry, an unusual accumulation from the Bridger Formation (middle Eocene) of southwestern Wyoming (USA); *in* Gunnell, G. F., ed., Eocene biodiversity: Unusual occurrences and rarely sampled habitats. New York, Kluwer Academic/Plenum Publishers, p. 361-401.

Murphy, N.L., Carpenter, K. and Trexler, D., 2013, New evidence for predation by a large tyrannosaurid; *in* Parrish, J.M., Molnar, R.E., Currie, P.J. and Koppelhus, E.B., eds., Tyrannosaurid paleobiology. Bloomington, Indiana University Press, p. 279–286.

Murphy, N.L., Trexler, D., and Thompson, M., 2006, “Leonardo,” a mummified *Brachylophosaurus* (Ornithischia: Hadrosauridae) from the Judith River Formation of Montana; *in* Carpenter, K., ed., Horns and beaks: Ceratopsian and ornithopod dinosaurs. Bloomington, Indiana University Press, p. 117-133.

Musil, R., 1962, Die Höhle “Sveduv stul,” ein typischer Höhlenhyänenhorst: Anthropos NS, v. 5, p. 97-260.

Muzzopappa, P., Martinelli, A.G., Garderes, J.P. and Rougier, G.W., 2021, Exceptional avian pellet from the Paleocene of Patagonia and description of its content: A new species of calyptocephalellid (Neobatrachia) anuran: Papers in Palaeontology, v. 7, p. 1133-1146.

Mustoe, G.E, 2000, Enigmatic origin of ferruginous “coprolites”: Evidence from the Miocene Wilkes Formation, southwestern Washington: Geological Society of America Bulletin, v. 113, p. 673-681.

Mychajliw, A.M., Rice, K.A., Tewksbury, L.R., Southon, J. R. and Lindsey, E. L., 2020a, Exceptionally preserved asphaltic coprolites expand the spatiotemporal range of a North American paleoecological proxy: Scientific Reports, v. 10, 5069, doi.org/10.1038/s41598-020-61996-y.

Mychajliw, A.M., Rick, T.C., Dagtas, N.D., Erlandson, J.M., Culleton, B.J., Kennett, D.J., Buckley, M. and Hofman, C.A., 2020b, Biogeographic problem-solving reveals the late Pleistocene translocation of a short-faced bear to the California Channel

Islands: Scientific Reports, v. 10, p.1-13. 10:15172, doi: .org/10.1038/s41598-020-71572-z.

Myers, T. S., 2004, Taphonomy of the Mother's Day quarry: Implications for gregarious behavior in sauropod dinosaurs [M.S. thesis]: Cincinnati, University of Cincinnati, 119 p.

Myers, T. S. and Storrs, G. W., 2007, Taphonomy of the Mother's Day Quarry, Upper Jurassic Morrison Formation, south-central Montana, USA: Palaios, v. 22, p. 652–66.

Myhrvold, N.P., 2011, A call to search for fossilised gastric pellets: Historical Biology, v. 24, p. 505–517.

Myrvold, K.S., Milàn, J. and Rasmussen, J.A., 2018, Two new finds of turtle remains from the Danian and Selandian (Paleocene) deposits of Denmark with evidence of predation by crocodilians and sharks: Bulletin of the Geological Society of Denmark, v. 66, p. 211–218.

Nagel-Myers, J. J., Dietl, G. P. and Brett, C. E. 2009, First report of sublethal breakage-induced predation on Devonian bivalves: Palaios, v. 24, p. 460-465.

Naish, D., 2014, The fossil record of bird behavior: Journal of Zoology, v. 292, p. 268-280.

Nakajima, Y. and Izumi, K., 2014, Coprolites from the upper Osawa Formation (upper Spathian), northeastern Japan: Evidence for predation in a marine ecosystem 5 Myr after the end-Permian mass extinction: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 414, p. 225-232.

Nakaya, H., 1989, Upper Cretaceous elasmosaurid (Reptilia, Plesiosauria) from Hobetsu, Hokkaido, northern Japan: Transactions and Proceedings of the Paleontological Society of Japan, New Series, v. 1989, no. 154, p. 96-116.

Napton, L.K. and Heizer, R.F., 1970, Analysis of human coprolites from archaeological contexts, with primary reference to Lovelock Cave, Nevada: Contributions of the University of California Archaeological Research Facility, v. 10, p. 87-129.

Nascimiento, P. M. and Zaher, H., 2010, A new species of *Baurusuchus* (Crocodyliformes, Meseucrocodylia) from the Upper Cretaceous of Brazil; with the first complete postcranial skeleton described for the family Baurusuchidae: Papéis Avulsos de Zoologia (São Paulo), v. 50, p. 323-361.

Nasif, N.L., Esteban, G.I. and Ortiz, P.E., 2009, Novedoso hallazgo de egagrópilas en el Mioceno tardío, Formación Andalhuala, provincia de Catamarca, Argentina: Serie Correlación Geológica, Temas de Paleontología I, v. 25, p. 105-114.

Navás, L., 1922, Algunos fosiles de Libros (Teruel): Boletín Sociedad Ibérica de Ciencias Naturales v. 21, p. 59-60, 172-173 (adiciones y correcciones).

Nebelsick, J., 1999, Taphonomic comparison between Recent and fossil sand dollars: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 349-358.

Neill, W.T., 1971, The last of the ruling reptiles: Alligators, crocodiles, and their kin. New York, Columbia University Press, 486 p.

Nelson, C.H., Johnson, K.R. and Barber, J.H., Jr., 1987, Gray whale and walrus feeding excavations on the Bering Shelf, Alaska: Journal of Sedimentary Petrology, v. 57, 419-430.

Nelson, C.H., Johnson, K.R., Barber, J.H. Jr. and Phillips, R.L., 1992, Gray Whale and walrus feeding excavation on the Bering Shelf, Alaska: Alaska OCS Region, Fourth Information Transfer Meeting Conference Proceedings. Anchorage, U.S. Department of the Interior Minerals Management Service, p. 87-104.

Nesbitt, S.J., Turner, A.H., Erickson, G.M. and Norell, M.A., 2006, Prey choice and cannibalistic behavior in the theropod *Coelophysis*: Biology Letters, v. 2, p. 611-614.

Nesov, L.A., 1995, [Dinosaurs of northern Eurasia: New data about assemblages, ecology and paleobiogeography]: Saint Petersburg, Izdatel'stvo Sankt-2 Peterburgskogo Universiteta, 156 p. [In Russian]

Nesov, L.A., 1997, [Cretaceous nonmarine vertebrates of northern Eurasia] (Posthumous Edition): Golovneva, L.B. and Averianov, A.O, eds., St. Petersburg, Izdatel'stvo Sankt-Peterburgskogo Universiteta, 218 p. [In Russian]

Neumann, C., 2000, Evidence of predation on Cretaceous sea stars from north-west Germany: Lethaia, v. 33, p. 65-70.

Neumann, C., 2003, Shell-breaking predation on Cretaceous sea urchins: Spatial and temporal patterns: Geological Society of America, Abstracts with Programs, v. 35(2), p. 7.

Neumann, C. and Hampe, O., 2018, Eggs for breakfast? Analysis of a probable mosasaur biting trace on the Cretaceous echinoid *Echinocorys ovata* Leske, 177: Mitteilungen aus dem Museum für Naturkunde in Berlin, Fossil Record, v. 21, p. 55-66.

Neumayer, L., 1904, Die Koprolithen des Perm von Texas: Palaeontographica, v. 51, p. 121–128.

Neumayer, L., 1929, Ein viviparer Fiisch aus dem lithographischen Schiefer von Kelheim. Centralblatt für Mineralogie, Geologie, und Paläontologie, Abtheilung B, v. 1929, p. 499-507.

Newell, N.D., 1952, Periodicity in invertebrate evolution: Journal of Paleontology, v. 26, p. 371-385.

Newell, N.D., 1962, Paleontological gaps and geochronology: Journal of Paleontology, v. 36, p. 592-610.

Newman, M. and Davidson, R., 2010, Early Devonian fish from the Midland Valley of Scotland: IPC3 Pre-Conference Field Trip. Aberdeen, University of Aberdeen, 38 p.

Newman, M.J. and Trewin, N.H., 2001, A new jawless vertebrate from the Middle Devonian of Scotland: Palaeontology, v. 44, p. 43-51.

Nicholls, E.L., 1988, Marine vertebrates of the Pembina Member of the Pierre Shale (Campanian, Upper Cretaceous) of Manitoba and their significance to the biogeography of the Western Interior seaway [Ph.D. dissertation]: Calgary, University of Calgary, 317 p.

Nicoll, R.S., 1977, Conodont apparatuses in Upper Devonian palaeoniscoid fish from the Canning Basin, western Australia: Journal of Australian Geology and Geophysics, v. 2, p. 217–228.

Niedźwiedzki, G., Gorzelak, P. and Sulej, T., 2010, Bite traces on dicynodont bones and the early evolution of large terrestrial predators: Lethaia, v. 44, p. 87–92.

Niedźwiedzki, G., Bajdek, P., Owocki, K. and Kear, B.P., 2016a, An Early Triassic polar predator ecosystem revealed by vertebrate coprolites from the Bulgo Sandstone (Sydney Basin) of southeastern Australia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 464, p. 5-15.

Niedźwiedzki, R., Surmik, D., Chećko, A. and Salamon, M.A., 2021, A regurgitalite of the Middle Triassic (Muschelkalk) from Upper Silesia (Poland): Geology, Geophysics and Environment, v. 47, p. 33-40.

Niedźwiedzki, G., Bajdek, P., Qvarnström, M., Sulej, T., Sennikov, A.G. and Golubev, V.K., 2016b, Reduction of vertebrate coprolite diversity associated with the end-Permian extinction event in Vyazniki region, European Russia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 450, p. 77-90.

Njau, J. K., 2006, The relevance of crocodiles to Oldowan hominin paleoecology at Olduvai Gorge, Tanzania [Ph.D. dissertation]: New Brunswick, Rutgers University, 325 p.

Njau, J.K. and R.J. Blumenschine, 2006, A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania: Journal of Human Evolution, v. 50, p. 142-162.

Njau, J.K. and Blumenschine, R.J., 2012, Crocodylian and mammalian carnivore feeding traces on hominid fossils from FLK 22 and FLK NN 3, Plio-Pleistocene, Olduvai Gorge, Tanzania: Journal of Human Evolution, v. 63, p. 408-417.

Njau, J.K. and Gilbert, H., 2016, Standardizing terms for crocodile-induced bite marks on bone surfaces in light of the frequent bone modification equifinality found to result from crocodile feeding behavior, stone tool modification, and trampling: FOROST (Forensic Osteology) Occasional Publications, v. 3, p. 1-13.

Noe-Nygaard, N., 1989, Man-made trace fossils on bones: Human Evolution, v. 4, p. 461-491.

Norell, M.A., Gaffney, E.S. and Dingus, L. 1995, Discovering dinosaurs in the American Museum of Natural History. New York, Alfred A.

Knopf, Inc., 204 p.

Noriega, J.I., Cione, A.L., Aceñolaza, F.G., 2007, Shark tooth marks on Miocene balaenopterid cetacean bones from Argentina: Neues Jahrbuch für Geologie und Paläontologie, v. 245, p. 185–192.

Norman, D.B., 1987, A mass-accumulation of vertebrates from the Lower Cretaceous of Nehden (Sauerland), West Germany: Proceedings of the Royal Society of London B, Biological Sciences, v. 230, p. 215-255.

Northwood, C., 1997, Palaeontological interpretations of the Early Triassic Arcadia Formation, Queensland [Ph.D. dissertation]: Melbourne, La Trobe University, 479 p.

Northwood, C., 2005, Early Triassic coprolites from Australia and their palaeobiological significance: Palaeontology, v. 48, p. 49-68.

Noto, C.R., Main, D.J. and Drumheller, S.K., 2012, Feeding traces and paleobiology of a Cretaceous (Cenomanian) crocodyliform: Example from the Woodbine Formation of Texas: Palaios, v. 27, p. 105-115.

Novis, L.K., 2012, A taphonomic study of marine reptiles from the Upper Jurassic of Svalbard [M.S. thesis]: Oslo, University of Oslo, 51 p.

Novitskaya, L. I. and Turner, S. 1998, *Turinia pagei* (Powrie): A new reconstruction of the soft organs of the cephalothorax: Memoirs of the Queensland Museum, v. 42, p. 533-544.

Nürnberger, L., 1934, Koproporhyrin im tertiären Krocodilkot: Nova Acta Leopoldina, Halle, v. 1, p. 324-325.

Nursall, J.R., 1996, Distribution and ecology of pycnodont fishes; *in* Arratia, G. and Viohl, G., eds., Mesozoic fishes: Systematics and paleoecology. München, Verlag Dr. Friedrich Pfeil, p. 115–124.

Nybelin, O., 1958, Ober die angebliche Viviparitat bei *Thrissops formosus* Agassiz: Arkiv for Zoologi, Series 2, v. 11, p. 447-455.

Nybelin, O., 1967, Versuch ein taxonomischen Revision der *Anaethalion* Arten des Weissjura Deutschlands: Acta Regiae Societatis scientiarum et litterarum Gothoburgensis: Zoologica, v. 2, 53 p.

Nybelin, O., 1974, A revision of the leptlepid fishes: Acta Regiae Societalis scientiarum et litterarum gothoburgensis, Zoologica, v. 9, p. 1-202.

Obruchev, D.V. and Mark-Kurik, E.Y., 1965, Psammosteidy (Agnatha, Psammosteidae) devona SSSR: Tallinn, Institute of Geology, Academy of Sciences of the Estonian SSR, 304 p. [In Russian]

Ochev, V.G., 1974, Some remarks on coprolites of Triassic vertebrates: Paleontological Journal, v. 1974, p. 253-255.

O'Connor, J.K., 2019, The trophic habits of early birds: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 513, p. 178-195.

O'Connor, J.K. and Zhou, Z., 2020, The evolution of the modern avian digestive system: Insights from paravian fossils from the Yanliao and Jehol biotas: Palaeontology, v. 63, p. 13-27.

O'Connor, J., Zhou, Z. and Xu, X., 2011, Additional specimen of *Microraptor* provides unique evidence of dinosaurs preying on birds: Proceedings of the National Academy of Sciences, v. 108, p. 19662-19665.

O'Connor, J., Zheng, X., Dong, L., Wang, X., Wang, Y., Zhang, X. and Zhou, Z., 2019, *Microraptor* with ingested lizard suggests non-specialized digestive function: Current Biology, v. 29, p. 2423-2429.

O'Connor, J., Wang, X., Sullivan, C., Wang, Y., Zheng, X., Hu, H., Zhang, X., Zhou, Z., 2018, First report of gastroliths in the Early Cretaceous basal bird *Jeholornis*: Cretaceous Research, v. 84, p. 200-208.

ÓGogáin, A., Falcon-Lang, H.J., Carpenter, D.K., Miller, R.F., Benton, M.J., Pufahl, P.K., Ruta, M., Davies, T.G., Hinds, S.J. and Stimson, M. R., 2016, Fish and tetrapod communities across a marine to brackish salinity gradient in the Pennsylvanian (early Moscovian) Minto Formation of New Brunswick, Canada, and their palaeoecological and palaeogeographical implications: Palaeontology, v. 59, p. 689-724.

O'Gorman, J.P., Oliveiro, E.B. and Cabrera, D., 2012, Gastroliths associated with a juvenile elasmosaur (Plesiosauria, Elasmosauridae) from Snow Hill Island Formation (upper Campanian-lower Maastrichtian), Vega Island, Antarctica: Alcheringa, v. 36, p. 531-541.

O'Gorman, J.P., Salgado, L., Cerda, I.A. and Gasparini, Z., 2013, First record of gastroliths associated with elasmosaur remains from La Colonia Formation (Campanian-Maastrichtian), Chubut, Patagonia, Argentina, with comments on the probable depositional paleo-environment of the source of the gastroliths: Cretaceous Research, v. 40, p. 212-217.

O'Gorman, J.P., Santillana, S., Otero, R., Reguero, M., 2019, A giant elasmosaurid (Sauropterygia; Plesiosauria) from Antarctica; New information on elasmosaurid body size and aristonectine evolutionary scenarios: Cretaceous Research, v. 102, p. 37-58.

O'Gorman, J.P., Oliveiro, E.B., Santillana, S., Everhart, M.J. and Reguero, M., 2014, Gastroliths associated with an *Aristonectes* specimen (Plesiosauria, Elasmosauriodae), López de Bertodano Formation (upper Maastrichtian) Seymour Island (*Is. Marambio*), Antarctic Peninsula: Cretaceous Research, v. 50, p. 228-237.

Oji, T., Ogaya, C. and Sato, T., 2003, Increase of shell-crushing predation recorded in fossil shell fragmentation: Paleobiology, v. 29, p. 520-526.

O'Keefe, F.R., Street, H.P., Cavigelli, J.P., Socha, J.J. and O'Keefe, R.D., 2009, A plesiosaur containing an ichthyosaur embryo as stomach contents from the Sundance Formation of the Bighorn Basin, Wyoming: Journal of Vertebrate Paleontology, 29, p. 1306-1310.

Oldenberg, H., 1688, Philosophical transactions: Giving some account of the present undertakings, studies and labours of the ingenious in many considerable parts of the world, Volume 3. London, S. Smith and B. Walford, p. 629-681.

Olson, E.C., 1966, Community evolution of the origin of mammals: Ecology, v. 47, p. 291-302.

Olson, E.C., 1971, A skeleton of *Lysorophus tricarinatus* (Amphibia: Lepospondyli) from the Hennessey Formation (Permian) of Oklahoma: Journal of Paleontology, v. 45, p. 443-449.

Olson, E.C., 1977, Permian lake faunas: A study in community evolution: Journal of the Palaeontological Society of India, v. 20, p. 146-163.

Olson, E.C. and Mead, J.G., 1982, The Vale Formation (Lower Permian): Its vertebrates and paleoecology: Texas Memorial Museum, Bulletin 29, 46 p.

Osborn, H.F., 1904, Fossil wonders of the West: The dinosaurs of the Bone-Cabin Quarry: Being the first description of the greatest "find" of extinct animals ever made: Century Illustrated Magazine (New Series), v. 168, p. 680-694.

Osborn, H.F., 1924, *Psittacosaurus* and *Protiguanodon*, two Lower Cretaceous iguanodonts from Mongolia: American Museum Novitates, no. 127, 16 p.

Ősi, A., Szabó, M., Tóth, E., Bodor, E., Lobitzer, H., Kvaček, J., Svobodová, M., Szente, I., Wagreich, M., Trabelsi, K. and Sames, B., 2021, A brackish to non-marine aquatic and terrestrial fossil assemblage with vertebrates from the lower Coniacian (Upper Cretaceous) Gosau Group of the Tiefengraben locality near St. Wolfgang im Salzkammergut, Austria: Cretaceous Research, v. 127, doi.org/10.1016/j.cretres.2021.104938.

Osmólska, H., 1993, Were the Mongolian "fighting dinosaurs" really fighting: Review de Paléobiologie Special, v. 7, p. 161-162.

Ostrom, J. H., 1964, A reconsideration of the paleoecology of hadrosaurian dinosaurs: American Journal of Science, v. 262, p. 975-997.

Ostrom, J. H., 1970, Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn basin area, Wyoming-Montana: Yale Peabody Museum of Natural History Bulletin, v. 35, 234 p.

Ostrom, J. H., 1978, The osteology of *Compsognathus longipes* Wagner: Zitteliana, v. 4, p. 73–118.

Otero, R.A., Soto-Acuna, S., Vargas, A.O. and Rubilar-Rogers, D., 2014, A new postcranial skeleton of an elasmosaurid plesiosaur from the Upper Cretaceous of central Chile and reassessment of *Cimoliasaurus andium* Deecke: Cretaceous Research, v. 50, p. 318-331.

Oyarzún-Ruiz, P., Pérez-Espinoza, S.A., González-Saldías, F., Martin, F. and Moreno, L., 2021, Paleoparasitological survey of coprolites of Darwin's ground sloth *Mylodon darwini* (Xenarthra, Folivora: Mylodontidae) from Cueva del Milodón Natural Monument, Chilean Patagonia: Archaeological and Anthropological Sciences, v. 13, p.1-8.

Owocki, K., Niedzwiedzki, G., Sennikov, A.G., Golubev, V.K., Janiszewska, K. and Sulej, T., 2012, Upper Permian vertebrate coprolites from Vyazniki and Gorokhovets, Vyatkian regional stage, Russian Platform: Palaios, v. 27, p. 867–877.

Packard, E.L. and Allison, I.S., 1980, Fossil bear tracks in Lake County, Oregon: Oregon Geology, v. 42, p. 1-2.

Paes Neto, V.D., Francischini, H., Martinelli, A.G., Marinho, T.D.S., Ribeiro, L.C.B., Soares, M.B. and Schultz, C.L., 2018, Bioerosion traces on titanosaurian sauropod bones from the Upper Cretaceous Marília Formation of Brazil: Alcheringa, v. 42, p. 415-426.

Paik, I.S., Kim, H.J., Lim, J.D., Huh, M. and Lee, H.I., 2011, Diverse tooth marks on an adult sauropod bone from the Early Cretaceous, Korea: Implications in feeding behaviour of theropod dinosaurs: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 309, p. 342-346.

Palmqvist, P. and Arribas, A., 2001, Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals: Paleobiology, v. 27, p. 512-530.

Palmqvist, P., Martínez-Navarro, B. and Arribas, A., 1996, Prey selection by terrestrial carnivores in a lower Pleistocene paleocommunity: Paleobiology, v. 22, p. 514-534.

Pan, Y., Sha, J., Zhou, Z., Fürsich, F.T., 2013, The Jehol Biota: Definition and distribution of exceptionally preserved relicts of a continental Early Cretaceous ecosystem: Cretaceous Research, v. 44, 30e38. https://doi.org/10.1016/ j.cretres.2013.03.007.

Pan, Y., Sha, J., Fürsich, F.T., Wang, Y., Zhang, X. and Yao, X., 2011, Dynamics of the lacustrine fauna from the Early Cretaceous Yixian Formation, China: Implications of volcanic and climatic factors: Lethaia, doi: 10.1111/j.1502-3931.2011.00284.x.

Pappa, S., Schreve, D.C. and Rivals, F., 2019, The bear necessities: A new dental microwear database for the interpretation of palaeodiet in fossil Ursidae: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 514, p. 168-188.

Pardo-Pérez, J.M., Kear, B.P., Mallison, H., Gómez, M., Moroni, M. and Maxwell, E.E., 2018, Pathological survey on *Temnodontosaurus* from the Early Jurassic of southern Germany: PLoS ONE, v. 13(10): e0204951, doi.org/10.1371/journal. pone.0204951.

Parker, L.R. and Balsley, J.K., 1989, Coal mines as localities for studying dinosaur trace fossils; *in* Gillette, D.D. and Lockley, M.G., eds., Dinosaur tracks and traces. Cambridge, Cambridge University Press, p. 353–359.

Parson, T.S. and Cameron, J.E., 1997, Internal relief of the digestive tract; *in* Gans, C. and Parsons, T.S., eds., Biology of the Reptilia. Volume 6. Morphology. New York, Academic Press, p. 159-314.

Patterson, C., 1975, The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase: Philosophical Transactions, Royal Society of London, Series B, Biological Sciences, v. 269, p. 282-283.

Patterson, C. and Rosen, D.E., 1977, Review of the icthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils: Bulletin of the American Museum of Natural History, v. 158, p. 83-172.

Paucă, M., 1933, Die fossile Fauna und Flora aus dem Oligozän von Suslaneşti-Muscel in Rumänien. Eine systematische und palaeobiologische Studie: Anuarul Institutului Geologic al României, Bucureşti, v. 16 [for 1931), 99 p.

Pavia, M., Davies, G.B., Gommery, D. and Kgasi, L., 2017, Mid-Pliocene bald ibis (*Geronticus* cf. *calvus*; Aves: Threskiornithidae) from the Cradle of Humankind, Gauteng, South Africa and its environmental and evolutionary implications: Paläontologische Zeitschrift, v. 91, p. 237-243.

Pearson, N.J., Gingras, M.K., Armitage, I.A. and Pemberton, S.G., 2007, Significance of Atlantic sturgeon feeding excavations, Mary's Point, Bay of Fundy, New Brunswick, Canada: Palaios, v. 22, p. 457–464.

Pedley, H.M., 1978, A new fish horizon from the Maltese Miocene and its palaeoecological significance: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 24, p. 73-83.

Peel, J.S., 2015, Bromalites from the Cambrian (Series 2 and 3) of North Greenland: GFF, v. 137, p. 181-194, doi: 10.1080/11035897.2014.995217.

Pemberton, S.G., 2012, William Buckland (1784-1856) and Henry De La Beche (1796-1855): The early history of coprolites: New Mexico Museum of Natural History and Science, Bulletin 57, p. 29-43.

Pemberton, S.G., McCrea, R., MacEachern, J.A., Gingras, M.K. and Sarjeant, W.A.S., 2007, The correspondences between the Reverend Henry Duncan and the Reverend William Buckland: Reports of the first vertebrate footprints: Ichnos, v. 15, p. 5–17.

Peñalver, E. and Gaudant, J., 2010, Limnic food web and salinity of the upper Miocene Bicorb palaeolake (eastern Spain): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 297, p. 683-696.

Pernkopf, E., 1929, Beitrage zur vergleichenden Anatomie des Vertebratenmagens: Zeitschrift für Anatomie und Entwicklungsgeschichte, v. 91, p. 329-390.

Perri, A.R., Heinrich, S., Gur-Arieh, S. and Saunders, J. J., 2017, Earliest evidence of *Toxocara* sp. in a 1.2-million-yr-old extinct hyena (*Pachycrocuta brevirostris*) coprolite from northwest Pakistan: Journal of Parasitology, v. 103, p. 138-141.

Perrotti, A.G., 2018, Pollen and *Sporormiella* evidence for terminal Pleistocene vegetation change and megafaunal extinction at Page-Ladson, Florida: Quaternary International, v. 466, p. 256-268.

Pervesler, P., Roetzel, R. and Steininger, F., 1995, Taphonomie der Sirenen in den marinen Flachwasserablagerungen (Burgschleinitz-Formation, Eggenburgium, Unter- miozän) der Gemeindesandgrube Kühnring (Niederösterreich): Jahrbuch der Geologischen Bundesandesanstallten, v. 138, p. 89-121.

Pesquero, M.D., Alcalá, L. and Fernández-Jalvo, Y., 2013a, Taphonomy of the reference Miocene vertebrate mammal site of Cerro de la Garita, Spain: Lethaia, v. 46, p. 378-398.

Pesquero, M.D., Souza-Egipsy, V., Alcalá, L., Ascaso, C. and Fernández-Jalvo, Y., 2013b, Calcium phosphate preservation of faecal bacterial negative moulds in hyaena coprolites: Acta Palaeontologica Polonica, v. 59, p. 997-1005.

Pesquero, M.D., Salesa, M.J., Espílez, E., Mampel, L., Siliceo, G. and Alcalá, L., 2011, An exceptionally rich hyaena coprolites concentration in the late Miocene mammal fossil site of La Roma 2 (Teruel, Spain): Taphonomical and palaeoenvironmental inferences: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 311, p. 30-37.

Peterson, J.E. and Daus, K.N., 2019, Feeding traces attributable to juvenile *Tyrannosaurus rex* offer insight into ontogenetic dietary trends: PeerJ7:e6573http://doi.org/10.7717/peerj.6573.

Peterson, J, E., Tseng, Z. and Brink, S., 2020, Bite force estimates in juvenile *Tyrannosaurus rex* based on simulated puncture marks: Society of Vertebrate Paleontology, 80th Annual Meeting Virtual 2020, October 12-16 2020, www.vertpaleo.org Conference Program, unnumbered page.

Peterson, J.E., Tseng, Z.J. and Brink S., 2021, Bite force estimates in juvenile *Tyrannosaurus rex* based on simulated puncture marks: PeerJ, v. 9:e11450 , doi:10.7717/peerj.11450.

Peterson, J.E., Henderson, M.D., Scherer, R.P. and Vittore, C.P., 2009, Face biting on a juvenile tyrannosaurid and behavioural implications: Palaios, v. 24, p. 780–784.

Petrigh, R.S., Martínez, J.G., Mondini, M. and Fugassa, M.H., 2019, Ancient parasitic DNA reveals *Toxascaris leonina* presence in final Pleistocene of South America: Parasitology, v. 146, p. 284-1288.

Petzold, H.G., 1967, Notizen zur Gewöllbildung be einen Bindenwarem (*Varanus salvator*) und einige allgemeine Bemerkungen über Repetilliengewölle: Der Zoologische Garten, v. 34, p. 134–138.

Peyer, B., 1968, Comparative odontology. Chicago, University of Chicago Press, 347 p.

Peyer, K., Carter, J.G., Sues, H.D., Novak, S.E. and Olsen, P.E., 2008, A new suchian archosaur from the Upper Triassic of North Carolina: Journal of Vertebrate Paleontology, v. 28, p. 363-381.

Peyrot-Clausade, M., Chabanet, P., Conand, C., Fontaine, M., Letourneur, Y. and Harmelinvivien, M., 2000, Sea urchin and fish bioerosion on La Réunion and Moorea reefs: Bulletin of Marine Science, v. 66, p. 477–485.

Phillips, A., 2008, A Late Cretaceous (Cenomanian) marine vertebrate-rich bioclastic horizon from the northeastern margin of the Western Interior Seaway, Canada [Ph.D. dissertation]: Ottawa, Carleton University, 237 p.

Phipps, K.J., 2008, Evidence of predation on *Gryphaea* (*Bilobissa*) *lituola* Lamarck, 1819, from the Oxford Clay Formation of South Cave Station Quarry, Yorkshire: Proceedings of the Geological Association, v. 119, p. 277-285.

Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P. and Brain, C.K., 2004, Beyond leopards: Tooth marks and the contribution of multiple carnivore taxa to the accumulation of the Swartkrans Member 3 fossil assemblage: Journal of Human Evolution, v. 46, p. 595–604.

Pickford, M., 1996, Fossil crocodiles (*Crocodylus lloydi*) from the lower and middle Miocene of southern Africa: Annales de Paléontologie, v. 82, p. 235-250.

Pieńkowski, G., 1985, Early Triassic trace fossil assemblages from the Holy Cross Mountains, Poland: Their distribution in continental and marginal marine environments; in Curran, H.A., ed., Biogenic structures: Their use in interpreting depositional environments: The Society of Economic Paleontologists and Mineralogists, Special Publication 35, p. 37-51.

Pierce, S.E., Angielczyk, K.D. and Rayfield, E.J., 2008, Patterns of morphospace occupation and mechanical performance in extant crocodilian skulls: A combined geometric, morphometric and finite element modeling approach: Journal of Morphology, v. 269, p. 840–864.

Pinna, G., 1979, Osteologia dello scheletro di *Kritosaurus notabilis* (Lambe, 1914) del Museo Civico di Storia Naturale di Milano: Memorie della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, v. 22, p. 34-55.

Pinna, G., Arduini, P., Pesarini, C. and Teruzzi, G., 1985, Some controversial aspects of the morphology and anatomy of *Ostenocaris cypriformis* (Crustacea, Thylacocephala): Transactions of the Royal Society of Edinburgh, Earth Sciences, 76, 373-379.

Pinto Llona, A.C. and Andrews, P., 2004, Taphonomy and paleoecology of *Ursus spelaeus* from northern Spain: Publications du Musée des Confluences, v. 2, p. 163-170.

Pirrone, C.A., Buatois, L.A. and Bromley, R.G. 2014, Ichnotaxobases for bioerosion trace fossils in bones: Journal of Paleontology, v. 88, p. 195-203.

Piveteau, J., 1926, Paleontologie de Madagascar, XIII. Amphibiens et reptiles permiens: Annales de Paleontologie, v. 15, p. 53-180.

Platt, S.G., Elsey, R.M., Bishop, N.D., Rainwater, T.R., Thongsavath, O., Labarre, D. and McWilliam, A.G., 2020, Using scat to estimate body size in crocodilians: Case studies of the Siamese crocodile and American alligator with practical applications: Herpetological Conservation and Biology, v. 15, p. 325-334.

Platt, S. G., Rainwater, T. R., Finger, A. G., Thorjarnarson, J. B., Anderson, T. A., McMurray, S. T., 2006, Food habits, ontogenetic partitioning and observation of foraging behavior of Morelet's crocodile (*Crocodylus moreletti*) in northern Belize: Herpetological Journal, v. 16, p. 281-290.

Poinar, H.N., Kuch, M., McDonald, G., Martin, P. and Pääbo, S., 2003, Nuclear gene sequences from a late Pleistocene sloth coprolite: Current Biology, v. 13, p. 1150-1152.

Poinar, H.N., Hofreiter, M., Spaulding, W.G., Martin, P.S., Stankiewicz, B.A., Bland, H., Evershed, R.P., Possnert, G. and Pääbo, S., 1998, Molecular coproscopy: Dung and diet of the extinct ground sloth *Nothrotheriops shastensis*: Science, v. 281, p. 402-406.

Pollard, J. E., 1968, The gastric contents of an ichthyosaur from the lower Lias of Lyme Regis, Dorset: Palaeontology, v. 11, p. 376-388.

Pollard, J.E., 1985, Coprolites and ostracods from the Dinantian of Foulden, Berwickshire, Scotland: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 76, p. 49-51.

Pollard, J.E., 1990, Evidence for diet; *in* Briggs, D.E.G. and Crowther, P.R., eds., Palaeobiology: A synthesis. Oxford, Blackwell, p. 362-367.

Pooley, A., and Gans, C., 1976, The Nile crocodile: Scientific American, v. 234, p. 114-124.

Poplin, C., 1986, Taphocoenoses et restes alimentaires de vertébrés carnivores: Bulletin du Muséum National d'Histoire Naturelle, Paris, Série C, v. 8, p. 257-267.

Poropat, S.F., White, M.A., Vickers-Rich, P. and Rich, T.H., 2019, New megaraptorid (Dinosauria: Theropoda) remains from the Lower Cretaceous Eumeralla Formation of Cape Otway, Victoria, Australia: Journal of Vertebrate Paleontology, v. 39:4, doi: 10.1080/02724634.2019.1666273.

Poropat, S.F., White, M.A., Ziegler, T., Pentland, A.H., Rigby, S.L., Duncan, R.J., Sloan, T. and Elliott, D.A., 2021, A diverse Late Cretaceous vertebrate tracksite from the Winton Formation of Queensland, Australia: PeerJ, v. 9:e11544, doi:10.7717/peerj.11544.

Portis, A., 1883, Nuovi studi sulle tracce attribuite all'uomo pliocenico: Memorie della Reale Accademia delle Scienze di Torino, v. 35, p. 2-35.

Posmoşanu, E., 2003, Iguanodontian dinosaurs from the Lower Cretaceous Bauxite site from Romania: Acta Paleontologica Romaniae, v. 4, p. 431-439.

Pough, F.H., Janis, C.M. and Heiser, J.B., 2002. Vertebrate life (Sixth Edition). Upper Saddle River, Prentice-Hall Inc., 699 p.

Powers, W. R. and Hoffecker, J. F., 1989, Settlement in the Nenana Valley, central Alaska. American Antiquity, v. 54, p. 263-289.

Powers, W. R., Guthries, R. D., Hoffecker, J. F., 1983, Archeology and paleoecology of a late Pleistocene Alaskan hunting camp: Report to National Park Service, Anchorage, contract #cx-9000-7-0047.

Prasad, V., Stromberg, C.A.E., Alimohammadian, H. and Sahni, A., 2005, Dinosaur coprolites and the early evolution of grasses and grazers: Science, v. 310, p. 1177-1180.

Price, P.H., 1927, The coprolite horizon of the Conemaugh Series in and around Morgantown, West Virginia: Annals of the Carnegie Museum, v. 17, p. 211-254.

Přikryl, T., Košťk, M., Mazuch, M. and Mikuláš, R., 2012, Evidence for fish predation on a coleoid cephalopod from the Lower Jurassic Posidonia Shale of Germany: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 263, p. 25-33.

Prothero, D.R., Liter, M.R., Barnes, L.G., Wang, X., Mitchell, E., McLeod, S., Whistler, D.P., Tedford, R.H. and Ray, C., 2008, Land mammals from the middle Miocene Sharktooth Hill Bonebed, Kern County, California: New Mexico Museum of Natural History and Science, Bulletin 44, p. 299-314.

Pryce, E., 1994, Grey louries *Corythaixoides concolor* feeding on clay: Babbler, v. 26-27, p. 23-24.

Puertolas-Pascual, E., Blanco, A., Brochu, C.A. and Canudo, J.I., 2016, Review of the Late Cretaceous-early Paleogene crocodylomorphs of Europe: Extinction patterns across the K-PG boundary: Cretaceous Research, v. 57, p. 565-590.

Pujos, F. and Salas-Gismondi, R., 2020. Predation of the giant Miocene caiman *Purussaurus* on a mylodontid ground sloth in the wetlands of proto-Amazonia: Biology Letters, v. 16: 20200239, dx.doi.

org/10.1098/rsbl.2020.0239.

Purdy, R.W., 1996. Paleoecology of fossil white sharks: The biology of *Carcharodon carcharias*; *in* Kinklei, A.P. and. Ainley, D.G., eds., Great white sharks: The biology of *Carcharodon carcharias*. New York, Academy Press, p. 67-78.

Purdy, R., Schneider, V.P., Applegate, S.P., McClellan, J.H., Meyer, R.L. and Slaughter, B. H., 2001, The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina; *in* Ray, C.E. and Bohaska, D.J., eds., Geology and paleontology of the Lee Creek Mine, North Carolina, Volume 3: Smithsonian Contributions to Paleobiology, v. 90, p. 71-202.

Quadrat, B., 1845, Über die Koprolithen von *Macropoma mantelli* (Agassiz), über fossile Haifischzähne, sowie über den Planerkalk von Bilin: Annalen der Chemie und Pharmacie, v. 55, p. 360-363.

Qvarnström, M., 2020a, Food web analysis of Eearly Mesozoic ecosystems shed new light on early dinosaur evolution: Society of Vertebrate Paleontology, 80th Annual Meeting Virtual 2020, October 12-16 2020, www.vertpaleo.org, unnumbered page.

Qvarnström, M., 2020b, Who ate whom? Paleoecology revealed through synchrotron microtomography of coprolites (fossil feces) [Ph.D. dissertation]: Uppsala, Acta Universitatis Upsaliensis, 49 p.

Qvarnström, M., Ahlberg, P.E. and Niedźwiedzki, G., 2019a, Tyrannosaurid-like osteophagy by a Triassic archosaur: Scientific Reports, v. 9, 925 (2019), doi.org/10.1038/s41598-018-37540-4.

Qvarnström, M., Niedźwiedzki, G. and Žigaitė, Ž., 2016, Vertebrate coprolites (fossil faeces): An underexplored Konservat-Lagerstätte: Earth-Science Reviews, v. 162, p. 44-57.

Qvarnström, M., Elgh, E., Owocki, K., Ahlberg, P.E. and Niedźwiedzki, G., 2019b, Filter feeding in Late Jurassic pterosaurs supported by coprolite contents: PeerJ, v. 7:e7375, doi.org/10.7717/peerj.7375.

Qvarnström, M., Niedźwiedzki, G., Tafforeau, P., Žigaitė, Ž. and Ahlberg, P.E., 2017, Synchrotron phase-contrast microtomography of coprolites generates novel palaeobiological data: Scientific Reports, v. 7, 2723 (2017), doi.org/10.1038/s41598-017-02893-9.

Qvarnström, M., Wernström, J.V., Piechowski, R., Tałanda, M., Ahlberg, P.E. and Niedźwiedzki, G., 2019c, Beetle-bearing coprolites possibly reveal the diet of a Late Triassic dinosauriform: Royal Society Open Science, v.6: 181042, dx.doi.org/10.1098/rsos.181042.

Qvarnström, M., Anagnostakis, S., Lindskog, A., Scheer, U., Vajda, V., Rasmussen, B.W., Lindgren, J. and Eriksson, M.E., 2019d, Multi-proxy analyses of Late Cretaceous coprolites from Germany: Lethaia, v. 52, p. 550-569.

Qvarnström, M., Fikáček, M., Wernström, J.V., Huld, S., Beutel, R.G., Arriaga-Varela, E., Ahlberg, P. E. and Niedźwiedzki, G., 2021, Exceptionally preserved beetles in a Triassic coprolite of putative dinosauriform origin: Current Biology, doi.org/10.1016/j.cub.2021.05.0.

Raath, M., 1974, Fossil vertebrate studies in Rhodesia: further evidence of gastroliths in prosauropod dinosaurs: Arnoldia, v. 7, p. 1-7.

Rabal-Garcés, R., Cuenca-Bescós, G., Ignacio Canudo, J. and De Torres, T., 2012. Was the European cave bear an occasional scavenger?: Lethaia, v. 45, p. 96-108.

Raczka, M.F., Bush, M.B., Folcik, A.M. and McMichael, C.H., 2016, *Sporormiella* as a tool for detecting the presence of large herbivores in the Neotropics: Biota Neotropica, v. 16(1): e20150090, dx. doi.org/10.1590/1676-0611-BN-2015-0090.

Radley, J.D., 1993, A derived Jurassic clast from the Wealden Group (Lower Cretaceous) of the Isle of Wight, southern England: Proceedings of the Geologists' Association, v. 104, p. 71-83.

Radley, J.D., 1994, Stratigraphy, palaeontology and palaeoenvironment of the Wessex Formation (Wealden Group, Lower Cretaceous) at Yaverland, Isle of Wight, southern England: Proceedings of the Geologists, Association, v. 105, p. 199-208.

Radley, J.D., 2005, Derived fossils in the southern English Wealden (non-marine Early Cretaceous): A review: Cretaceous Research, v. 26, p. 657-664.

Rahmat, S., Muñiz, F., Toscano, A., Esperante, R. and Koretsky, I., 2018, First European record of *Homiphoca* (Phocidae: Monachinae: Lobodontini) and its bearing on the paleobiogeography of the genus: Historical Biology, p.1-9, doi: 10.1080/08912963.2018.1507030.

Rakshit, N., Bhat, M.S., Mukherjee, D. and Ray, S., 2019, First record of Mesozoic scroll coprolites: Classification, characteristics, elemental composition and probable producers: Palaeontology, v. 62, p. 451-471.

Randle, E. and Sansom, R.S. 2019a, Bite marks and predation of fossil jawless fish during the rise of jawed vertebrates: Proceedings of the Royal Society, Series B, doi.org/10.1098/rspb.2019.1596.

Randle, E. and Sansom, R.S. 2019b, Data from: Bite marks and predation of fossil jawless fish during the rise of jawed vertebrates: Proceedings of the Royal Society, Series B, v. 5, Dataset, https://doi.org/10.5061/dryad.f32p5g7.

Rasmussen, H.W., 1950, Cretaceous Asteroidea and Ophiuroidea with special reference to the species found in Denmark: Danmarks Geologiske Undersùgelse, v. 77, p. 1-134.

Rayner, D., Mitchell, T., Rayner, M. and Clouter, F., 2009, London Clay fossils of Kent and Essex. Sevenoaks, Caxton and Holmesdale Press and Medway Fossil and Mineral Society, 228 p.

Rayner, D.H., 1963, The Achanarras Limestone of the Middle Old Red Sandstone, Caithness, Scotland: Proceedings of the Yorkshire Geological Society, v. 34, p. 117-138.

Rea, A.M., 1973, Turkey vultures casting pellets: Auk, v. 90, p. 209–210.

Rieber, H., 1970, *Phragmoteuthis ?ticinensis* n. sp., ein Coleoida-Rest aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kt. Tessin, Schweiz): Paläontologische Zeitschrift, v. 44, p. 32-40.

Reinhard, K.J., 1988, Diet, parasitism, and anemia in the Prehistoric Southwest [Ph.D. dissertation]: College Station, Texas A&M University, 201 p

Reinhard, K.J. and Bryant, V.M., Jr., 1992, Coprolite analysis: A biological perspective on archaeology: University of Nebraska, Lincoln, Papers in Natural Resources, v. 46, p. 245-288.

Reinhard, W. and Vogel, Z., 1980, Die Nattern; *in* Grzimek, B., Hediger, H., Klemmer, K., Kuhn, O. and Wermuth, H., eds., Grzimeks Tierleben, 6, Kriechtiere. München, Deutscher Taschenbuch-Verlag, p. 390-423.

Reiss, J. and Frey, E., 1991, The evolution of underwater flight and the locomotion of plesiosaurs; *in* Rayner, J.V.M., Wooten, R.J., eds., Biomechanics of evolution. Cambridge, Cambridge University Press, p. 131-144.

Reisz, R.R. and Tsuji, L.A., 2006, An articulated skeleton of *Varanops* with bite marks: The oldest known evidence of scavenging among terrestrial vertebrates: Journal of Vertebrate Paleontology, v. 26, p. 1021-1023.

Reisz, R.R., MacDougall, M.J. and Modesto, S.P., 2014, A new species of the parareptile genus *Delorhynchus*, based on articulated skeletal remains from Richards Spur, lower Permian of Oklahoma: Journal of Vertebrate Paleontology, v. 34, p. 1033-1043.

Repenning, C.A. and Packard, E.L., 1990, Locomotion of a desmostylian and evidence of ancient shark predation; *in* Boucot, A. J., ed., Evolutionary paleobiology of behavior and coevolution. Elsevier, Amsterdam p. 199-203.

Retallack, G.J., 1983, Late Eocene and Oligocene paleosols from Badlands National Park, South Dakota: Geological Society of America, Special Paper 193, 82 p.

Retallack, G.J. and Krull, E.S., 1999, Permian coprolites from Graphite Peak, Antarctica: U.S. Antarctic Journal, v. 30, p. 7-9.

Reuss, A.E., 1856, Über Koprolithen im Rothliegen Böhmens: Sitzsungberichte Berlin Akademie der Wissenschaft Wien, mathematische-naturhistorische Klasse Vienna, v. 18, p. 124-132.

Rice, K., Mychajliw, A., Tewksbury, L. and Lindsey, E., 2019, Stable isotope analysis of asphaltic coprolites reveals stability of woodrat diet (*Neotoma* sp.) from Rancho La Brea, Los Angeles, California: AGU Fall Meeting Abstracts, v. 2019, p. PP42C-17.

Richardson, E.S., Jr., 1980, Life at Mazon Creek; *in* Langenheim, R.L., Jr. and Mann, C.J., eds., Middle and Late Pennsylvanian strata on margin of Illinois Basin. 10th Annual Field Conference of the Society of Economic Paleontologists and Mineralogists, Great Lakes Section. Urbana, University of Illinois, p. 217-224.

Richardson, E. S., Jr. and Johnson, R.G., 1971, The Mazon Creek fauna: Proceedings of the North American Paleontology Convention II, Lawrence, p. 1222-1235.

Richter, A.E., 2009, Ammoniten-Gehäuse mit Bissspuren: Berliner paläobiologische Abhandlungen, v. 10, p. 297-305.

Richter, G., 1987, Untersuchungen zur Ernährung eozäner Säuger aus der Fossilfundstätte Messel bei Darmstadt: Courier Forschungsinstitut Senckenberg, v. 91, p. 1-33.

Richter, G., 1988, Problems in the analysis of stomach contents of Eocene mammals from the Messel Oil Shale-layers: Courier Forschunginstitut Senckenberg, v. 107, p. 105-117.

Richter, G., 1992, Fossilized gut contents: Analysis and interpretation; *in* Schaal, S. and Ziegler, W., eds., Messel: An insight into the history of life and of the earth. Oxford, Oxford University Press, p. 285-289.

Richter, G. and Baszio, S., 2001a, First proof of planctivory/insectivory in a fossil fish: *Thaumaturus intermedius* from the Eocene Lake Messel (FRG): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 173, p. 75-85.

Richter, G. and Baszio, S., 2001b, Traces of a limnic food web in the Eocene Lake Messel—a preliminary report based on fish coprolite analyses: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 166, p. 345-368.

Richter, G. and Baszio, S., 2006, First evidence of size-related change of diet (“switching”) in a fossil fish: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 270-279.

Richter, R. and Storch, G., 1980, Beiträge zur Ernährungs-biologie eozäner Fledermause aus der “Grube Messel:” Natur und Museum Frankfurt, v. 110, p. 353-367.

Richter, G. and Wedmann, S., 2005, Ecology of the Eocene Lake Messel revealed by analysis of small fish coprolites and sediments from a drilling core: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 223, p. 147-161.

Richter, R., 1981, Untersuchungen zur Enährung von *Messelobunodon schaeferi* (Mammalia, Artiodactl: Senckenbergiana Lethaea, v. 61, p. 355-370.

Ridgwell, N.M., Chin, K., Upchurch, G. and Sertich, J., 2015, Rare direct evidence of angiosperm consumption by dinosaurs based on coprolites from the Kaiparowits Formation of Utah: Journal of Vertebrate Paleontology, v. 24 (supplement to no. 3), p. 203.

Rieber, H., 1970, *Phragmoteuthis*? *ticinensis* n. sp., ein Coleoidea-Rest aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kt. Tessin, Schweiz): Paläontologische Zeitschrift, v. 44, p. 32-40.

Riggs, E., 1939, A specimen of *Elasmosaurus serpentinus:* Field Museum of Natural History, Geological Series v. 6, p. 385-391.

Riggs, E.S., 1944, A new polycotolid plesiosaur: University of Kansas, Bulletin, 30, 77-87.

Rinehart, L.F., Lucas, S.G. and Spielmann, J.A. 2006. Bite marks on tetrapod bones from the Upper Triassic Chinle Group representing a new genus: New Mexico Museum of Natural History and Science, Bulletin 37, p. 160-163.

Rinehart, L.F., Lucas, S.G., Heckert, A.B., Spielmann, J.A. and Celeskey, M.D., 2009, The paleobiology of *Coelophysis bauri* (Cope) from the Upper Triassic (Apachean) Whitaker quarry, New Mexico, with detailed analysis of a single quarry block: New Mexico Museum of Natural History and Science, Bulletin 45, 260 p.

Ringuelet, R.A., 1957, Restos de probables huevos de nematodes en el estiercol del edentado extinguido *Mylodon listai* (Ameghino): Ameghiniana, v. 1, p. 15-16.

Ristevski, J., Young, M.T., De Andrade, M.B. and Hastings, A.K., 2018, A new species of *Anteophthalmosuchus* (Crocodylomorpha, Goniopholididae) from the Lower Cretaceous of the Isle of Wight, United Kingdom, and a review of the genus: Cretaceous Research, v. 84, p. 340-383.

Ritchie, A., 1991, Return of the great sea monsters: Australian Natural History, v. 23, p. 538-545.

Rivett, W. E. E., 1956, Reptilian bones from the Weald Clay: Proceedings of the Geological Society of London, v. 1540, p. 110-111.

Rivera-Sylva, H.E., Frey, E. and Guzmán-Gutiérrez, J.R., 2009, Evidence of predation on the vertebra of a hadrosaurid dinosaur from the Upper Cretaceous (Campanian) of Coahuila, Mexico: Carnets de Géologie Letter, v. 2, p.1–5.

Rivera-Sylva, H.E., Hone, D.W.E. and Dodson, P., 2012, Bite marks of a large theropod on a hadrosaur limb bone from Coahuila, Mexico: Boletín de la Sociedad Geológica Mexicana, v. 64, p. 155–159.

Rivera-Sylva, H.E., Frey, E., Guzmán-Gutierrez, J.R., Palomino-Sánchez, F. and Stinnesbeck, W., 2011, Un *Deinosuchus riograndensis* (Eusuchia: Alligatoroidea) de Coahuila, norte de México: Revista Mexicana de Ciencias Geológicas, v. 28, p. 267-274.

Roberts, A.E., 1958, Geology and coal resources of the Toledo-Castle Rock District, Cowlitz and Lewis Counties, Washington: U.S. Geological Survey, Bulletin 1062, 71 p.

Robertson, D., 1834, [untitled]: Bulletin de la Société Géologique de France, series 1, v. 4, p. 415.

Robin, N., Foldi, I., Godinot, M. and Petit, G., 2016. Scale insect larvae preserved in vertebrate coprolites (Le Quesnoy, France, Lower Eocene): Paleoecological insights: The Science of Nature, v. 103(9), doi: 10.1007/s00114-016-1412-x.

Robinson, R.F., Jasinski, S.E. and Sullivan, R.M., 2015, Theropod bite marks on dinosaur bones: Indications of a scavenger, predator or both?; and their taphonomic implications: New Mexico Museum of Natural History and Science, Bulletin 68, p. 275-282.

Rodriguez-de la Rosa, R.A., 2003, Pterosaur tracks from the latest Campanian Cerro del Pueblo Formation of southeastern Coahuila, Mexico; *in* Buffetaut, E. and Mazin, J.M., eds., Evolution and palaeobiology of pterosaurs. Geological Society of London, Special Publications, v. 217, p. 275–282.

Rodríguez de la Rosa, R.A., Cevallo-Ferriz, S.R.S. and Silva-Pineda, A., 1998, Paleobiological implications of Campanian coprolites: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 142, p. 231-254.

Rodríguez de la Rosa, R.A., Fernández-Barajas, M. del R., Valdes-Vergara, N.A. and Prado-Escamilla, E., 2021, Fish trace fossils from the Lower Cretaceous of Pueblo, Mexico: Journal of South American Earth Science, v. 112, https://doi.org/10.1016/j.james.2021103547.

Rogers, J.V., 2003, *Pachycheilosuchus trinquei*, a new procoelous crocodyliform from the Lower Cretaceous (Albian) Glen Rose Formation of Texas: Journal of Vertebrate Paleontology, v. 23, p. 128-145.

Rogers, R.R., 1990, Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of northwestern Montana: Evidence for drought-related mortality: Palaios, v. 5, p. 394-413.

Rogers, R.R. and Krause, D.W., 2007, Tracking an ancient killer: Scientific American, v. 296(2), p. 42-51.

Rogers, R.R., Krause, D.W., Curry Rogers, K., Rasoamiaramanana, A.H. and Rahantrisoa, L., 2004, Paleoenvironment and paleoecology of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar; *in* Sampson, S.D. and Krause, D.W., eds., *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar: Journal of Vertebrate Paleontology, Memoir, v. 8, p. 21-31.

Rogers, R.R., Krause, D.W., Kast, S.C., Marshall, M.S., Rahantarisoa, L., Robins, C.R. and Sertich, J.J., 2013, A new, richly fossiliferous member comprised of tidal deposits in the Upper Cretaceous Maevarano Formation, northwestern Madagascar: Cretaceous Research, v. 44, p.12-29.

Rolfe, W. D. I., 1973, Excursion 15: Silurian arthropod and fish assemblages from Lesmahagow, Lanarkshire; *in* Bluck, B. J., ed., Excursion guide to the geology of the Glasgow District. Glasgow, Geological Society of Glasgow, p. 119-126.

Romer, A.S., 1933, Eurypterid influence on vertebrate history: Science, v. 78, p. 114–117.

Romer, A.S., 1962, The vertebrate body (Third Edition). Philadelphia, W.B. Saunders, 627 p.

Romer, A.S. and Parsons, T.S., 1977, The vertebrate body (Fifth Edition). Philadelphia, W. B. Saunders, 624 p.

Romer, A.S., and Price, L.I., 1940, Review of the Pelycosauria: Geological Society of America, Special Paper, v. 28, p. 1-538.

Romilio, A. and Salisbury, S.W., 2011, A reassessment of large theropod dinosaur tracks from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia: A case for mistaken identity: Cretaceous Research, v. 32, p.135-142.

Romilio, A., Tucker, R.T. and Salisbury, S.W., 2013, Reevaluation of the Lark Quarry dinosaur tracksite (late Albian–Cenomanian Winton Formation, central-western Queensland, Australia): No longer a stampede?: Journal of Vertebrate Paleontology, v. 33, p. 102-120.

Romo-de-Vivar-Martínez, P.R., Martinelli, A.G., Paes Neto, V.D. and Soares, M.B., 2017, Evidence of osteomyelitis in the dentary of the Late Triassic rhynchocephalian *Clevosaurus brasiliensis* (Lepidosauria: Rhynchocephalia) from southern Brazil and behavioural implications: Historical Biology, v. 29, p. 320-327.

Röper, M., 2005, Field trip C: Lithographic limestones and Plattenkalk deposits of the Solnhofen and Mörnsheibm formations near Eichstätt and Solnhofen: Zitteliana, v. 26, p. 71-85.

Rothschild, B. M., 2015, Unexpected behavior in the Cretaceous: Tooth-marked bones attributable to tyrannosaur play: Ethology, Ecology and Evolution, v. 27, p. 325-334.

Rothschild, B.M. and Biehler-Gomez, L., 2021, Non-destructive recognition and differentiation of quasi-spherical structures of biologic interest: International Journal of Osteoarchaeology, v. 2021, p. 1-22,doi.org/10.1002/ oa.301.

Rothschild, B. M., and DePalma, R., 2013, Skin pathology in the Cretaceous: Evidence for probable failed predation in a dinosaur: Cretaceous Research, v. 42, p. 44-47.

Rothschild, B. and Everhart, M.J., 2015, Co-ossification of vertebrae in mosasaurs (Squamata, Mosasauridae): Evidence of habitat interactions and susceptibility to bone disease: Transactions of the Kansas Academy of Science, v. 118, p. 265-275.

Rothschild, B.M. and Martin, L.D., 1993, Paleopathology: Disease in the fossil record. Baton Rouge, CRC Press, 386 p.

Rothschild, B.M. and Molnar, R.E., 2008, Tyrannosaurid pathologies as clues to nature and nurture in the Cretaceous; *in* Larson, P. L. and Carpenter, K., eds., *Tyrannosaurus rex,* the Tyrant King. Bloomington, Indiana University Press, p. 287-304.

Rothschild, B.M., Clark, N.D. and Clark, C.M., 2018, Evidence for survival in a Middle Jurassic plesiosaur with a humeral pathology: What can we infer of plesiosaur behaviour?: Palaeontologia Electronica, v. 21, p. 1-11.

Rothschild, B.M., Martin, L.D. and Schulp, A.S., 2005, Sharks eating mosasaurs, dead or alive?: Netherlands Journal of Geosciences - Geologie en Mijnbouw, v. 84, p. 335-340.

Rowe, T., Cifelli, R. L., Lehman, T. M. and Weil, A., 1992, The Campanian Terlingua local fauna, with a summary of other vertebrates from the Aguja Formation, Trans-Pecos Texas: Journal of Vertebrate Paleontology, v. 12, p. 472-493.

Royo, J. and Gomez, J. 1960, Los vertebratos de la formation Uranco, Estado Falcon: Tercero Congreso Geológico Venezoelano, Memoir, v. 11, p. 509.

Rozada, L., Allain, R., Vullo, R., Goedert, J., Augier, D., Jean, A., Marchal, J., Peyre de Fabrègues, C., Qvarnström, M. and Royo-Torres, R., 2021, A Lower Cretaceous Lagerstätte from France: A taphonomic overview of the Angeac-Charente vertebrate assemblage: Lethaia, v. 54, p. 141-165.

Ruben, J. A., 1990, Evidence of convergent behavioral patterns in male crocodilians and phytosaurs; *in* Boucot, A. J., 1990, ed., Evolutionary paleobiology of behavior and coevolution, Elsevier, Amsterdam p. 427-428.

Rummy, P., Halaclar, K. and Chen, H., 2021, The first record of exceptionally-preserved spiral coprolites from the Tsagan-Tsab Formation (Lower Cretaceous), Tatal, western Mongolia: Scientific Reports, v. 11, 7891 (2021), doi.org/10.1038/s41598-021-87090-5.

Runnegar, B., 1983, A *Diprotodon* ulna chewed by the marsupial lion, *Thylacoleo carnifex*: Alcheringa, v. 7, p. 23-25.

Rusconi, C., 1947, Primeros hallazgos de coprolitos de reptile en el triásico de El Challao, Mendoza: Ciencia e Investigación, v. 10, p. 521-523.

Rusconi, C., 1949, Coprolitos Triassicos de Mendoza: Revista del Museo de Historia Natural de Mendoza, v. 3, p. 241-251.

Russell, E.S., 1982, Form and function: A contribution to the history of animal morphology (Second Edition). Chicago, University of Chicago Press, 383 p.

Ruedemann, R., 1929, Fossils from the Permian tillite of San Paulo, Brazil, and their bearing on the origin of the tillite: Geological Society of America Bulletin, v. 40, p. 417-426.

Ruf, I. and Lehmann, T., 2018, Rodents – gnawing their way to success; *in* Smith, K.T., Schaal, S.F.K. and Habersetzer, J., eds., Messel – ancient greenhouse ecosystem. Frankfurt am Main, Senckenberg Gesellschaft für Naturforschung, p. 263-269.

Runge, A.K.W., Hendy, J., Richter, K.K., Masson-MacLean, E., Britton, K., Mackie, M., McGrath, K., Collins, M., Cappellini, E. and Speller, C., 2021, Palaeoproteomic analyses of dog palaeofaeces reveal a preserved dietary and host digestive proteome: Proceedings of the Royal Society B, v. 288: 20210020, doi.org/10.1098/rspb.2021.0020.

Russo, G., Raia, P. and Lauteri, M., 2015, Coprolite specimens from Pietraroja (lower Cretaceous, southern Italy): Morphological analysis by scanning electron microscopy: Microscopie, v. 12, p. 53-59.

Rybakiewicz, S., Rivera-Sylva, H. E., Stinnesbeck, W., Frey, E., José Rubén Guzmán-Gutiérrez, J. R., González, R. V., Nava Rodríguez, R. L. and Padilla-Gutiérrez, J. M., 2019, Hadrosaurs from Cañada Ancha (Cerro del Pueblo Formation; upper Campanian-?lower Maastrichtian), Coahuila, northeastern Mexico: Cretaceous Research, v. 104, p. 104-199.

Rybczynski, N., 2008, Woodcutting behavior in beavers (Castoridae, Rodentia): Estimating ecological performance in a modern and a fossil taxon: Paleobiology, v. 34, p. 389-402.

Sahle, Y., El Zaatari, S. and White, T.D., 2017, Hominid butchers and biting crocodiles in the African Plio–Pleistocene: Proceedings of the National Academy of Sciences of the USA, v. 114, p. 13164-13169.

Sainte-Saint, P. de, 1949, Les poisons des calcaires lithographiques de Cerin (Ain): Nouvelles Archives du Muséum d'Histoire Naturelle de Lyons, v. 2, p. 1-357.

Sala, N., Algaba, M., Arsuaga, J.L., Aranburu, A. and Pantoja, A., 2012, A taphonomic study of the Búho and Zarzamora caves. Hyenas and humans in the Iberian Plateau (Segovia, Spain) during the late Pleistocene: Journal of Taphonomy, v. 10, p. 477-497.

Salamon, M. A. and Gorzelak, P., 2008, Signs of predation on Middle Triassic crinoids from Poland; *in* Andreas Kroh, A. and Schmid, B., eds., 4. Arbeitstreffen deutschsprachiger Echinodermenforscher, 4th Workshop of German and Austrian Echinoderm Research Abstracts. Wien, Naturhistorisches Museum Wien, p. 43-44.

Salamon, M. and Gorzelak, P., 2010, Late Cretaceous crinoids (Crinoidea) from eastern Poland: Palaeontographica Abteilung A, v. 291, p. 1-43.

Salamon, M.A., Gorzelak, P., Niedźwiedzki, R., Trzęsiok, D. and Baumiller, T.K., 2014, Trends in shell fragmentation as evidence of mid-Paleozoic changes in marine predation: Paleobiology, v. 40, p. 14-23.

Salamon, M.A., Niedźwiedzki, R., Gorzelak, P., Lach, R. and Surmik, D., 2012, Bromalites from the Middle Triassic of Poland and the rise of the Mesozoic Marine Revolution: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 321, p. 142-150.

Salesa, M.J., Antón, M., Turner, A. and Morales, J., 2010, Functional anatomy of the forelimb in *Promegantereon ogygia* (Felidae, Machairodontinae, Smilodontini) from the late Miocene of Spain and the origins of the sabre-toothed felid model: Journal of Anatomy, v. 216, p. 381-396.

Sallan, L.C. and Coates, M.I., 2010, End-Devonian extinction and a bottleneck in the early evolution of modern jawed vertebrates: Proceedings of the National Academy of Sciences of the USA, v. 107, p. 10131-10135.

Sallan, L.C and Galimberti, A.K., 2015, Body-size reduction in vertebrates following the end-Devonian mass extinction: Science, v. 350, p. 812-815.

Sallan, L.C., Kammer, T.W., Ausich, W.I. and Cook, L.A., 2011, Persistent predator–prey dynamics revealed by mass extinction: Proceedings of the National Academy of Sciences, v. 108, p. 8335-8338.

Salo, O.J., 1942, Gizzard stones, true and false: Mineralogist, v. 10(10), p.301-302.

Sánchez, I. M., Quiralte, V., Ríos, M., Morales, J. and Pickford, P., 2015, First African record of the Miocene Asian mouse-deer *Siamotragulus* (Mammalia, Ruminantia, Tragulidae): Implications for the phylogeny and evolutionary history of the advanced selenodont tragulids: Journal of Systematic Palaeontology, v. 13, p. 543-556.

Sandau, S.D., 2005, A Uintan (Late Middle Eocene) flora and fauna from the Uinta Basin, Utah [M.S. thesis]: Provo, Brigham Young University, 106 p.

Sander, P.M., 1989, Early Permian depositional environments and pond bonebeds in central Archer County, Texas: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 69, p. 1-21.

Sander, P. M., Rieppel, O. C. and Bucher, H., 1997, A new pistosaurid (Reptilia, Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of plesiosaurs: Journal of Vertebrate Paleontology, v. 17, p. 526-533.

Sanders, F. H. and Carpenter, K., 1998, Gastroliths from a camarasaurid in the Cedar Mountain Formation: Journal of Vertebrate Paleontology, v. 18 (supplement to no. 3), p. 74A.

Sanders, F. H., Manley, K. and Carpenter, K., 2001, Gastroliths from the Lower Cretaceous sauropod *Cedarosaurus weiskopfae*; *in* Tanke, D. and Carpenter, K., eds., Mesozoic vertebrate life. Bloomington, Indiana University Press, p. 166-180.

Sanders, W.J., Trapani, J. and Mitani, J.C., 2003, Taphonomic aspects of crowned hawk-eagle predation on monkeys: Journal of Human Evolution, v. 44, p. 87-105.

Saneyoshi, M., Watabe, M., Suzuki, S. and Tsogtbaatar, K., 2011, Trace fossils on dinosaur bones from Upper Cretaceous eolian deposits in Mongolia: Taphonomic interpretation of paleoecosystems in ancient desert environments: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 311, p. 38-47.

Sanford, E., 1999, Regulation of keystone predation by small changes in ocean temperature: Science, v. 283, p. 2095-2097.

Sansom, I.J., Davies, N.S., Coates, M.I., Nicoll, R.S. and Ritchie, A., 2012, Chondrichthyan-like scales from the Middle Ordovician of Australia: Palaeontology, v. 55, p. 243–247.

Sansom, I.J., Smith, M.M. and Smith, M.P., 1996, Scales of thelodont and shark-like fishes from the Ordovician of Colorado: Nature, v. 379, p. 628-630.

Sansom, R.S. Gabbott, S.E. and Purnell, M.A. 2010, Nonrandom decay of chordate characters causes bias in fossil interpretation: Nature, v. 463, p. 797–800.

Santi, G. and Stoppini, M., 2005, Predator-prey interaction in the Permian of the Orobic basin (North Italy): PalArch Vertebrate Palaeontology, v. 4, p. 7-18.

Santos, A., Mayoral, E., Muñiz, F., Bajo, I. and Adriaensens, O., 2003, Bioerosión en erizos irregulares (Clypeasteroidea) del Mioceno Superior en el sector suroccidental de la cuenca del Guadalquivir (Provincia de Sevilla): Revista Española de Paleontología, v. 18, p. 131-141.

Sanz, J.L., Chiappe, L.M., Fernádez-Jalvo, Y., Ortega, F., Sánchez-Chillón, B., Poyatoariza, F.J., and Pérez-Moreno, B.P., 2001, An Early Cretaceous pellet: Nature, v. 409, p. 998-1000.

Sanz, P.M., Chiappe, L.M., Pérez-Moreno, B., Buscalioni, A.D., Moratalla, J.J., Ortega, F. and Poyata-Ariza, F.J., 1996, An Early Cretaceous bird from Spain and its implications for the evolution of avian flight: Nature, v. 382, p. 442–445.

Sardella, R., Bellucci, L., Bona, F., Cherin, M., Iurino, D.A. and Rook, L., 2018, Before and after the earliest *Homo* dispersal in Europe: Evidence from the early Pleistocene sites of the Italian Peninsula: Comptes Rendus Palevol, v. 17, p. 287-295.

Sato, T., and Storrs, G. W., 2000, An early polycotylid plesiosaur (Reptilia: Sauropterygia) from the Cretaceous of Hokkaido, Japan: Journal of Paleontology, v. 74, p. 907–914.

Sato, T., and Tanabe, K., 1998, Cretaceous plesiosaurs ate ammonites: Nature, v. 394, p. 629– 630.

Sato, T., Hasegawa, Y., Manabe, M., 2006, A new elasmosaurid plesiosaur from the Upper Cretaceous of Fukushima, Japan: Palaeontology, v. 49, p. 467-484.

Saul, L.R., 1979, A hollow spined *Anapachydiscus peninsularis* with possible mosasaur bite impressions: Contributions in Science, Natural History Museum of Los Angeles County, v. 304, p. 1-8.

Savage, T., E., 1915, The loess in Illinois: Its origin and age: Illinois State Academy of Science Transactions, v. 8, p. 100-117.

Sawyer, G.T. and Erickson, B.R., 1998, Paleopathology of the Paleocene crocodile *Leidyosuchus*: Science Museum of Minnesota, Monograph, v. 4, 38 p.

Scanferla, A. and Smith, K.T., 2020, Exquisitely preserved fossil snakes of Messel: Insight into the evolution, biogeography, habitat preferences and sensory ecology of early boas: Diversity, v. 12, p. 100, doi:10.3390/d12030100.

Schaal, S., 2004, *Palaeopython fischeri* n. sp. (Serpentes: Boidae), eine Riesenschlange aus dem Eozän (MP 11) von Messel: Courier Forschunginstitut Senckenberg, v. 252, p. 35–45.

Schaal, S.K.F., 2016, The Messel pit fossil site; *in* Fraser, N. and Sues H.-D., eds., Terrestrial conservation Lagerstätten: Windows into the evolution of life on land: Dunedin, Dunedin Academic Press, 450 p.

Schaeffer, B. and Patterson, C., 1984, Jurassic fishes from the western United States, with comments on Jurassic fish distribution: American Museum Novitates, no. 2796, 86 p.

Schaffner, D., 1928, Gastroliths in the lower Dakota of northern Kansas: Transactions of the Kansas Academy of Science, v. 41, p. 225-226.

Schaumberg, G., 1979, Neue Nachweise von Bryozoen und Brachiopoden als Nahrung des permischen Holocephalen *Janassa bituminosa* (Schlotheim): Ein Beitrag zur Ökologie des Kupferschiefers: Philippia, v. 4, p. 3–11.

Schein, J.P. and Poole, J.C., 2014, A shark-bitten dinosaur (Hadrosauridae) femur from the latest Maastrichtian basal Hornerstown Formation, New Jersey, U.S.A: The Mosasaur, v. 8, p. 15–22.

Scherpner, C., 1980, Die Krokodile; *in* Grzimek, B., Hediger, H., Klemmer, K., Kuhn, O. and Wermuth, H., eds., Grzimeks Tierleben, 6, Kriechtiere. München, Deutscher Taschenbuch-Verlag, p. 128-147.

Scheyer, T. M., Delfino, M., Klein, N., Bunbury, N., Fleischer-Dogley, F. and Hansen, D.M., 2018, Trophic interactions between larger crocodylians and giant tortoises on Aldabra Atoll, Western Indian Ocean, during the Late Pleistocene: Royal Society Open Science, v. 5:171800, dx.doi.org/10.1098/rsos.171800.

Schindewolf, O. H., 1953, Über die Faunenwende vom Paläozoikum zum Mesozoikum: Zeitschrift der Deutsche Geologische Gesellschaft, v. 105, p. 153–183.

Schmeisser, R. L. and Flood, T. P., 2004, A proposed method for recognizing selected paleogastroliths using a scanning electron microscope: Geological Society of America, Abstracts with Programs, v. 36, p. 61.

Schmeisser, R. L. and Flood, T. P., 2008, Recognition of paleogastroliths from the Lower Cretaceous Cedar Mountain Formation, Utah using a scanning electron microscope: Ichnos, v. 15, p. 72-77.

Schmeisser, R. L. and Gillette, D. D., 2009, Unusual occurrence of gastroliths in a polycotylid plesiosaur from the Upper Cretaceous Tropic Shale, southern Utah: Palaios, v. 24, p. 453-459.

Schmidt, G.D., Duszynski, D.W. and Martin, P.S., 1992, Parasites of the extinct Shasta Ground Sloth, *Nothrotheriops shastensis*, in Rampart Cave, Arizona: Journal of Parasitology, v. 78, p. 811-816.

Schmitz, M., 1991, Die Koprolithen mitteleozäner Vertebraten der Grube Messel bei Darmstadt: Courier Forschungsinstitut Senckenberg, Band 137, 1-159.

Schmitz, M. and Benda, P.L., 1991, Coprolites from the Maastrichtian Whitemud Formation of southern Saskatchewan: Morphological classification and interpretation of diagenesis: Paläontologische Zeitschrift, v. 65, p. 199-211.

Schneider, V.P. and Fierstine, H.L., 2004, Fossil tuna vertebrae punctured by istiophorid billfishes: Journal of Vertebrate Paleontology, v. 24, p. 253-255.

Schoch, R.R., 2012, Dicynodont mandible from the Triassic of Germany forms the first evidence of large herbivores in the Central European Carnian: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 263, p. 119-123.

Schoch, R.R., Nesbitt, S., Müller, J., Lucas, S.G. and Boy, J.A., 2010, The reptile assemblage from the Moenkopi Formation (Middle Triassic) of New Mexico: Neues Jahrbuch für Geologie und Paläontologie Abheilung, v. 255, p. 345-369.

Schoenwetter, J., 1974, Pollen analysis of prehistoric human feces from Salts Cave, Kentucky; *in* Watson, P., ed., The archeology of the Mammoth Cave area. New York, Academic Press, p. 49-58.

Scholze, F., Schneider, J. W. and Lucas, S. G., 2021, Conchostracans from the Late Pennsylvanian Kinney Brick Quarry Konservat Lagerstätte, New Mexico (USA) – taxonomy, biostratigraphy, and paleoecology: New Mexico Museum of Natural History and Science, Bulletin 84, p. 287-299.

Schormann J., 1987, Bißspuren an Seeigeln: Arbeitskreis Paläontologie Hannover, v. 15, p. 73–75.

Schroeder-Adams, C., Cumba, S.L., Bloch, A.J., Leckie, D.A., Craig, J., Seif El-Dein, S.A., Simons, D.J. and Kenig, D.E., 2001, Late Cretaceous (Cenomanian to Campanian) paleoenvironmental history of the eastern Canadian margin of the Western Interior seaway: Bonebeds and anoxic events: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 17, p. 311- 365.

Schultze, H.-P., 1972, Early growth stages in coelacanth fishes: Nature New Biology, v. 236, p. 90-91.

Schumacher, B.A., 1993, Biostratigraphy of Mosasauridae (Squamata, Varanoidea) from the Smoky Hill Chalk Member, Niobrara Chalk (Upper Cretaceous) of western Kansas [M.S. thesis]: Hays, Fort Hays State University, 68 p.

Schumacher, B. and Everhart, M. J., 2005, A stratigraphical and taxonomic review of plesiosaurs from the old "Fort Benton Group" of central Kansas: A new assessment of old records: Paludicola, v. 5, p. 33-54.

Schwartz, D., Ikejiri, T., Breithaupt, B.H., Sander, P.M., Klein, N., 2007, A nearly complete skeleton of an early juvenile diplodocid (Dinosauria: Sauropoda) from the lower Morrison Formation (Late Jurassic) of north central Wyoming and its implications for early ontogeny and pneumaticity in sauropods: Historical Biology, v. 19, p. 225-253.

Schwarzhans, W. W., Murphy, T. D. and Frese, M., 2018, Otoliths *in situ* in the stem teleost *Cavenderichthys talbragarensis* (Woodward, 1895), otoliths in coprolites, and isolated otoliths from the Upper Jurassic of Talbragar, New South Wales, Australia: Journal of Vertebrate Paleontology, v. 38, no. 6: e1539740, doi: 10.1080/02724634.2018.1539740.

Schweigert, G. and Dietl, G., 2012, Vertebrate coprolites from the Nusplingen lithographic limestone (Upper Jurassic, SW-Germany): New Mexico Museum of Natural History and Science, Bulletin 57, p. 215-220.

Schweigert, G., Dietl, G. and Wild, R., 2001, Miscellanea aus dem Nusplinger Plattenkalk (Ober-Kimmeridgium, Schwäbische Alb). 3. Ein Speiballen mit Flugsaurierresten: Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins Band, v. 83, p. 357 – 364.

Schwenk, K., 2000, Feeding: Form, function and evolution in tetrapod vertebrates. London, Elsevier, 537 p.

Schwenk, K. and Rubega, M., 2005, Diversity of vertebrate feeding systems; *in* Starck, J.M. and Wang, T., eds., Physiological and ecological adaptations to feeding in vertebrates. Enfield, Science Publishers, p. 1-41.

Schwimmer, D.R., 2010, Bite marks of the giant crocodilian *Deinosuchus* on Late Cretaceous (Campanian) bones: New Mexico Museum of Natural History and Science, Bulletin 51, p. 183–190.

Schwimmer, D.R., Stewart, J.D. and Williams G.D., 1997, Scavenging by sharks of the genus *Squalicorax* in the Late Cretaceous of North America: Palaios, v. 12, p. 71–83.

Schwimmer, D.R., Weems, R.E. and Sanders, A.E., 2015a, A Late Cretaceous shark coprolite with baby freshwater turtle vertebrae inclusions: Palaios, v. 30, p. 707-713.

Schwimmer, D.R., Sanders, A.E., Erickson, B.R., and Weems, R.E., 2015b, A Late Cretaceous dinosaur and reptile assemblage from South Carolina, U.S.A.: Transactions of the American Philosophical Society, v. 105, 157 p.

Scott, A. C., 1991, Evidence for plant-arthropod interactions in the fossil record: Geology Today, v. 7, p. 58-61.

Scott, E.E., Clemens, M.E., Ryan, M.J., Jackson, G. and Boyle, J.T., 2012, A *Dunkleosteus* suborbital from the Cleveland Shale, northeastern Ohio, showing possible arthrodire-inflicted bite marks: Evidence for agonistic behavior, or postmortem scavenging?: Geological Society of America, Abstracts with Programs, v. 44, p. 61.

Scott, L., 1987, Pollen analysis of hyena coprolites and sediments from Equus Cave Taung, Southern Kalahari (South Africa): Quaternary Research, v. 28, p. 144-156.

Scott, R., Ungar, P., Bergstrom, T., Brown, C. A., Grine, F. E., Teafordd, M. F. and Walker, A., 2005, Dental microwear texture analysis shows within-species diet variability in fossil hominins: Nature, v. 436, p. 693–695.

Scott, W. B. and Jepsen, G. L., 1936, The mammalian fauna of the White River Oligocene. Part I. Insectivora and Carnivora: Transactions of the American Philosophical Society, v. 28, p. 1–153.

Secord, R., Gingerich, P.D. and Bloch, J.I., 2002, *Mylanodon rosei*, a new metacheiromyid (Mammalia, Palaeanodonta) from the late Tiffanian (late Paleocene) of northwestern Wyoming: Contributions of the Museum of Paleontology, University of Michigan, v. 30, p. 385–399.

Seeley, H.G., 1877, On *Mauisaurus gardneri* Seeley, an elasmosaur from the base of the Gault of Folkestone: Quarterly Journal of the Geological Society of London, v. 33, p. 541-546.

Segesdi, M., Botfalvai, G., Bodor, E.R., Ősi, A., Buczkó, K., Dallos, Z., Tokai, R. and Földes, T., 2017, First report on vertebrate coprolites from the Upper Cretaceous (Santonian) Csehbánya Formation of Iharkút, Hungary: Cretaceous Research, v. 74, p. 87-99.

Seilacher, A., 1953, Studien zur Palichnologie. I. Über die Methoden der Palichnologie: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 96, p. 421–452.

Seilacher, A., 1964, Biogenic sedimentary structures; *in* Imbrie, J. and Newell, N., eds., Approaches to paleoecology. New York, Wiley, p. 296–316.

Seilacher, A., 1967, Bathymetry of trace fossils: Marine Geology, v. 5, p. 413–428.

Seilacher, A., 1998, Mosasaurs, limpets or diagenesis: How *Placenticeras* shells got punctured: Mitteilungen aus dem Museum für Naturkunde in Berlin. Fossil Record, v. 1, p. 93-102.

Seilacher, A., 2002, Non olet: The strange taphonomy of coprolites and cololites; *in* De Renzi, M., Alonso, M. V. P., Belinchón, M., Peñalver, E., Montoya, P. and Márquez-Aliaga, A., eds., Current topics on taphonomy and fossilization. Valencia, Collecció Encontres, p. 233-240.

Seilacher, A., Marshall, C., Skinner, H.C.W. and Tsuihiji, T., 2001, A fresh look at sideritic "coprolites:" Paleobiology, v. 27, p. 7-13.

Selden, P. A., 1979, Functional morphology of *Baltoeurypterus* [Ph.D. dissertation]: Cambridge, University of Cambridge, 190 p.

Selden, P.A., 1984, Autecology of Silurian eurypterids: Special Papers in Palaeontology, 32, p. 39-54.

Sennikov, A.G. and Golubev, V.K., 2012, On the faunal verification of the Permo-Triassic boundary in continental deposits of Eastern Europe: 1. Gorokhovets–Zhukov Ravine: Paleontological Journal, v. 46, p. 313–323.

Sereno, P. C., 1990, Psittacosauridae; *in* Weishampel, D. B. Dodson, P. and Osmólska, H., eds., The Dinosauria. Berkeley, University of California Press, p. 579-592.

Sereno, P.C. and Novas, F.E., 1994, The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*: Journal of Vertebrate Paleontology, v. 13, p. 451-476.

Sereno, P.C., Larsson, H.C., Sidor, C.A. and Gado, B., 2001, The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa: Science, v. 294, p. 1516-1519.

Sereno, P.C., Tan, L., Brusatte, S.L., Kriegstein, H.J., Zhao, X. and Cloward, K., 2009, Tyrannosaurid skeletal design first evolved at small body size: Science, v. 326, p. 418–422.

Serrano-Brañas, C.I. and Espinosa-Chavez, B., 2017, Taphonomic history of a 'duck-bill' dinosaur (Dinosauria: Ornithopoda) from the Cerro del Pueblo Formation (Upper Cretaceous, Campanian) Coahuila, Mexico: Preservational and paleoecological implications: Cretaceous Research, v. 74, p. 165-174.

Seuss, B., Mapes, R.H., Klug, C., and Nützel, A. 2012, Exceptional cameral deposits in a sublethally injured Carboniferous orthoconic nautiloid from the Buckhorn Asphalt Lagerstätte in Oklahoma, USA: Acta Palaeontologica Polonica, v. 57, p. 375–390.

Seymour, R., 1982, Physiological adaptations to aquatic life; *in* Gans, C., ed., The biology of the Reptilia. Volume 13. New York, Academic Press, p. 1-51.

Shabica, C. W. and Godfrey, S. J., 1997, Coprolites and trace fossils (biogenic structures); *in* Shabica, C.W. and Hay, A.A., eds., Richardson's guide to the fossil fauna of Mazon Creek. Chicago, Northeastern Illinois University, p. 275-280.

Shaler, N., 1891, The origin and nature of soils: Twelfth Annual Report of the Director of the U. S. Geological Survey. Part I Geology, p. 213-345.

Sharma, M.K. and Patnaik, R., 2010, Coprolites from the lower Miocene Baripada beds of Orissa: Current Science, v. 99, p. 804-808.

Sheldon, R.P., 1964, Paleolatitudinal and paleogeographic distribution of phosphorite: U. S. Geological Survey, Professional Paper 501, p. C106-C113.

Shen, C., Pratt, B.R. and Zhang, X.-G., 2014, Phosphatized coprolites from the middle Cambrian (Stage 5) Duyun fauna of China: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 410, p. 104–112, doi: 10.1016/j.palaeo.2014.05.035.

Shillito, L.-M., Blong, J.C., Green, E.J. and Van Asperen, E., 2020, The what, how and why of archaeological coprolite analysis: Earth Science Reviews, v. 207, p.103-196, doi.org/10.1016/j.earscirev.2020.103196.

Shillito, L.-M., Matthews, W., Bull, I.D., Williams, J., 2013b, Biomolecular investigations of faecal biomarkers at Sheik-e Abad and Jani; *in* Matthews, R., Matthews, W. and Mohammadifar, Y., eds., The earliest Neolithic of Iran: 2008 Excavations at Sheikh e Abad and Jani. Oxford, Oxbow and British Institute for Persian Studies, p. 105–115.

Shimada, K., 1997, Paleoecological relationships of the Late Cretaceous lamniform shark *Cretoxyrhina mantelli* (Agassiz): Journal of Paleontology, v. 71, p. 926-933.

Shimada, K. and Everhart, M. J., 2004, Shark–bitten *Xiphactinus audax* (Teleostei: Ichthyodectiformes) from the Niobrara Chalk (Upper Cretaceous) of Kansas: The Mosasaur, v. 7, p. 35–39.

Shimada, K. and Hooks, G.E., III., 2004, Shark–bitten protostegid turtles from the Upper Cretaceous Mooreville Chalk, Alabama: Journal of Paleontology, v. 78, p. 205–210.

Shimada, K., Tsuihiji, T., Sato, T. and Hasegawa, Y., 2010, A remarkable case of a shark-bitten elasmosaurid plesiosaur: Journal of Vertebrate Paleontology, v. 30, p. 592-597.

Shimada, K., Schumacher, B.A., Parkin, J.A. and Palermo, J.M., 2006, Fossil marine vertebrates from the lowermost Greenhorn Limestone (Upper Cretaceous: Middle Cenomanian) in southeastern Colorado: Memoir of the Paleontological Society, v. 63, Journal of Paleontology, supplement to v. 80(2), p. 1-45.

Shu, D., 2008, Cambrian explosion: Birth of tree of animals: Gondwana Research, v. 14, p. 219–240.

Shu, D.-G., Conway Morris, S., Han, J., Zhang, Z.-F., Yasui, K., Janvier, P., Chen, L., Zhang, X.-L., Liu, J.-N., Li, Y. and Liu, H.-Q., 2003, Head and backbone of the early Cambrian vertebrate *Haikouichthys*: Nature, v. 421, p. 526-529.

Shu, D.-G., Conway Morris, S., Zhang, Z.-F., Liu, J.N., Han, J., Chen, L., Shu, D.-G., Luo, H.-L., Conway Morris, S., Zhang, X.-L., Hu, S.-X., Chen, L., Han, J., Zhu, M., Li, Y. and Chen, L.-Z., 1999, Lower Cambrian vertebrates from South China: Nature, v. 402, p. 42-46.

Shubin, N. H., Daeschler, E. B. and Coates, M. I., 2004, The early evolution of the tetrapod humerus: Science, v. 304, p. 90-93.

Shuler, E., 1950, A new elasmosaur from the Eagle Ford Shale of Texas: Modern Science Series 1, Part 2, University Press, Dallas, p. 18-24.

Shumacher, B. A., 2007, A new polycotylid plesiosaur (Reptilia: Sauropterygia) from the Greenhorn Limestone (Upper Cretaceous: lower upper Cenomanian), Black Hills, South Dakota: Geological Society of America, Special Paper, v. 27, p. 133-146.

Signor III, P.W. and Brett, C.E., 1984, The mid-Paleozoic precursor to the Mesozoic marine revolution: Paleobiology, v. 10, p. 229-245.

Sillen, A., Hall, G. and Armstrong, R., 1995, Strontium–calcium ratios (Sr/Ca) and strontium isotopic ratios (87Sr/Sr86) of *Australopithecus robustus* and *Homo* sp. from Swartkrans: Journal of Human Evolution, v. 26, p. 227–285.

Silva, R.R., Ferigolo, J., Bajdek, P. and Piñeiro, G., 2017, The feeding habits of Mesosauridae: Frontiers in Earth Science, v. 5:23, doi:10.3389/feart.2017.00023.

Simpson, E.L., Hilbert-Wolf, H.L., Wizevich, M.C., Tindall, S.E., Fasinski, B.R., Storm, L.P. and Needle, M.D., 2010, Predatory digging behavior by dinosaurs: Geology, v. 38, p. 699-702.

Simpson, G.G. and Elftman, H. O., 1928, Hind limb musculature and habits of a Palaeocene multituberculate: American Museum Novitates, no. 333, 19 p.

Sims, D.W., Andrews, P.L.R. and Young, J.Z., 2000, Fish behaviour: Stomach rinsing in rays: Nature, v. 404, p. 566.

Sims, M.S., Boston, W.B. and Mapes, R.H., 1987, Predation on an upper Carboniferous ammonoid *Gonioloboceras*: Geological Society of America, Abstracts with Program, v. 9, p. 57–58.

Sinclair, W.J., 1922, Entelodonts from the Big Badlands of South Dakota in the Geological Museum of Princeton University: Proceedings of the American Philosophical Society, v. 60, p. 467-495.

Sinclair, W.J. and Granger, W., 1914, Paleocene deposits of the San Juan Basin, New Mexico: Bulletin of the American Museum of Natural History, v. 33, p. 297–316.

Skoczylas, R., 1978, Physiology of the digestive tract; *in* Gans, C. and Gans, K. A., eds., Biology of the Reptilia. Volume 8. Physiology B. London, Academic Press, p. 589-717.

Slodownik, M. and Wings, O., 2015, Bite marks on *Europasaurus* bones from the Langenberg Quarry near Goslar (Lower Saxony, Germany): 13th Annual Meeting of the European Association of Vertebrate Palaeontologists Opole, Poland, 8-12 July 2015, Abstracts, p. 141.

Slon, V., Mafessoni, F., Vernot, B., de Filippo, C., Grote, S., Viola, B., Hajdinjak, M., Peyrégne, S., Nagel, S., Brown, S. and Douka, K., 2018, The genome of the offspring of a Neanderthal mother and a Denisovan father: Nature, v. 561, p. 113-116.

Slotta, F., Korn, D., Klug, C., Kröger, B. and Keupp, H., 2011, Sublethal shell injuries in Late Devonian ammonoids (Cephalopoda) from Kattensiepen (Rhenish Mountains): Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, v. 261, p. 321-336.

Smith, A. S., 2007, Anatomy and systematics of the Rhomaleosauridae (Sauropyterygia: Plesiosauria) [Ph.D. dissertation]: Dublin, National University of Ireland, 278 p.

Smith, C.L., Rand, C.S. B. Schaeffer, B. and Atz, J.W., 1975*, Latimeria*, the living coelacanth, is ovoviviparous: Science, v. 190, p. 1105–1106.

Smith, H.F., Hutchison, J.H., Townsend, K.E.B. and, Adrian, B. and Jager, D., 2017, Morphological variation, phylogenetic relationships, and geographic distribution of the Baenidae (Testudines), based on new specimens from the Uinta Formation (Uinta Basin), Utah (USA): PLoS ONE, v. 12(7):e0180574, doi.org/10.1371/journal.pone.0180574.

Smith, K.T. and Wuttke, M., 2015, Avian pellets from the late Oligocene of Enspel, Germany-ecological interactions in deep time: Palaeobiodiversity and Palaeoenvironments, v. 95, p. 103–113.

Smith, K.T., Čerňanský, A., Scanferia and Schaal, S.F.K., 2018, Lizards and snakes – Warmth-loving sunbathers; *in* Smith, K.T., Schaal, S.F.K. and Habersetzer, J., eds., Messel – Ancient greenhouse ecosystem. Frankfurt am Main, Senckenberg Gesellschaft für Naturforschung, p. 123-147.

Smith, M.M. and Sansom, I.J., 1997, Exoskeletal micro-remains of an Ordovician fish from the Harding Sandstone of Colorado: Palaeontology, v. 40, p. 645–658.

Smith, R.M.H., 1993, Vertebrate taphonomy of late Permian floodplain deposits in the southwestern Karoo Basin of South Africa: Palaios, v. 8, p. 45-67.

Smith, R.M.H. and Botha-Brink, J., 2011, Morphology and composition of bone-bearing coprolites from the late Permian Beaufort Group, Karoo Basin, South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 312, p. 40-53.

Snyder, K., McLain, M., Wood, J. and Chadwick, A., 2020, Over 13,000 elements from a single bonebed help elucidate disarticulation and transport of an *Edmontosaurus* thanatocoenosis. PLoS ONE, v. 15(5): e0233182, doi.org/10.1371/journal.pone.0233182.

Sobolik, K., 1988, The importance of pollen concentration values from coprolites: An analysis of Southwest Texas samples: Palynology, v. 12, p. 201-214.

Sobolik, K.D., 1994, Paleonutrition of the Lower Pecos region of the Chihuahuan Desert; *in* Sobolik, K.D., ed., Paleonutrition: The diet and health of Prehistoric Americans: Carbondale, Southern Illinois University, Center for Archaeological Investigations, Occasional Paper No. 22, p. 247-264.

Sohn, I.G., and Chatterjee, S., 1979, Freshwater ostracodes from Late Triassic coprolite in central India: Journal of Paleontology, v. 53, p. 578- 586.

Sokol, O., 1971, Lithophagy and geophagy in reptiles: Journal of Science, v. 5, p. 69-71.

Soler-Gijón, R., 1995, Evidence of predator-prey relationship in xenacanth sharks of the upper Carboniferous (Stephanian C) from Puertollano; Spain: Geobios, v. 28, p. 151-156.

Sorbini, L., 1972, I Fossili di Bolca. Verona, Edizioni Corev, 132 p.

Souto, P.R.F., 2001, Tetrapod coprolites from the Middle Triassic of Southern Brazil: GAIA, v. 16, p. 51-57.

Souto, P.R.F., 2007, Os coprólitos da Bacia de São José de Itaboraí. Estado do Rio de Janeiro, Brasil; *in* Ismar de Souza Carvalho et al., eds., Paleontologia: Cenários da vida. 1. Rio de Janeiro, Interciência, p. 811-818.

Souto, P. R.F., 2008, Coprólitos do Brasil: Principais ocorrências e estudo. Rio de Janeiro, Publit, 89 p.

Souto, P.R.F., 2010, Crocodylomorph coprolites from the Bauru Basin, Upper Cretaceous, Brazil: New Mexico Museum of Natural History and Science, Bulletin 51, p. 201–208.

Souto, P.R.F. and Fernandes, M.A., 2015, Fossilized excreta associated to dinosaurs in Brazil: Journal of South American Earth Sciences, v. 57, p. 32–38.

Souto, P.R.F. and Schwanke, C., 2010, Ocorrência de coprólitos de vertebrados na bacia de Alagoas, Cretáceo Inferior: Boletim Do Museu Paraense Emílio Goeldi, Ciências Naturais, v. 5, p. 189-194.

Spallanzani, L., 1785, Versuche über das Verdauungsgeschäft des Menschen und verschiedener Tierarten. Leipzig, Ueberf, p. 18-24.

Spencer, P. K., 1993, The “coprolites” that aren’t: The straight poop on specimens from the Miocene of southwestern Washington: Ichnos, v. 2, p. 231-236.

Sperling, E.A., Frieder, C.A., Raman, A.V., Girguis, P.R., Levin, L.A. and Knoll, A.H., 2013, Oxygen, ecology, and the Cambrian radiation of animals: Proceedings of the National Academy of Sciences, v. 110, p. 13446-13451.

Sperry, G., 1957, Collecting gizzard stones in Utah: Desert Magazine, v. 20, p. 4-5, 7.

Spielmann, J.A., Lucas, S.G., Hunt, A.P. and Heckert, A.B., 2006, Reinterpretation of the holotype of *Malerisaurus langstoni*, a diapsid reptile from the Upper Triassic Chinle Group of West Texas: New Mexico Museum of Natural History and Science, Bulletin 37, p. 543-547.

Spillmann, F., 1929, Das südamerikanische Mastodon als Zeitgenose dês Menschen majoiden Kulturkeises: Paläontologische Zeitschrift, v. 11, p.170-177.

Špinar, Z.V., 1972, Tertiary frogs from central Europe. Prague, Academia, 286 p.

Spindler, F., Lauer, R., Tischlinger, H. and Mäuser, M., 2021, The integument of pelagic crocodylomorphs (Thalattosuchia: Metriorhynchidae): Palaeontologia Electronica, v. 24(2):a25, doi.org/10.26879/1099 palaeo-electronica.org/content/2021/3399-metriorhynchid-skin.

Stanley, S.M., 2008, Predation defeats competition on the seafloor: Paleobiology, v. 34, p. 1–21.

Starck, J.M., 1999a. Structural flexibility of the gastro-intestinal tract of vertebrates. Implications for evolutionary morphology: Zoologische Anzeiger, v. 238, p. 87-101.

Starck, J.M., 1999b, Phenotypic flexibility of the avian gizzard: rapid, reversible and repeated changes of organ size in response to changes in dietary fibre content: Journal of Experimental Biology, v. 202, p. 3171-3179.

Stauffer, C., 1945, Gastroliths from Minnesota: American Journal of Science, v. 6, p. 336-342.

Steadman, D.W., Franz, R., Morgan, G.S., Albury, N.A., Kakuk, B., Broad, K., Franz, S.E., Tinker, K., Pateman, M.P., Lott, T.A. and Jarzen, D.M., 2007, Exceptionally well preserved late Quaternary plant and vertebrate fossils from a blue hole on Abaco, The Bahamas: Proceedings of the National Academy of Sciences, v. 104, p. 19897-19902.

Stein, W. W., 2021, The paleontology, geology and taphonomy of the Tooth Draw Deposit; Hell Creek Formation (Maastrictian), Butte County, South Dakota: The Journal of Paleontological Sciences, v. 9, p. 1-108.

Stensiö, E.A., 1939, A new anaspid from the Upper Devonian of Scaumenac Bay in Canada, with remarks on the other anaspids: Kungliga Svenska Vetenskapsakademiens Handlingar, v. 18(3), p. 3-25.

Sternberg, C.H. 1917, Hunting dinosaurs in the badlands of the Red Deer River, Alberta, Canada. Lawrence, San Diego, Charles H. Sternberg, 232 p.

Sternberg, C.H., 1922, Exploration of the Permian of Texas and the Chalk of Kansas, 1918: Transactions of the Kansas Academy of Science, v. 30, p. 119-120.

Stevens, C.E. and Hume, I. D., 1995, Comparative physiology of the vertebrate digestive system (Second Edition). Cambridge, Cambridge University Press, 400 p.

Stevens, K., Mutterlose, J. and Schweigert, G., 2014, Belemnite ecology and the environment of the Nusplingen Plattenkalk (Late Jurassic, southern Germany): Evidence from stable isotope data: Lethaia, v. 47, p. 512-523.

Stewart, A., 1899, *Pachyrhizodus minimus*, a new species of fish from the Cretaceous of Kansas: Kansas University Quarterly, v. 8, p. 37-38.

Stewart, I. and Nicoll, R.S., 2003, Multi-element apparatus structure of the Early Ordovician conodont *Oepikodus evae* Lindström from Australia and Sweden; *in* Mawson, R. and Talent, J. A., eds., Contributions to the Second Australian conodont Symposium (AUSCOS II) held in conjunction with Palaeontology Down Under 2000 in Orange, Australia, 3–7 July 2000: Courier Forschungsinstitut Senckenberg, 2, v. 45, p. 361-387.

Stewart, J.D., 1978, Enterospirae (fossil intestines) from the Upper Cretaceous Niobrara Formation of western Kansas; *in* Chorn, J., Reavis, E.A., Stewart, J.D. and Whetstone, K.N., eds., Fossil fish studies: The University of Kansas Paleontological Contributions, Paper 89, p. 9-16.

Stewart, J. D. and Carpenter, K., 1990, Examples of vertebrate predation on cephalopods in the Late Cretaceous of the Western Interior; *in* Boucot, A. J., 1990, ed., Evolutionary paleobiology of behavior and coevolution. Elsevier, Amsterdam p. 203-207.

Stewart, J. D. and Martin, J. E., 1993. Late Cretaceous selachians and associated marine vertebrates from the Dakota Rose Granite Quarry, Grant County, South Dakota: Proceedings of the South Dakota Academy of Science, v. 72, p. 241-248.

Stiner, M.C., 2004, Comparative ecology and taphonomy of spotted hyenas, humans, and wolves in Pleistocene Italy: Revue de Paléobiologie, v. 23, p. 771-785.

Stinnesbeck, W., Frey, E., Rivas, L., Pérez, J.P., Cartes, M.L., Soto, C.S. and Lobos, P.Z., 2014, A Lower Cretaceous ichthyosaur graveyard in deep marine slope channel deposits at Torres del Paine National Park, southern Chile: Geological Society of America Bulletin, v. 126, p. 1317-1339.

Stirling, E. C., and Zietz, A. H. C., 1900, Fossil remains of Lake Callabona. II. *Genyornis newtoni*. A new genus and species of fossil struthious bird: Memoirs of the Royal Society of South Australia, v. 1, p. 41-80.

Stirton, R. A., 1959, Time, life and man. New York, Wiley, 558 p.

Stokes, W., 1942, Some field observations bearing on the origin of the Morrison gastroliths: Science, v. 95, p. 18-19.

Stokes, W., 1944, Morrison Formation and related deposits in and adjacent to the Colorado Plateau: Geological Society of America Bulletin, v. 55, p. 969-983.

Stokes, W., 1952, Lower Cretaceous in Colorado Plateau: Bulletin of the American Association of Petroleum Geologists, v. 36, p. 1766-1773.

Stokes, W. L., 1964. Fossilized stomach contents of a sauropod dinosaur: Science, 143, 576-577.

Stokes, W., 1987, Dinosaur gastroliths revisited: Journal of Paleontology, v. 61, p. 1242-1246.

Storch, G., 2001, Paleobiological implications of the Messel mammalian assemblage; *in* Gunnell, G.F., eds., Eocene biodiversity: unusual occurrences and rarely sampled habitats. New York, Kluwer Academic/Plenum, p. 215-235.

Storch, G. and Richter, G., 1992, Pangolins: Almost unchanged for 50 million years; *in* Schaal and Ziegler, W., eds., Messel: An insight into the history of life and of the Earth. Oxford, Clarendon Press, p. 201-207.

Storch, G. and Richter, G., 1994, Zur Paläobiologie der Messeler Igel: Natur und Museum, v. 124(3), p. 81-90.

Storrs, G. W., 1981, A review of occurrences of the Plesiosauria (Reptilia: Sauropterygia) in Texas with description of new material [M.S. thesis]: Austin, University of Texas, 226 p.

Storrs, G. W., 1993, Function and phylogeny in sauropterygian (Diapsida) evolution: American Journal of Science, v. 293, p. 63-90.

Storrs, G.W., 1995, A juvenile specimen of ?*Plesiosaurus* sp. from the Lias (Lower Jurassic, Pliensbachian) near Charmouth, Dorset, England: Proceedings of the Dorset Natural History and Archaeological Society, v. 116, p. p. 71-76.

Storrs, G. W., 1999, An examination of Plesiosauria (Diapsida: Sauropterygia) from the Niobrara Chalk (upper Cretaceous) of central North America: University of Kansas Paleontological Contributions (New Series), v. 11, 15 p.

Storrs, G.W., Oser, S.E. and Aull, M., 2013, Further analysis of a Late Jurassic dinosaur bone-bed from the Morrison Formation of Montana, USA, with a computed three-dimensional reconstruction: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 103, pp 443-458, doi:10.1017/S1755691013000248.

Stovall, J.W. and Strain, W.S., 1936, A hitherto undescribed coprolite from the White River badlands of South Dakota: Journal of Mammalogy, v. 17, p. 27-28.

Strickland, H., E. and Hooker, J., 1853, On the distribution and organic contents of the "Ludlow Bone Bed" in the Districts of Woolhope and May Hill with a note on the seed-like bodies found in it: Quarterly Journal of the Geological Society, v. 9, p. 8-12.

Stringer, G.L. and King, L., 2012, Late Eocene shark coprolites from the Yazoo Clay in northeastern Louisiana: New Mexico Museum of Natural History and Science, Bulletin 57, p. 275-309.

Strganac, C., Jacobs, L.L., Polcyn, M.J., Mateus, O., Myers, T.S., Salminen, J., May, S.R., Araújo, R., Ferguson, K.M., Gonçalves, A.O. and Morais, M.L., 2015, Geological setting and paleoecology of the Upper Cretaceous Bench 19 marine vertebrate bonebed at Bentiaba, Angola: Netherlands Journal of Geosciences, v. 94, p. 121-136.

Stuart, C. and Stuart, T., 2000, A field guide to the tracks and signs of Southern and East African Wildlife: Cape Town, Struick Nature (Random House Struick), 310 p.

Stubbs, T.L. and Benton, M.J., 2016, Ecomorphological diversifications of Mesozoic marine reptiles: The roles of ecological opportunity and extinction: Paleobiology, v. 42, p. 547-573.

Stuetzer, P. H., 1972, Morphologie, Taxonomie und Phylogenie der Ionoscopidae (Actinopterygii, Pisces) [Ph.D. dissertation]: München, Ludwig-Maximilians Universität, 141 p.

Su, D.F. and Harrison, T., 2008, Ecological implications of the relative rarity of fossil hominins at Laetoli: Journal of Human Evolution, v. 55, p. 672-681.

Suazo, T.L., Cantrell, A.K., Lucas, S.G., Spielmann, J.A. and Hunt, A.P., 2012, Coprolites across the Cretaceous/Tertiary boundary, San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 57, p. 263-274.

Sues, H.D., Olsen, P.E., Carter, J.G. and Scott, D.M., 2003, A new crocodylomorph archosaur from the Upper Triassic of North Carolina: Journal of Vertebrate Paleontology, v. 23, p. 329-343.

Sulimski, A., 1964, Pliocene Lagomorpha and Rodentia of Weze 1 (bone breccia): Acta Palaeontologica Polonica, v. 9, p. 149-261.

Sullivan, R.M., 1987, A reassessment of reptilian diversity across the Cretaceous-Tertiary boundary: Contributions in Science, Natural History Museum of Los Angeles County, v. 391, p. 1-26.

Sullivan, R.M, 2000, *Prenocephale edmontonensis* (Brown and Schlaikjer) new comb. and *P. brevis* (Lambe) new comb. (Dinosauria: Ornithischia: Pachycephalosauria) from the Upper Cretaceous of North America: New Mexico Museum of Natural History and Science, Bulletin 17, p. 177-190.

Sullivan, R.M. and Jasinski, S.E., 2012, Coprolites from the Upper Cretaceous Fruitland, Kirtland and Ojo Alamo formations, San Juan Basin, New Mexico: New Mexico Museum of Natural History and Science, Bulletin 57, p. 255-262.

Sumner, D., 1991, Palaeobiology, taphonomy and diagenesis of a lower Carboniferous fish fauna [Ph.D. dissertation]: St Andrews, University of St. Andrews, 165 p.

Sumner, D., 1994, Coprolites from the Visean of East Kirkton, West Lothian, Scotland: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 84, p. 413-416.

Sundell, K.A., 1999, Taphonomy of a multiple *Poebrotherium* kill site: An *Archeotherium* meat cache: Journal of Vertebrate Paleontology, v. 19 (supplement to no. 3), p. 79A.

Sutcliffe, A.J., 1970, Spotted hyaena: Crusher, gnawer, digester and collector of bones: Nature, v. 227, p. 1110–1113.

Sutcliffe, A. J., 1973, Similarity of bones and antlers gnawed by deer to human artifacts: Nature, v. 246, p. 428-430.

Sweetman, S. C. and Underwood, C. J., 2006, A neoselachian shark from the non-marine Wessex Formation (Wealden Group: Early Cretaceous, Barremian) of the Isle of Wight, southern England: Palaeontology, v. 49, p. 457-465.

Swift, A. and Duffin, C.J., 1999, Trace fossils; *in* Swift, A. and Martill, D.M., eds., Fossils of the Rhaetian Penarth Group: Palaeontological Association, Field Guides to Fossils, no. 9, p. 239-250.

Swift, C.C. and Barnes, L.G., 1996, Stomach contents of *Basilosaurus cetoides*: Implications for the evolution of cetacean feeding behavior, and the evidence for vertebrate fauna of epicontinental Eocene seas: Paleontological Society Special Publications, v. 8, p. 380.

Syed, R. and Sengupta, S., 2019, First record of parrotfish bite mark on larger Foraminifera from the Middle Eocene of Kutch, Gujarat, India: Current Science, v. 116, p. 363-365.

Szczygielski, T. and Surmik, D., 2020, A tough turtle – healed damage on a *Mongolemys* shell from the Late Cretaceous of Mongolia: Society of Vertebrate Paleontology, 80th Annual Meeting Virtual 2020, October 12-16 2020, www.vertpaleo.org Conference Program, unnumbered page.

Szrek, P., Salwa, S., Niedźwiedzki, G., Dec, M., Ahlberg, P.E. and Uchman, A., 2016, A glimpse of a fish face—an exceptional fish feeding trace fossil from the Lower Devonian of the Holy Cross Mountains, Poland: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 454, p. 113-124.

Taggart, R.E. and Cross, A.T., 1997, The relationship between land plant diversity and productivity and patterns of dinosaur herbivory; *in* Wolberg, D.L., Stump, E. and Rosenberg, G., eds., Dinofest International: Proceedings of a symposium held at Arizona State University. Philadelphia, National Academy of Sciences, p. 403-416.

Takakuwa, Y., 2014, A dense occurrence of teeth of fossil "mako" shark ("*Isurus*" *hastalis*: Chondrichthyes, Lamniformes), associated with a balaenopterid-whale skeleton of the Late Miocene Pisco Formation, Peru, South America: Bulletin of the Gunma Museum of Natural History, v. 18, p. 77–86.

Takeda, Y. and Tanabe, K., 2014, Low durophagous predation on Toarcian (Early Jurassic) ammonoids in the northwestern Panthalassa shelf basin: Acta Palaeontologica Polonica, v. 60, p. 781-794.

Tanke, D. and Currie, P.J., 1998, Head-biting behavior in theropod dinosaurs: Paleopathological evidence: Gaia, v. 15, p. 167-184.

Tanke, D. H., Rothschild, B. M., 2002, Dinosores: An annotated bibliography of dinosaur paleopathology and related topics: New Mexico Museum of Natural History and Science, Bulletin 20, 96 p.

Tanke, D.H. and Rothschild, B.M., 2014, Paleopathology in Late Cretaceous Hadrosauridae from Alberta, Canada with comments on a putative *Tyrannosaurus* bite injury on an *Edmontosaurus* tail; *in* Eberth, D. and Evans, D., eds., Hadrosaurs. Bloomington, Indiana University Press, p. 540-571.

Tanke, D.H., Currie, P.J. and Larson, P.L., 1992, Once bitten twice shy: Predator tooth marks on oreodont (Mammalia: Merycoidodontoidae) skulls, middle ND upper Oligocene, Brule Formation of South Dakota and Nebraska, USA: Journal of Vertebrate Paleontology, v. 12 (supplement to no. 3), p. 54-55A.

Tapanila, L., Roberts, E.M., Bouaré, M.L., Sissoko, F. and O'Leary, M. A., 2004, Bivalve borings in phosphatic coprolites and bone, Cretaceous-Paleogene, northeastern Mali: Palaios, v.19, p. 565-573.

Tapanila, L., Roberts, E.M., Bouaré, M.L., Sissoko, F. and O'Leary, M.A., 2008, Phosphate taphonomy of bone and coprolite conglomerates: A case study from the Eocene of Mali, NW Africa: Palaios, v. 23, p.139-152.

Taquet, P. and Russell, D.A. 1999, A massively-constructed iguanodont from Gadoufaoua, Lower Cretaceous of Niger: Annales de Palaeontologie, v. 85, p. 5-96.

Tarlo, L. B., 1959, *Pliosaurus brachyspondylus* Owen from the Kimmeridge Clay: Palaeontology, v. 1, p. 83–291.

Tarrant, P.R., 1991, The ostracoderm *Phialaspis* from the Lower Devonian of the Welsh Borderland and South Wales. Palaeontology, 34(2), p. 399-438.

Tasch, P. 1973, Paleobiology of the invertebrates. New York, John Wiley and Sons, Inc. 946 p.

Tasnadi-Kubacska, A., 1962, Paläopathologie. Jena, Gustav Fischer Verlag, 269 p.

Tauber, A.A., Palacios, M.E. and Cardozo, S.A., 2007, Coprólitos da Formación Santa Cruz (Mioceno Inferior-Medio), Patagônia, Republica Argentina: Congresso Argentino De Paleontologia y Bioestratigrafia, 9, Resúmenes, p. 294.

Taylor, M.A., 1987, How tetrapods feed in water: A functional analysis by paradigm: Zoological Journal of the Linnean Society, v. 91, p. 171–195.

Taylor, M.A., 1992, Taxonomy and taphonomy of *Rhomaleosaurus zetlandicus* (Plesiosauria: Reptilia) from the Toarcian (Lower Jurassic) of the Yorkshire coast: Proceedings of the Yorkshire Geological Society, v. 49, p. 49-55.

Taylor, M.A., 1993, Stomach stones for feeding or buoyancy? The occurrence and function of gastroliths in marine tetrapods: Philosophical Transactions Royal Society London, Series B, v. 341, p. 163-175.

Taylor, M.A., 1994, Stone, bone or blubber? Buoyancy control strategies in aquatic tetrapods; *in* Maddock, L., Bone, Q. and Rayner, J. M. V., eds., Mechanics and physiology of animal swimming. Cambridge, Cambridge University Press, p. 151-161.

Taylor, M.A., Norman, D.B. and Cruickshank, A.R.I., 1993, Remains of an ornithischian dinosaur in a pliosaur from the Kimmeridgian of England: Palæontology, v.36 p. 357–360.

Teaford, M.F. and Walker, A., 1984, Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*: American Journal of Physical Anthropology, v. 64, p. 191-200.

Tedford, R.H. and Harington, C.R., 2003, An Arctic mammal fauna from the early Pliocene of North America: Nature, v. 425, p. 388-390.

Terry, R.C., 2007, Inferring predator identity from skeletal damage of small-mammal prey remains: Evolutionary Ecology Research, v. 9, p. 199-219.

Terry, R.C., 2010, On raptors and rodents: Testing the ecological fidelity and spatiotemporal resolution of cave death-assemblages: Paleobiology, v. 36, p. 137 –160.

Thies, D., 1985, Bißspuren an Seeigel-Gehäusen der Gattung Echinocorys Leske, 1778 aus dem Maastrichtium von Hemmoor (NW-Deutschland): Mitteilungen des Geologisch-Paläontologischen Institutes der Universität Hamburg, v. 59, p.71-82.

Thies, D. and Hauff, R.B., 2012, A Speiballen from the Lower Jurassic Posidonia Shale of South Germany: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 267, p. 117–124.

Thies, D. and Rief, W.-E., 1985, Phylogeny and evolutionary ecology of Mesozoic Neoselachii: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 169, p. 333-361.

Thies, D., Stevens, K. and Stumpf, S., 2019, Stomach contents of the Early Jurassic fish †*Lepidotes* Agassiz, 1832 (Actinopterygii, Lepisosteiformes) and their palaeoecological implications: Historical Biology, doi.org/10.1080/08912963.2019.1665040.

Thomas, D.A. and Farlow, J.O., 1997, Tracking a dinosaur attack: Scientific American, v. 277, p. 74-79.

Thompson, D.W., 1917, On growth and form. Cambridge, Cambridge University Press, 1116 p.

Thompson, W.A., Martin, J.E. and Requero, M., 2007, Comparison of gastroliths within plesiosaurs (Elasmosauridae) from the Late Cretaceous marine deposits of Vega Island, Antarctic Peninsula and the Missouri River area, South Dakota: Geological Society of America Special Paper, v. 427, p. 146-153.

Thorson, R.M. and Hamilton, T.D., 1977, Geology of Dry Creek site: Quaternary Research, v. 7, p. 149-176.

Thouzeau, C., Peters, G., Le Bohec, C. and Le Maho, Y., 2004, Adjustments of gastric pH, motility and temperature during long-term preservation of stomach contents in free-ranging incubating king penguins: Journal of Experimental Biology, v. 207, p. 2715–2724.

Thulborn, R.A., 1991, Morphology, preservation and palaeobiological significance of dinosaur coprolites: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 83, p. 341-366.

Thulborn, R.A., 2013, Lark Quarry revisited: A critique of methods used to identify a large dinosaurian track-maker in the Winton Formation (Albian–Cenomanian), western Queensland, Australia: Alcheringa, v. 37, p. 312-330.

Thulborn, T., 2017, Behaviour of dinosaurian track-makers in the Winton Formation (Cretaceous, Albian–Cenomanian) at Lark Quarry, western Queensland, Australia: Running or swimming?: Ichnos, v. 24, p. 1-18.

Thulborn, T. and Turner, S., 1993, An elasmosaur bitten by a pliosaur: Modern Geology, v. 18, p. 489-501.

Thulborn, R.A. and Wade, M., 1979, Dinosaur stampede in the Cretaceous of Queensland: Lethaia, v. 12, p. 275-279.

Thulborn, R.A. and Wade, M., 1984, Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland: Memoirs of the Queensland Museum, v. 21, p. 413-517.

Tichy, G. and Urbanek, E., 2004, Biss-Spuren eines Sauriers an *Pinacoceras parma* Mojsisovics, ein Ammonit der Halleiner Obetrias: GeoAlp, v. 1, p. 87-90.

Tietze, E., Barberena, R. and Beltrame, M.O., 2019, Parasite assemblages from feline coprolites through the Pleistocene-Holocene transition in Patagonia: Cueva Huenul 1 Archaeological Site (Argentina): Environmental Archaeology, v. p. 1-11, doi: 10.1080/14614103.2019.1689893.

Tischlinger, H., 2001, Bemerkungen zur Insekten Taphonomie der Solnhofer Plattenkalke: Archaeopteryx, v. 19, p. 29-44.

Tobien, H., 1980, Ein anthracotherioider Paahufer (Artiodactlyla, Mammalia) aus dem Eozän von Messel bei Darmstadt (Hessen): Geologisches Jahrbuch Hessen, v. 108, p. 11-22.

Tobler, M.W., Carrillo-Percastegui, S.E. and Powell, G., 2009, Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru: Journal of Tropical Ecology, v. 25, p. 261-270.

Tolmacheva, T. Y., 1996, New conodont clusters from the Lower Ordovician of central Kazakhstan; *in* Dzik, J., ed., Sixth European Conodont Symposium, Abstracts. Warszawa, Instytut Paleobiologii PAN, p. 57.

Tolmacheva, T.Y. and Purnell, M.A., 2002, Apparatus composition, growth, and survivorship of the Lower Ordovician conodont *Paracordylodus gracilis* Lindström, 1955: Palaeontology, v. 45, p. 209-228.

Tomassini, R.L. and Montalvo, C.I., 2010, Coprolitos en la Formación Monte Hermoso (Mioceno tardío-Plioceno temprano), Farola Monte Hermoso, Buenos Aires, Argentina: Ameghiniana, v. 47, p. 111-115.

Tomassini, R.L. and Montalvo, C.I., 2013, Taphonomic modes on fluvial deposits of the Monte Hermoso Formation (early Pliocene), Buenos Aires Province, Argentina: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 369, p. 282-294.

Tomassini, R.L., Kaufmann, C.A., Frontini, R. and Vecchi, R.J., 2019, Modern guanaco (*Lama guanicoe*, Camelidae) bezoars: An approach towards identification in the fossil record: International Journal of Paleopathology, v. 26, p. 111-121.

Tomassini, R.L., Montalvo, C.I., Bargo, M.S., Vizcaíno, S.F. and Cuitiño, J.I., 2019, *Sparassodonta* (Metatheria) coprolites from the early-mid Miocene (Santacrucian age) of Patagonia (Argentina) with evidence of exploitation by coprophagous insects: Palaios, v. 34, p. 639-651.

Toots, H. and Voorhies, M.R., 1965, Strontium in fossil bones and the reconstruction of food chain: Science, v. 149, p. 854–855.

Tournal, P., 1833, Considérations générales sur le phénomène des cavernes à ossemens: Annales de Chimie et de Physique, v. 52, p. 161-181.

Tournepiche, J.F. and Couture, C., 1999, The hyena den of Rochelot Cave (Charente, France): Monographien des Römisch-Germanischen Zentralmuseums, v. 42, p. 89–101.

Traquair, R.H., 1879, Evidence as to the predaceous habits of the larger Palaeoniscidae: Proceedings of the Royal Physical Society of Edinburgh, v. 5, p. 128-130.

Trevor-Deutsch, B., and. Bryant, V.M, Jr., 1978, Analysis of suspected human coprolites from Terra Amata, Nice, France: Journal of Archaeological Science, v. 5, p. 387-90.

Trewin, N.H., 1986, Palaeoecology and sedimentology of the Achanarras fishbed of the Middle Old Red Sandstone, Scotland: Transactions of the Royal Society of Edinburgh: Earth Sciences, v. 77, p. 21-46.

Trewin, N. H., 2008, Fossils alive! Or new walks in an old field. Edinburgh, Dunedin Academic Press, 211 p.

Trewin, N.H., and Davidson, R. G., 1996, An Early Devonian lake and its associated biota in the Midland Valley of Scotland: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 86, p. 233-246.

Tripp, M., Wiemann, J., Hope, J.M., Brocks, J.J., Mayer, P., Lidgard, S. and Grice, K., 2021, Molecular biomarkers in coprolites illuminate dietary interactions in the Carboniferous Mazon Creek ecosystem: IMOG 2021 (European Association of Geoscientists and Engineers) Conference Proceedings, p. 1-2, doi; https://doi.org/10.3997/2214-4609.202134169.

Tryon, C., 2002, Exotic minerals or ostrich gastroliths? An alternative explanation for some evidence of hominin non-utilitarian behavior at Wonderwerk Cave, South Africa: Journal of Taphonomy, v. 8, p. 235-242.

Tschanz, K., 1989, *Lariosaurus buzzii* n. sp. from the Middle Triassic of Monte San Giorgio (Switzerland) with comments on the classification of nothosaurs: Palaeontographica Abteilung A, Paläozoologie, Stratigraphie, v. 208, p. 153-179.

Tseng, Z.J. and Wang, X., 2010, Cranial functional morphology of fossil dogs and adaptation for durophagy in *Borophagus* and *Epicyon* (Carnivora, Mammalia): Journal of Morphology, v. 271, p.1386-1398.

Tseng, Z.J. and Wang, X., 2011, Do convergent ecomorphs evolve through convergent morphological pathways? Cranial shape evolution in fossil hyaenids and borophagine canids (Carnivora, Mammalia): Paleobiology, v, 37, p. 470-489.

Tsujita, C.J. and Westermann, G.E., 1998, Ammonoid habitats and habits in the Western Interior Seaway: A case study from the Upper Cretaceous Bearpaw Formation of southern Alberta, Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 144, p. 135-160.

Tsujita C.J. and Westermann, G.E., 2001, Were limpets or mosasaurs responsible for the perforations in the ammonite *Placenticeras*?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 169, p. 245-270.

Tucker, E.A. and Tucker, M. E., 2018, Crayfish gastroliths: Geology Today, v. 35, p. 26-28.

Tumanova, T., Gallagher, W.B., Dodson, P. and Axel, L., 1998, Computerized tomography of Asian ankylosaur skulls: Damage and repair in a *Tarchia* skull; *in* Wolberg, D.L., Gittis, K.., Miller, S., Carey L. and. Raynor A., eds., The Dinofest Symposium. Philadelphia, Academy of Natural Sciences, p. 60-61.

Turner, S., 1999, The importance of coprolite events: Ichthyolith Issues, v. 20, p. 37-38.

Turner, S., Burrow, C.J., Schultze, H.P., Blieck, A., Reif, W.E., Rexroad, C.B., Bultynck, P. and Nowlan, G.S., 2010, False teeth: Conodont-vertebrate phylogenetic relationships revisited: Geodiversitas, v. 32, p. 545-594.

Tuuling, T., 2015, A specimen of *Psammolepis* in the Gauja Formation (Estonia)[B.S. thesis]: Tartu, University of Tartu, 31 p.

Tweet, J.S., Chin, K. and Ekdale, A.A., 2016, Trace fossils of possible parasites inside the gut contents of a hadrosaurid dinosaur, Upper Cretaceous Judith River Formation, Montana: Journal of Paleontology, v. 90, p. 279-287

Tweet, J. S., Santucci, V. L. and Hunt, A. P., 2012, An inventory of packrat (*Neotoma* spp.) middens in National Park Service areas: New Mexico Museum of Natural History and Science, Bulletin 57, p. 355-368.

Tweet, J.S., Chin, K., Murphy, N.L., and Braman, D.R., 2008, Probable gut contents within a specimen of *Brachylophosaurus canadensis* (Dinosauria: Hadrosauridae) from the Upper Cretaceous Judith River Formation of Montana: Palaios, v. 28, p. 624–635.

Tyborowski, D., 2016, A new ophthalmosaurid ichthyosaur from the Late Jurassic of Owadów-Brzezinki Quarry, Poland: Acta Palaeontologica Polonica, v. 61, p. 791-804.

Uchman, A., Torres, P., Johnson, M.E., Berning, B., Ramalho, R.S., Rebelo, A.C., Melo, C.S., Baptista, L., Madeira, P., Cordeiro, R. and Avila, S.P., 2018, Feeding traces of recent ray fish and occurrences of the trace fossil *Piscichnus waitemata* from the Pliocene of Santa Maria Island, Azores (northeast Atlantic): Palaios, v. 33, p. 361-375.

Uhen, M.D., 2004, Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): An archaeocete from the middle to late Eocene of Egypt: University of Michigan Papers on Paleontology, v. 34, p. 1–222.

Ukraintseva, V.V., 1981, Vegetation of warm late Pleistocene intervals and the extinction of some large herbivorous mammals: Polar Geography and Geology, v. 5, p. 189-203.

Ukraintseva, V.V., 1993, Vegetation cover and environment of the Mammoth Epoch in Siberia; *in* Agenbroad, L.D., Mead, J.I. and Hevly, R.H., eds. Rapid City, The Mammoth Site of Hot Springs, 309 p.

Ullmann, P.V., Shaw, A., Nellermoe, R. and Lacovara, K.J., 2017, Taphonomy of the Standing Rock hadrosaur site, Corson County, South Dakota: Palaios, v. 32, p. 779-796.

Umamaheswaran, R., Prasad, G.V.R., Rudra, A. and Dutta, S., 2019, Biomarker signatures in Triassic coprolites: Palaios, v. 34, p. 458-467.

Underwood, C.J., 2006, Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous: Paleobiology, v. 32, p. 215-235.

Underwood, C.J. and Cumbaa, S.L., 2010, Chondrichthyans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada: Palaeontology, v. 53, p. 903-944.

Ungar, P.S., Scott, J.R. and Steininger, C.M., 2016, Dental microwear differences between eastern and southern African fossil bovids and hominins: South African Journal of Science, v. 112, p.1-5.

Unterrassner, L., 2009, The anterior appendicular morphology and the stomach content of the first theropod skeleton (Saurischia, Dinosauria) of Switzerland (Late Triassic; Frick, Canton Aargau) [M.S. thesis]: Zurich, University of Zurich, 123 p.

Upchurch, P. and Barrett, P. M., 2020, The evolution of sauropod feeding mechanisms; *in* Sues, H.-D., ed., Evolution of herbivory in terrestrial vertebrates: Perspectives from the fossil record. Cambridge, Cambridge University Press, p. 79-122.

Upeniece, I., 2001, The unique fossil assemblage from the Lode quarry (Upper Devonian, Latvia): Mitteilungen Museum Naturkunde Berlin Geowissenschaften Reihe, 4, p. 101-119.

Upeniece, I., 2011, Palaeoecology and juvenile individuals of the Devonian placoderm and acanthodian fishes from Lode site, Latvia [Ph.D. dissertation]: Disertations Geologicae Universitas Latviensis, v. 21, p. 1-221.

Uriona, T. J., Lyon, M. and Farmer, C. G., 2018, Lithophagy prolongs voluntary dives in American alligators (*Alligator mississippiensis*): Integrative Organismal Biology, 1-4, doi: 10.1093/iob/oby008.

Urlichs, M., Wild, R. and Ziegler, N., 1994, Der Posidonien-Schiefer des unteren Juras und seine Fossilien: Stuttgarter Beiträge zur Naturkunde Serie C, v. 36, p. 1-95.

Vajda, V., Fernández, M.D.P., Villanueva-Amadoz, U., Lehsten, V. and Alcalá, L., 2016, Dietary and environmental implications of Early Cretaceous predatory dinosaur coprolites from Teruel, Spain: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 464, p. 134-142.

Vallon, L. R., 2012, Digestichnia (Vialov, 1972) - an almost forgotten ethological class for trace fossils: New Mexico Museum of Natural History and Science, Bulletin 57, p. 131-135.

Vallon, L. H., Rindsberg, A. K. and Martin, A. J., 2015, The use of the terms trace, mark and structure: Annales Societatis Geologorum Poloniae, v. 85, p. 527–528.

Van Geel, B., Pals, J.P. Van Reenen, G. and Mol. D., 2004, Plant remains in the Yukagir mammoth dung and an environmental reconstruction; *in* The Yukagir Mammoth: Outcome of the first stage of research work. Proceedings of International Scientific Practical Conference. Yakutsk, SB RAS Publishing House, p. 58–59.

Van Geel, B., Guthrie, R.D. Altmann, J.G. Broekens, P., Bull, I. D., Gill, F. L., Jansen, B., Nieman, A. M. and Gravendeel, B., 2011, Mycological evidence of coprophagy from the feces of an Alaskan Late Glacial mammoth: Quaternary Science Reviews, v. 30, p. 2289–2303.

Van Geel, B., Aptroot, A., Baittinger, C., Birks, H.H., Bull, I.D., Cross, H.B., Evershed, R.P., Gravendeel, B., Kompanje, E.J., Kuperus, P. and Mol, D., 2008, The ecological implications of a Yakutian mammoth's last meal: Quaternary Research, v. 69, p. 361-376.

Van Geel, B., Protopopov, A., Bull, I., Duijm, E., Gill, F., Lammers, Y., Nieman, A., Rudaya, N., Trofimova, S., Tikhonov, A.N. and Vos, R., 2014, Multiproxy diet analysis of the last meal of an early Holocene Yakutian bison: Journal of Quaternary Science, v. 29, p. 261-268

Van Nest, J., 2002, The good earthworm: How natural processes preserve upland Archaic archaeological sites of western Illinois, U. S. A.: Geoarchaeology: An International Journal, v. 17, p. 53-90.

Vannier, J. and Chen, J., 2005, Early Cambrian food chain: New evidence from fossil aggregates in the Maotianshan Shale biota: Palaios, v. 20, p. 3–26.

Van Zyl, W., Badenhorst, S. and Brink, J. S., 2016, Pleistocene Bovidae from X Cave on Bolt's Farm in the Cradle of Humankind in South Africa: Annals of the Ditsong National Museum of Natural History, v. 6, p. 39–73.

Varricchio, D.J., 1995a, Jack's birthday site, a diverse dinosaur bonebed from the Cretaceous Two Medicine Formation of Montana [Ph.D. dissertation]: Bozeman, Montana State University, 105 p.

Varricchio, D.J., 1995b, Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 114, p. 297–323.

Varricchio, D.J., 2001, Gut contents from a Cretaceous tyrannosaurid: Implications for theropod dinosaur digestive tracts: Journal of Paleontology, v. 75, p. 401-406.

Varrichio, D.J., Sereno, P.C., Zhao, X., Tan, L., Wilson, J.A. and Lyon, G.H., 2008, Mud-trapped herd captures evidence of distinctive dinosaur sociality: Acta Palaeontologica Polonica, v. 53, p. 567-578.

Vasconcellos, F.M., Morato, L., Marinho, T.S. and Carvalho, I. S., 2008, Occurrence of gastroliths in *Baurusuchus* (Baurusuchidae, Meseucrocodylia) from Adamantina Formation, Bauru basin: Boletin de Resumos do VI Simpósio Brasileiro de Paleontologia de Vertebrados, Ribeirão Preto, p. 200-202.

Vasileiadou, K., Hooker, J.J. and Collinson, M.E., 2007, Taphonomic evidence of a Paleogene mammalian predator–prey interaction: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 243, p. 1–22.

Vasileiadou, K., Hooker, J.J. and Collinson, M.E., 2009, Paleocommunity reconstruction and accumulation of micromammalian remains (late Eocene, southern England): Palaios, v. 24, p. 553-567.

Vasse, D. and Hua, S., 1998, Diversité des crocodiliens du Crétace Supérieur et du Paléogene: Influences et limites de la crise Maastrichtien-Paléocéne et des "Terminal Eocene Events:" Oryctos, v. 1, p. 65-77.

Vega-Dias, C. and Schultz, C.L., 2007, Evidence of archosauriform feeding on dicynodonts in the Late Triassic of southern Brazil: Paleobios, v. 27, p. 62–67.

Venczel, M., Vasile, Ș. and Csiki-Sava, Z., 2015, A Late Cretaceous madtsoiid snake from Romania associated with a megaloolithid egg nest – paleoecological inferences: Cretaceous Research, v. 55, p. 152-163.

Verde, M. and Ubilla, M., 2002, Carnivore mammal coprolites from the Sopas Formation (Upper Pleistocene, Lujanian Stage) of Uruguay: Ichnos, v. 9, p. 77-80.

Vermeij, G.J. 1977, The Mesozoic marine revolution; evidence from snails, predators and grazers: Paleobiology, v. 3, p. 245–258.

Verzi, D.H., Montalvo, C.I. and Deschamps, C.M., 2008, Biostratigraphy and biochronology of the late Miocene of central Argentina: Evidence from rodents and taphonomy: Geobios, v. 41, p. 145-155.

Vijaya, Prasad, G.V.R. and Singh, K., 2009, Late Triassic palynoflora from the Pranhita–Godavari Valley, India: Evidence from vertebrate coprolites: Alcheringa, v. 33, p. 91-111.

Vincent, P., Allemand, R., Taylor, P.D., Suan, G. and Maxwell, E.E., 2017, New insights on the systematics, palaeoecology and palaeobiology of a plesiosaurian with soft tissue preservation from the Toarcian of Holzmaden, Germany: The Science of Nature, v. 104:51, doi:10.1007/s00114-017- 1472-6.

Viohl, G., 1983, Forschungsprojekt "Solnhofer Plattenkalke:" Archaeopteryx, v. 1, p. 3-23.

Viohl, G., 1990, Piscivorous fishes of the Solnhofen lithographic limestone; *in* Boucot, A. J., 1990, ed., Evolutionary paleobiology of behavior and coevolution. Amsterdam, Elsevier, p. 285-303.

Viohl, G., 2015, Die lithographischen Plattenkalke im engeren Sinne; *in* Arratia, G., Schultze, H.P., Tischlinger, H. and Viohl, G., eds., Solnhofen - ein Fenster in die Jurazeit. München, Verlag Dr. F. Pfeil, p. 78-100.

Vogeltanz, R., 1965, Austrocknungsstruckturen bei Koprolithen: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 3, p. 362-371.

Vogeltanz, R., 1967, Erganzends Mitteilung über Koprolithen Untersuchungen aus dem Unteroligozän von Nebraska: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 7, p. 188-191.

Voigt, E., 1934, Die Fische aus der mitteleozänen Braunkohle des geiseltales mit besonderer Berücksichtigung der ehaltenen eichteile: Nova Acta Leopoldina, Halle, v. 2, p. 21-146.

von Koenigswald, W., Richter, G. and Storch, G., 1981, Nachweis von Hornshuppen bei *Eomanis waldi* aus der "Grube Messel" bei Darmstadt (Mammalia, Pholidota): Senckenbergeana Lethaea, v. 61, p. 291-298.

von Koenigswald, W., Storch, G. and Richter, G., 1992, Primitive insectivores, extraordinary hedgehogs, and long fingers; *in* Schaal, S. and Ziegler, W., eds., Messel: An insight into the history of life and of the Earth. London, Clarendon Press, p. 161-177.

von Koenigswald, W., Gunnell, G., Lehmann, T., Rose, K. D. and Ruf, I., 2018, Four archaic yet highly specialized mammals; *in* Smith, K.T., Schaal, S.F.K. and Habersetzer, J., eds., Messel – Ancient greenhouse ecosystem. Frankfurt am Main, Senckenberg Gesellschaft für Naturforschung, p. 223-233.

von Münster, R. G. 1831, *in*: Goldfuss, A., ed., Petrefacta Germaniae. Leipzig, Arnz and Co., 252 p.

von Münster, G., 1842, Beitrag zur Kenntnis einiger neuen seltenen Versteinerungen aus den lithographischen Schiefern in Baiern: Neues Jahrbuch für Mineralogie, Geologie und Pälaontologie Monatshefte, v. 1842, p. 35-46.

von Wurstemberger, A.R., 1876, Über lias epsilon: Schweizerbart. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, v. 32, p. 192-233.

Voorhies, M.R., 1980, Pompei of prehistoric animals in Nebraska: National Geographic, v. 159, p. 66-75.

Voss, M., Antar, M.S.M., Zalmout, I.S. and Gingerich, P.D., 2019, Stomach contents of the archaeocete *Basilosaurus isis*: Apex predator in oceans of the late Eocene: PLoS ONE, v. 14(1): e0209021, doi.org/10.1371/journal. pone.0209021.

Vremir, M., Kellner, A.W., Naish, D. and Dyke, G.J. 2013, A new azhdarchid pterosaur from the Late Cretaceous of the Transylvanian Basin, Romania: Implications for azhdarchid diversity and distribution: PLoS ONE, v. 8(1): e54268, doi.org/10.1371/journal. pone.0054268.

Vullo, R., 2011, Direct evidence of hybodont shark predation on Late Jurassic ammonites: Naturwissenschaften, v. 98, p. 545-549.

Wagner, A., 1860, Zur Charakeristick de Gattungen *Sauropsis* und *Pachycormus* nebst ihren Verwandten: Gelehrte Anzeigen der Königlich Bayerischen Akademie eder Wissenschaften Gelehrt, v. 1, p. 209-227.

Wagner, T. and Boyce, A.J., 2006, Pyrite metamorphism in the Devonian Hunsrück Slate of Germany: Insights from laser microprobe sulfur isotope analysis and thermodynamic modeling: American Journal of Science, v. 306, p. 525-552.

Wahl, A.M., Martin, A.J. and Hasiotis, S.T., 1998, Vertebrate coprolites and coprophagy traces, Chinle Formation (Late Triassic), Petrified Forest National Park; *in* Santucci, V.L. and McClelland, L., eds., National Park Service Paleontological Research. National Park Service Geological Resources Division Technical Report NPS/ NRGRD/GRDTR-98/01, p. 144-148.

Wahl, W., 1998, Plesiosaur gastric contents from the upper Redwater Shale (lower Oxfordian) of the Sundance Formation (Jurassic) of Wyoming: Journal of Vertebrate Paleontology, v. 18 (supplement to no. 3), p. 84A.

Wahl, W.R., 2006, A juvenile plesiosaur (Reptilia: Sauropterygia) assemblage from the Sundance Formation (Jurassic), Natrona County, Wyoming: Paludicola, v. 5, p. 255-261.

Wahl, W.R., 2008, Bite marks on an ammonite; re-evaluation of the limpet home marks versus mosasaur predation and preservation of an aborted attack; *in* Everhart, M.J., ed., Proceedings of the Second Mosasaur Meeting, p. 1-6.

Wahl W.R., 2012, Gastric contents of a plesiosaur from the Sundance Formation of Hot Springs County, Wyoming, and implications for the paleobiology of cryptocleidid plesiosaurs: Paludicola, v. 9, p. 32–39.

Waldman, M. and Hopkins, W.S., Jr., 1970, Coprolites from the Upper Cretaceous of Alberta, Canada, with a description of their microflora: Canadian Journal of Earth Sciences, v. 7, p. 1295-1303.

Walkden, G. M., Fraser, N. C., Muir, J., 1987, A new specimen of *Steneosaurus* (Mesosuchia, Crocodilia) from the Toarcian of the Yorkshire Coast: Proceedings of the Yorkshire Geological Society, v. 46, p. 279-287.

Walker, A., Hoeck, H.N. and Perez, L., 1978, Microwear of mammalian teeth as an indicator of diet: Science, v. 201, p. 908-910.

Walker, E.P., 1968, Mammals of the World (Second Edition). Baltimore, Johns Hopkins University Press, 1500 p.

Walker, M.V., 2006, The impossible fossil – revisited: Kansas Academy of Science, Transactions, v. 109, p. 87-96.

Walker, S. E. and Brett, C. E., 2002, Post-Paleozoic patterns in marine predation: Was there a Mesozoic and Cenozoic marine predatory revolution?: Paleontological Society Papers, v. 8, p. 119-193.

Walmsley, C.W., Smits, P.D., Quayle, M.R., McCurry, M.R., Richards, H.S., Oldfield, C.C., Wroe, S., Clausen, P.D. and McHenry, C.R., 2013, Why the long face? The mechanics of mandibular symphysis proportions in crocodiles: PLoS ONE, v. 8(1): e53873, doi:10.1371/journal.pone.0053873.

Walsh, S.A. and Hume, J.P., 2001, A new Neogene marine avian assemblage from north-central Chile: Journal of Vertebrate Paleontology, v. 21, p. 484-491.

Walther, J. and Weigelt, J., 1932, Die eozäne Lebewelt in der Braunkohle des Geiseltals; *in* Abderhalden, E., ed., Die Wirbeltierfundstellen im Geiseltal: Nova Acta Leopoldina, N. F., v. 1, p. 1-27.

Walton, A. H., 1990, Owl pellets and the fossil record; *in* Boucot, A. J., 1990, ed., Evolutionary paleobiology of behavior and coevolution. Amsterdam, Elsevier, p. 233-241.

Wang, M. and Zhou, Z., 2016, A new adult specimen of the basalmost ornithuromorph bird *Archaeorhynchus spatula* (Aves: Ornithuromorpha) and its implications for early avian ontogeny: Journal of Systematic Paleontology, v. 15, p. 1-18.

Wang, M., Zhou, Z. and Sullivan, C., 2016, A fish-eating enantiornithine bird from the Early Cretaceous of China provides evidence of modern avian digestive features: Current Biology, v. 26, p. 1170-1176.

Wang, X., Miao, D. and Zhang, Y., 2005, Cannibalism in a semi-aquatic reptile from the Early Cretaceous of China: China Science Bulletin, v. 50, p. 281-283.

Wang, X.-R., Ji, Q., Teng, F.-F. and Jin, K.-M., 2013, A new species of *Yanornis* (Aves: Ornithurae) from the Lower Cretaceous strata of Yixian, Liaoning Province: Geological Bulletin of China, v. 32, p. 601-606.

Wang, X., Kellner, A.W., Zhou, Z. and de Almeida Campos, D., 2008. Discovery of a rare arboreal forest-dwelling flying reptile (Pterosauria, Pterodactyloidea) from China: Proceedings of the National Academy of Sciences, v. 105, p. 1983-1987.

Wang, X., White, S.C., Balisi, M., Biewer, J., Sankey, J., Garber, D. and Tseng, Z.J., 2018, First bone-cracking dog coprolites provide new insight into bone consumption in *Borophagus* and their unique ecological niche: eLife 2018, v. 7:e34773, doi: https://doi.org/10.7554/eLife.347737, p.e34773.

Wang, X., O'Connor, J.K., Maina, J.N., Pan, Y., Wang, M., Wang, Y., Zheng, X. and Zhou, Z., 2018, *Archaeorhynchus* preserving significant soft tissue including probable fossilized lungs: Proceedings of the National Academy of Sciences, v. 115, p. 11555-11560.

Wang, X., Bachmann, G.H., Hagdorn, H., Sander, P.M., Cuny, G., Chen, X., Wang, C., Chen, L., Long, C., Meng, F., and Xu, G., 2008, The Late Triassic black shales of the Guanling area, Guizhou Province, south-west China: A unique marine reptile and pelagic crinoid fossil Lagerstätte: Palaeontology, v. 51, p. 27-61.

Wang, Y., M., Wang, M., O'Connor, J.K., Wang, X., Zheng, X. and Zhang, X., 2016, A new Jehol enantiornithine bird with three-dimensional preservation and ovarian follicles: Journal of Vertebrate Paleontology. doi 10.1080/02724634.2015.1054496.

Wanless, H.R., 1923, Stratigraphy of the White River beds of South Dakota: Proceedings of the American Philosophical Society, v. 62, p. 190-269.

Ward, D.J. and Hollingworth, N.T., 1990, The first record of a bitten ammonite from the Middle Oxford Clay (Callovian, Middle Jurassic) of Bletchley, Buckinghamshire: Mesozoic Research, v. 2, p. 153-161.

Ward, D.J., Duffin, C.J. and Ward, A., 2020, Are spiral bromalites enterospirae or coprolites? A brief review with some additional evidence: Society of Vertebrate Paleontology, 80th Annual Meeting Virtual 2020, October 12-16 2020, www.vertpaleo.org Conference Program, unnumbered page.

Warner, A.C.I., 1981, Rate of passage of digesta through the gut of mammals and birds: Nutrition Abstracts and Reviews Series B, v. 51, p. 789–820.

Warren, A. A. and Hutchinson, M. N., 1987, The skeleton of a new hornless rhystidosteid (Amphibian, Temnospondyli): Alcheringa, v. 11, p. 291-302.

Warren, A.A., Rubidge, B.S., Stanistreet, I.G., Stollhofen, H., Wanke, A., Latimer, E.M., Marsicano, C.A. and Damiani, R.J., 2001, Oldest known stereospondylous amphibian from the early Permian of Namibia: Journal of Vertebrate Paleontology, v. 21, p. 34-39

Washburn, S.L., 1957, Australopithecines: The hunters or the hunted?: American Anthropologist, v. 59, p. 612-614.

Watson, D.M.S., 1927, The reproduction of the coelacanth: Proceedings of the Zoological Society of London, v. 28, p. 453-457.

Watson, D.M.S., 1937, The acanthodian fishes: Philosophical Transactions of the Royal Society of London, Series B, v. 228, p. 49-146.

Watson, P.J., and. Yarnell, R.A., 1966, Archaeological and paleoethnobotanical investigations in Salts Cave, Mammoth Cave National Park, Kentucky: American Antiquity, v. 31, p. 842-49.

Weber, S., 2004, *Ornatocephalus metzleri* gen. et spec. nov. (Lacertilia, Scincoida): Taxonomy and paleobiology of a basal scincoid lizard from the Messel Formation (Middle Eocene: basal Lutetian, Geiseltalium): Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, v. 561, p. 1-159.

Wedmann, S., Uhl, D., Lehmann, T., Garrouste, R., Nel, A., Gomez, B., Smith, K. and Schaal, S.F.K., 2018, The Konservat-Lagerstätte Menat (Paleocene; France)–an overview and new insights: Geologica Acta, v. 16, p. 189-213.

Weems, R.E., 2018, A synopsis of the vertebrate fauna from the Culpeper Basin (Upper Triassic-Lower Jurassic, Maryland and Virginia): New Mexico Museum of Natural History and Science, Bulletin 79, p. 749-768.

Weems, R.E., 2020, Behavioral patterns of the Late Triassic *Kayentapus minor* trackmakers at the Culpeper Quarry near Stevensburg, Virginia USA: New Mexico Museum of Natural History and Science, Bulletin 82, p. 439-454.

Weems, R.E., Culp, M. J. and Wings, O., 2007, Evidence for prosauropod dinosaur gastroliths in the Bull Run Formation (Upper Triassic, Norian) of Virginia: Ichnos, v. 14, p. 271-295.

Weidenreich F. 1941, The extremity bones of *Sinanthropus pekinensis*: Palaeontologica Sinica, New Series, D, v. 5, p. 1-50

Weigelt, J., 1927, Rezente Wirbeltierleichen und ihre Paläobiologische Bedeutung. Leipzig, Max Weg, 227 p.

Weigelt, J., 1928a, Die Pflanzenreste des mitteldeutschen Kupferschiefers und ihre Einschaltung ins Sediment: Eine palökologische Studie: Fortschritte der Geologie und Paläontologie, v. 6, p. 395-592.

Weigelt, J., 1928b, Ganoidfischleichen in Kupferschiefer und in der Gegenwart: Palaeobiologica, v. 1, p. 323-356.

Weigelt, J., 1930a Über die vermutliche Nahrung von *Protorosaurus* und über einen körperlich erhaltenen Fruchtstand von *Archaeopodocarpus germanicus* aut: Leopoldina, v. 6, p. 269-280.

Weigelt, J., 1930b, Wichtige Fischreste aus dem Mansfelder Kupferschiefer: Leopoldina, v.6, p. 601-624.

Weiler, W., 1922, Beiträge zur Kenntnis der Tertiären Fische des Mainzer Beckens I: Abhandlungen der Hessischen Geologischen Landesanstalt zu Darmstadt, v. 6, p. 71-135.

Weiler W, 1931, Beiträge zum Oberrheinischen Fossilienkatalog Nr. 7. Revision der Fischfauna des Septarientones von Wiesloch bei Heidelberg: Sitzungsberichte Heidelberger Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, v. 11, p. 1-14.

Weiler, W., 1934, Ein fossiler Cybiide mit Magenhalt: Palaeobiologica, v. 6, p. 17-24.

Weinbaum, J.C., 2013, Postcranial skeleton of *Postosuchus kirkpatricki* (Archosauria: Paracrocodylomorpha), from the Upper Triassic of the United States: Geological Society, London, Special Publications, v. 379, p. 525-553.

Weishampel, D.B., 1984, The evolution of jaw mechanisms in ornithopod dinosaurs: Advances in Anatomy, Embryology and Cell Biology, v. 87, p. 1–110.

Weishampel, D. B. and Norman, D. B., 1989, Vertebrate herbivory in the Mesozoic; jaws, plants, and evolutionary metrics: Geological Society of America, Special Paper, v. 238, p. 87-100.

Welles, S. and Bump, J., 1949, *Alzadasaurus pembertoni,* a new elasmosaur from the Upper Cretaceous of South Dakota: Journal of Paleontology, v. 23, p. 522-523, 534.

Wellnhofer, P., 1964, Zur Pelecypodenfauna der Neuburger Bankkalke (Mitteltithon): Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Neue Folge, v. 119, p. 1 –143.

Wellnhofer, P., 1970, Die Pterodacyloidea (Pterosauria) der Oberjura-Plattenkalke Süddeutschlands: Bayerische Akademie der Wissenschaften, Mathematisch Wissenschaftlichen Klasse, Abhandlugen, v. 141, p. 1-133.

Wellnhofer, P., 1975a, Die Rhamphorhynchoidea (Pterosauria) der Oberjura Plattenkalke Süddeutschlands: Palaeontographica, v. 148, p. 1-186.

Wellnhofer, P., 1975b, Die Rhamphorhynchoidea (Pterosauria) der Oberjura Plattenkalke Süddeutschlands: Palaeontographica, v. 149, p. 1-30.

Wellnhofer, P., 1991, The illustrated encyclopedia of pterosaurs. London, Salamander Books Ltd., 192 p.

Wells, N.A., Ferber, C.T. and Ohman, S.C., 1993, Discriminant analysis of fish-bearing deposits in the Eocene Green River Formation of Utah and Wyoming: Palaios, v. 8, p. 81-100.

Welton, B.J., and Farish, R.F., 1993, The collector's guide to fossil sharks and rays from the Cretaceous of Texas: Lewisville, Before Time, 204 p.

Werneburg, R., 1986, Die Stegocephalen (Amphibia) der Goldlauterer Schichten (Unterrotliegendes, Perm) des Thüringer Waldes, Teil I: *Apateon flagrifer* (Whitt.): Freiberger Forschungshefte Hefte C, v. 410, p. 87–100.

Werneburg, R., 1988, Die Stegocephalen der Goldlauterer Schichten (Unterrotliegendes, Unterperm) des Thüringer Waldes, Teil II: *Apateon kontheri* n. sp., *Melanerpeton eisfeldi* n. sp. und andere: Freiberger Forschungshefte Hefte C, v. 427, p. 7–29.

Werneburg, R., 1989, Die Amphibienfauna der Manebacher Schichten (Unterrotliegendes, Unterperm) des Thüringer Waldes: Naturhistorisches Museum Schloss Bertholdsburg, Schleusingen, Veröffentlichungen, v. 4, p. 55–68.

Werneburg, R., 2020, On the morphology of large branchiosaurids (Amphibamiformes) from the Rotliegend (Lower Permian) of the Saar-Nahe basin, Germany: Semana, v. 35, p. 39-54.

Werneburg, R., Ronchi, A. and Schneider, J.W., 2007, The early Permian branchiosaurids (Amphibia) of Sardinia (Italy): systematic palaeontology, palaeoecology, biostratigraphy and palaeobiogeographic problems: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 252, p. 383-404.

Werneburg, R., Schneider, J.W. and Lucas, S.G., 2013, The dissorophoid *Milnererpeton huberi* (Temnospondyli) from the Late Pennsylvanian Kinney Brick Quarry in New Mexico restudied – paleontology, paleoenvironment, and age: New Mexico Museum of Natural History and Science, Bulletin 59, p. 349-370.

Werneburg, R., Schneider, J.W. and Lucas, S.G., 2021, The new dvinosaurian *Bermanerpeton kinneyi* (Temnospondyli), with a few "branchiosaurid" characters, from the Late Pennsylvanian Kinney Brick Quarry in New Mexico: New Mexico Museum of Natural History and Science, Bulletin 84, p. 433-451.

West, D.L. and Hasiotis, S.T., 2007, Trace fossils in an archaeological context: Examples from bison skeletons, Texas, US; *in* Miller, W. III, ed., Trace fossils: Concepts, problems, prospects. New York, Elsevier, p. 545-561.

Westaway, M.C., Thompson, J.C., Wood, W.B. and Njau, J., 2011, Crocodile ecology and the taphonomy of early Australasian sites: Environmental Archaeology, v. 16, p. 124-136.

Westphal, F., 1962, Die Krokodiler des deutschen und englischen Oberen Lias: Palaeontographica, A, v. 118, p. 23-118.

Wetmore, A., 1943, The occurrence of feather impressions in the Miocene deposits of Maryland: The Auk, v. 60, p. 440-441.

Wetzel, W., 1953 Die Bielefelder Garantianen-Knollen als palaobiologisches Objekt: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 104, p. 499-505.

Wetzel, W., 1960, Nachtrag zum Fossilarchiv der *Fuiriquina*-Schichten: Neues Jahrbuch fur Geologie und Paläontologie Monatshefte, v. 1960, p. 439-446.

Wetzel, W., 1964, Mikroorganismen aus jurassischen und kretazischen Saurier-Gewöllen: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 1964, p. 867-874.

Whitmore, F.C. and Stewart, R.H., 1965, Miocene mammals and Central American seaways: Fauna of the Canal Zone indicates separation of Central and South America during most of the Tertiary: Science, v. 148, p. 180-185.

Whitten, D. G. A. and Brooks, J. R. V., 1983, A dictionary of geology. Middlesex, Penguin Books Ltd., 495 p.

Whittle, C.H. and Everhart, M. A., 2000, Apparent and implied evolutionary trends in lithophagic vertebrates from New Mexico and elsewhere: New Mexico Museum of Natural History and Science, Bulletin 17, p. 75-82.

Whittle, C.H. and Onorato, L., 2000, On the origins of gastroliths–determining the weathering environment of rounded and polished stones by scanning-electron-microscope examination: New Mexico Museum of Natural History and Science, Bulletin 17, p. 69-73.

Wickes, W.H., 1908, Pebble swallowing animals. A sequel to "The Rhaetic Bone Beds:" Proceedings of the Bristol Natural Society, Series 4, v. 11, p. 25-31.

Wieland, G., 1906, Dinosaurian gastroliths: Science, v. 23, p. 819-821.

Wieland, G., 1907, Gastroliths: Science, v. 25, p. 66-67.

Wieland, G., 1920, The longneck sauropod *Barosaurus:* Science, v. 51, p. 528-530.

Wiest, L.A., Esker, D. and Driese, S.G., 2016, The Waco Mammoth National Monument may represent a diminished watering-hole scenario based on preliminary evidence of post-mortem scavenging: Palaios, v. 31, p. 592-606.

Wiffen, J., and Moisley, W. L., 1986, Late Cretaceous reptiles (families Elasmosauridae and Pliosauridae) from the Mangahouanga Stream, North Island, New Zealand: New Zealand Journal of Geology and Geophysics, v. 29, p. 202-252.

Wiffen, J. de Bufrenil, V., de Riclès, A. and Mazin, J.M., 1995, Ontogenetic evolution of bone structure in the Late Cretaceous Plesiosauria from New Zealand: Geobios, v. 28, p. 625-640.

Wilby, P.R. and Martill, D.M., 1992, Fossil fish stomachs: a microenvironment for exceptional preservation: Historical Biology, v. 6, p. 25-36.

Wild, R., 1978, Die Flugsaurier (Reptilia, Pterosauria) aus der Oberen Trias von Cene bei Bergamo, Italien: Bolletino delta Societa Paleontologies Italiana, v. 17, p. 176-256.

Wilde, V. and Hellmund, M., 2010, First record of gut contents from a middle Eocene equid from the Geiseltal near Halle (Saale), Sachsen-Anhalt, central Germany: Palaeobiodiversity and Palaeoenvironments, v. 90, p. 153-162.

Williams, E.E., 1952, Additional notes on fossil and subfossil bats from Jamaica: Journal of Mammalogy, v. 33, p. 171-179.

Williams, F.L.E. and Patterson, J.W., 2010, Reconstructing the paleoecology of Taung, South Africa from low magnification of dental microwear features in fossil primates: Palaios, v. 25, p. 439-448.

Williams, J.P. 2003, Bones of comprehension: The analysis of small mammal predator-prey interactions; *in* Kelley, P.H., Kowalewski, M. and Hansen, T.A., eds., Predator-prey interactions in the fossil record. New York, Kluwer Academic/Plenum Publishers, p. 341-358.

Williams, M.E., 1972, The origin of "spiral coprolites:" University of Kansas Palaeontological Contributions, v. 59, p. 1–19.

Williams, M.E., 1990, Feeding behavior in Cleveland Shale fishes; *in* Boucot, A. J., 1990, ed., Evolutionary paleobiology of behavior and coevolution, Elsevier, Amsterdam p. 273-287.

Williams-Dean, G.J., 1978, Ethnobotany and cultural ecology of Prehistoric Man in southwest Texas [Ph.D. dissertation]: College Station, Texas A&M University, 287 p.

Williams-Dean, G. and Bryant, V.M., 1975, Pollen analysis of human coprolites from Antelope House, Canyon de Chelly National Monument, Arizona: Kiva, v. 41, p. 97-111.

Williamson, W.E., 1996, ?*Brachychampsa sealeyi*, sp. nov., (Crocodylia, Alligatoroidea) from the Upper Cretaceous (Lower Campanian) Menefee Formation, northwestern New Mexico: Journal of Vertebrate Paleontology, v. 16, p. 421-431.

Williston, S.W., 1891, An interesting food habit of the plesiosaurs: Transactions of the Kansas Academy of Science, v. 13, p. 120-122.

Williston, S.W., 1898, Mosasaurs: Kansas University, Geological Survey, Paleontology, v. 4, p. 81–221.

Williston, S.W., 1899, Some additional characters of the mosasaurs: Kansas University Quarterly, v. 8, p.3 9-41.

Williston, S., 1904, The stomach stones of the plesiosaurs: Science, v. 20, p. 565.

Williston, S.W., 1906, North American plesiosaurs: *Elasmosaurus*, *Cimoliasaurus* and *Polycotylus*: American Journal of Science, v. 21, p. 221-236.

Williston, S.W., 1914, Water reptiles of the past and present. Chicago, University of Chicago Press, 251 p.

Williston, S. W. and Moodie, R.L., 1917, *Ogmodirus martinii*, a new plesiosaur from the Cretaceous of Kansas: The University of Kansas Science Bulletin, v. 10, p. 61-73.

Wilmsen, M. and Niebuhr, B., 2002, Stratigraphic revision of the upper Lower and Middle Cenomanian in the lower Saxony basin (northern Germany) with special reference to the Salzgitter area: Cretaceous Research, v. 23, p. 445-460.

Wilson, J.A., Mohabey, D.M., Peters, S.E. and Head, J.J., 2010, Predation upon hatchling dinosaurs by a new snake from the Late Cretaceous of India: PLoS Biol, v. 8(3): e1000322, doi:10.1371/journal.pbio.1000322.

Wilson, M.A., Borszcz, T. and Zatoń, M., 2014, Bitten spines reveal unique evidence for fish predation on Middle Jurassic echinoids: Lethaia, v. 48, p. 4-9.

Wilson, M.A., Feldman, H.R. and Krivicich, E.B., 2010, Bioerosion in an equatorial Middle Jurassic coral-sponge reef community (Callovian, Matmor Formation, southern Israel): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 289, p. 93–101.

Wilson, M.V.H., 1977a, Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia: Canadian Journal of Earth Sciences, v. 14, p. 953-962.

Wilson, M.V.H., 1977b, Middle Eocene freshwater fishes from British Columbia: Royal Ontario Museum, Life Sciences Contributions, v. 113, p. 1-61.

Wilson, M.V.H., 1980, Eocene lake environments: Depth and distance-from-shore variation in fish, insect, and plant assemblages: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 32, p. 21-44.

Wilson, M.V.H., 1987, Predation as a source of fish fossils in Eocene lake sediments: Palaios, v. 2, p. 497-504.

Wilson, M.V. H. and Caldwell, M.W., 1993, New Silurian and Devonian fork-tailed 'thelodonts' are jawless vertebrates with stomachs and deep bodies: Nature, v. 361, p. 442-444.

Wilson, M.V.H. and Caldwell, M.W., 1998, The Furcacaudiformes, a new order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from northern Canada: Journal of Vertebrate Paleontology, v. 18, p. 10-29.

Winkler, D.A., 1987, Vertebrate-bearing eolian unit from the Ogallala Group (Miocene) in northwestern Texas: Geology, v. 15, p. 705-708.

Winkler, D.E., Schulz-Kornas, E., Kaiser, T.M. and Tütken, T., 2019, Dental microwear texture reflects dietary tendencies in extant Lepidosauria despite their limited use of oral food processing: Proceedings of the Royal Society, Series B 20190544, dx.doi.org/10.1098/rspb.2019.0544.

Wings, O., 2003, Observations on the release of gastroliths from ostrich chick carcasses in terrestrial and aquatic environments: Journal of Taphonomy, v. 1, p. 97-103.

Wings O., 2004, Identification, distribution, and function of gastroliths in dinosaurs and extant birds with emphasis on ostriches (*Struthio camelus*) [Ph.D. dissertation]: Bonn, Rheinische Friedrich-Wilhelms-Universität, 187 p.

Wings, O., 2007, A review of gastrolith function with implications for fossil vertebrates and a revised classification: Acta Palaeontologica Polonica, v. 52, p. 1-16.

Wings, O., 2009, A simulated bird gastric mill and its implications for fossil gastrolith authenticity: Fossil Record, v. 12, p. 91-97.

Wings, O., 2012, Gastroliths in coprolites—a call to search!: New Mexico Museum of Natural History and Science, Bulletin 57, p. 73-77.

Wings, O., 2015a, The Langenberg Quarry near Goslar: Unique window into a terrestrial Late Jurassic ecosystem in Northern Germany: Abstract Volume of the 12th Symposium on Mesozoic Terrestrial Ecosystems, p. 99-100.

Wings, O., 2015b, The rarity of gastroliths in sauropod dinosaurs—a case study in the Late Jurassic Morrison Formation, western USA: Fossil Record, v. 18, p. 1-16.

Wings, O. and Sander, P.M., 2007, No gastric mill in sauropod dinosaurs: New evidence from analysis of gastrolith mass and function in ostriches: Proceedings of the Royal Society of London, Series B, v. 274, p. 635-640.

Wiseman, K.D., Greene, H.W., Koo, M.S. and Long, D.J., 2019, Feeding ecology of a generalist predator, the California kingsnake (*Lampropeltis californiae*): Why rare prey matter: Herpetological Conservation and Biology, v. 14, p. 1-30.

Witmer, L.M., 1995, The extant phylogenetic bracket and the importance of reconstructing soft issues in fossils; *in* Thomason, J., ed., Functional morphology in vertebrate paleontology. Cambridge, Cambridge University Press, p. 19-33.

Witton, M.P., 2013, Pterosaurs: Natural history, evolution, anatomy. Princeton, Princeton University Press, 291 p.

Witton, M.P., 2018, Pterosaurs in Mesozoic food webs: A review of fossil evidence; *in* Hone, D. W.E., Witton, M.P. and Martill, D.M., eds., New perspectives on pterosaur palaeobiology: Geological Society of London, Special Publications, v. 455, p. 7–23.

Witzmann, F., 2009, Cannibalism in a small growth stage of the early Permian branchiosaurid *Apateon gracilis* (Credner, 1881) from Saxony: Fossil Record, v. 12, p. p. 7-11.

Wong, K., 2003, Stranger in a new land: Scientific American, v. 289(5), p. 74-83.

Wood, J.R., Wilmshurst, J.M., Worthy, T.H. and Cooper, A., 2011, *Sporormiella* as a proxy for non-mammalian herbivores in island ecosystems: Quaternary Science Reviews, v. 30, p. 915–920.

Wood J.R., Wilmshurst, J.M., Worthy, T.H. and Cooper, A., 2012a, First coprolite evidence for the diet of *Anomalopteryx didiformis*, an extinct forest ratite from New Zealand: New Zealand Journal of Ecology, v. 36, p. 164–170.

Wood, J.R., Rawlence, N.J., Rogers, G.M., Austin, J.J., Worthy, T.H. and Cooper, A., 2008, Coprolite deposits reveal the diet and ecology of the extinct New Zealand megaherbivore moa (Aves, Dinornithiformes): Quaternary Science Reviews, v. 27, p. 2593-2602.

Wood, J.R., Wilmshurst, J.M., Wagstaff, S.J., Worthy, T.H., Rawlence, N.J. and Cooper, A., 2012b, High-resolution coproecology: Using coprolites to reconstruct the habits and habitats of New Zealand's extinct upland moa (*Megalapteryx didinus*): PLoS ONE, v. 7(6): e40025, doi.org/10.1371/journal.pone.0040025.

Woodward, A.S., 1901, Catalog of fossil fishes in the British Museum (Natural History). Part VI. Containing the Actinopterygian Teleostomi of the Suborders Isospondyli (in Part), Ostariophysi, Apodes, Percesoces Hemibranchii, Acanthopterygii, and Anacanthini. London, British Museum (Natural History), 636 p.

Woodward, J., 1729, An attempt towards a natural history of the fossils of England in a catalogue of the English fossils in the collection of John Woodward, M.D., Volume 2: London, J. Senex, J. Osborn and T. Longman, 115 p.

Wretman, L. and Kear, B.P., 2014, Bite marks on an ichthyodectiform fish from Australia: Possible evidence of trophic interaction in an Early Cretaceous marine ecosystem: Alcheringa, v. 38, p. 170-176.

Wright, C. W. and Wright, E. V., 1940, Notes on Cretaceous Asteroidea: Geological Society of London, Quarterly Journal, v. 94, p. 231-248.

Wright, J.L., Unwin, D.M., Lockley, M.G. and Rainforth, E.C., 1997, Pterosaur tracks from the Purbeck Limestone Formation of Dorset, England: Proceedings of the Geologists' Association, v. 108, p. 39-48.

Wroe, S., Chamoli, U., Parr, W.C., Clausen, P., Ridgely, R. and Witmer, L., 2013, Comparative biomechanical modeling of metatherian and placental saber-tooths: A different kind of bite for an extreme pouched predator: PLoS ONE, v. 8(6): e66888, doi: 10.1371/journal.pone.0066888.

Wu, F.X., Sun, Y.L., Hao, W.C., Jiang, D.Y. and Sun, Z.Y., 2015, A new species of *Saurichthys* (Actinopterygii; Saurichthyiformes) from the Middle Triassic of southwestern China, with remarks on pattern of the axial skeleton of saurichthyid fishes: Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, v. 275, p. 249-267.

Wu, X.C., Brinkman, D.B., Eberth, D.A. and Braman, D.R., 2007, A new ceratopsid dinosaur (Ornithischia) from the uppermost Horseshoe Canyon Formation (upper Maastrichtian), Alberta, Canada: Canadian Journal of Earth Sciences, v. 44, p. 1243-1265.

Wu, Y., 2021, Molecular phyloecology suggests a trophic shift concurrent with the evolution of the first birds: Communications Biology, v. 4, p. 1-13. doi.org/10.1038/s42003-021-02067-4.

Wuttke, M. and Poschmann, M., 2010, First finding of fish in the diet of a water-dwelling extinct frog *Palaeobatrachus* from the upper Oligocene Fossil-Lagerstätte Enspel (Westerwald Mountains, Western Germany): Palaeobiodiversity and Palaeoenvironments, v. 90, p. 59-64.

Xing, L., Niu, K. and Evans, S.E., 2019, Inter-amphibian predation in the Early Cretaceous of China: Scientific Reports, v. 9, 7751, doi.org/10.1038/s41598-019-44247-7.

Xing, L., Bell, P.R., Currie, P.J., Shibata, M., Tseng, K. and Dong, Z., 2012, A sauropod rib with an embedded theropod tooth: Direct evidence for feeding behaviour in the Jehol Group, China: Lethaia, v. 45, p. 500-506.

Xing, L., Rothschild, B.M., Randolph-Quinney, P.S., Wang, Y., Parkinson, A.H. and Ran, H., 2018, Possible bite-induced abscess and osteomyelitis in *Lufengosaurus* (Dinosauria: sauropodomorph) from the Lower Jurassic of the Yimen Basin, China: Scientific Reports, v. 8, 5045 (2018), doi.org/10.1038/s41598-018-23451-x.

Xing, L., Bell, P.R., Persons, W.S. IV, Ji, S., Miyashita, T., Burns, M.E., Ji,, Q. and Currie, P.J., 2012, Abdominal contents from two large Early Cretaceous compsognathids (Dinosauria: Theropoda) demonstrate feeding on confuciusornithids and dromaeosaurids: PLoS ONE, v. 7(8): e44012, doi:10.1371/journal.pone.0044012.

Xing, L., Persons IV, W.S., Bell, P.R., Xu, X., Zhang, J., Miyashita, T., Wang, F. and Currie, P.J., 2013, Piscivory in the feathered dinosaur *Microraptor*: Evolution, v. 67, p. pp.2441-2445.

Xu, X., 1997, A new psittacosaur (*Psittacosaurus mazongshanensis* sp. nov.) from Mazongshan area, Gansu Province, China; *in* Dong, Z., ed., Sino-Japanese Silk Road dinosaur expedition. Beijing, China Ocean Press, p. 48-67.

Xu, X., Forster, C., Clark, J. and Mo, J., 2006, A basal ceratopsian with traditional features from the Late Jurassic of northwestern China: Proceedings of the Royal Society of London, Series B., v. 273, p. 2135-2140.

Xu, X., Clark, J. M., Mo, J., Chorniere, J., Forster, C.A., Erickson, G.M., Hone, D.W.E., Sullivcan, C., Eberth, D.A., Nesbitt, S., Zhao, Q., Hernandez, R., Jia, C., Han, F. and Guo, Y., 2009, A Jurassic ceratosaur from China helps clarify avian digital homologies: Nature, v. 459, p. 940-944.

Yabumoto, Y. and Brito, P.M., 2013, The second record of a mawsoniid coelacanth from the Lower Cretaceous Crato Formation, Araripe Basin, northeastern Brazil, with comments on the development of coelacanths; *in* Arratia, G., Schultze, H.P. and Wilson M.V., eds., Mesozoic fishes 5. Global diversity and evolution. München, Verlag Dr. F. Pfei, p. 489-497.

Yang, H. and Yang, S., 1994, The Shanwang fossil biota in eastern China: A Miocene Konservat-Lagerstätte in lacustrine deposits: Lethaia, v. 27, p. 345-354.

Yates A.M., Neumann, F.H. and Hancox, P.J., 2012, The earliest post-Paleozoic freshwater bivalves preserved in coprolites from the Karoo Basin, South Africa: PLoS ONE, v. 7, e30228, doi:10.1371/journal.pone.0030228.

Yeh, H., 1981, Third note on a fossil bird from Miocene of Lingwu, Shandong: Vertebrata Palasiatica, v. 18, p. 149-155.

Yelinek, K.D., 2005, Taphonomy of *Daemonelix*: Implications for the preservation of terrestrial vertebrate burrows and description of associated invertebrate burrows [M.S. thesis]: Boulder, University of Colorado, 50 p.

Yoshikawa, H., 2000, *Juglans ailanthifolia* Carr gnawed by large Japanese field mice, *Apodemus speciosus* (Temminck), from the middle Pleistocene Sahama Mud in Hanamatsu City, Shizuoka Prefecture, central Japan: Science Report of the Toyohashi Museum of Natural History, v. 10, p. 23-30.

You, H., Dodson, P. M., 2004, Basal Ceratopsia; *in* Weishampel, D. B., Dodson, P. and Osmólska, H., eds., The Dinosauria. Berkeley, University of California Press, p. 478-493.

Young, B. H., 1910, The prehistoric men of Kentucky. Louisville, Filson Club Publications, 25 p.

Young, C. C., 1964, New fossil crocodiles from China: Vertebrata PalAsiatica, v. 8, p. 189-210.

Young, D. J., 1967, Loess deposits of the west coast of the South Island, New Zealand: New Zealand Journal of Geology and Geophysics, v. 10, p. 647-658.

Young, M. T., Rabi, M., Bell, M. A., Foffa, D., Steel, L., Sachs, S., and Peyer, K., 2016, Big-headed marine crocodyliforms and why we must be cautious when using extant species as body length proxies for long-extinct relatives: Palaeontologia Electronica, v. 19.3.30A: 1-14, https://doi.org/10.26879/648. palaeo-electronica.org/content/2016/1554-teleosaurid-size-estimation

Young, M.T., Hua, S., Steel, L., Foffa, D., Brusatte, S. L., Thüring, S., Mateus, O., Ruiz-Omeñaca, J. I., Havlik, P., Lepage, Y. and De Andrade, M. B., 2014, Revision of the Late Jurassic teleosaurid genus *Machimosaurus* (Crocodylomorpha, Thalattosuchia): Royal Society Open Science, v. 1:140222, dx.doi.org/10.1098/rsos.140222

Youngman, P.M., 1994, Beringian ferrets: Mummies, biogeography and systematics: Journal of Mammalogy, v. 75, p. 454-461.

Yun, C., 2019, Comments on the ecology of Jurassic theropod dinosaur *Ceratosaurus* (Dinosauria: Theropoda) with critical reevaluation for supposed semiaquatic lifestyle: Volumina Jurassica, v. 17, p. 111-116.

Zahner, M. and Brinkmann, W., 2019, A Triassic averostran-line theropod from Switzerland and the early evolution of dinosaurs: Nature Ecology and Evolution, v. 8, p. 1146-1152.

Zajíc, J., 2014, Permian fauna of the Krkonoše Piedmont Basin (Bohemian Massif, Central Europe): Acta Musei Nationalis Pragae, Series B-Historia Naturalis, v. 70, p. 131-142.

Zakharenko, G.V., 2008, Possible evidence of predation in placoderms (Pisces) of the Evlanovo basin of central Russia: Paleontological Journal, v. 42, p. 522-525.

Zaleha, M. J. and Wiesemann, S. A., 2005, Hyperconcentrated flows and gastroliths: Sedimentology of diamictites and wackes of the upper Cloverly Formation, Lower Cretaceous, Wyoming, U.S.A.: Journal of Sedimentary Research, v. 75, p. 43-54.

Zammit, M., 2011, The Australian Cretaceous ichthyosaur

Platypterygius australis: Understanding its taxonomy, morphology, and palaeobiology [Ph.D. dissertation]: Adelaide, University of Adelaide, 106 p.

Zammit, M. and Kear, B., 2011, Healed bite marks on a Cretaceous ichthyosaur: Acta Palaeontologica Polonica; v. 56, p. 859–863.

Zangerl, R., 1953, The vertebrate fauna of the Selma Formation of Alabama. Part 4. The turtles of the family Toxochelyidae: Fieldiana, Geology, Memoirs, v. 3, p .133-277.

Zangerl, R. and Richardson, E.S., 1963, The paleoecological history of two Pennsylvanian black shales: Fieldiana, Geological Memoirs, v. 4, 352 p.

Zanno, L.E. and Makovicky, P.J., 2011, Herbivorous ecomorphology and specialization patterns in theropod evolution: Proceedings of the National Academy of Sciences, v. 108, p. 232-237.

Zapfe, H., 1981, Ein Schädel von *Mesopithecus* mit Biss-Spuren: Folia Primatologica, v. 35, p. 248-258.

Zatoń, M. and Rakociński, M., 2014, Coprolite evidence for carnivorous predation in a Late Devonian pelagic environment of southern Laurussia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 394, p. 1-11.

Zatoń, M. and Salamon, M.A., 2008, Durophagous predation on Middle Jurassic molluscs, as evidenced from shell fragmentation: Palaeontology, v. 51, p. 63-70.

Zatoń, M., Villier, L., and Salamon, M. A., 2007, Signs of predation in the Middle Jurassic of south-central Poland: Evidence from echinoderm taphonomy: Lethaia, v. 40, p. 139–151.

Zatoń, M., Broda, K., Qvarnström, M., Niedźwiedzki, G. and Ahlberg, P.E., 2017, The first direct evidence of a Late Devonian coelacanth fish feeding on conodont animals: The Science of Nature, v. 104, 26 (2017). https://doi.org/10.1007/s00114-017-1455-7

Zatoń, M., Niedźwiedzki, G., Marynowski, L., Benzerara, K., Pott, C., Cosmidis, J., Krzykawski, T. and Filipiak, P., 2015, Coprolites of Late Triassic carnivorous vertebrates from Poland: An integrative approach: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 430, p. 21-46.

Zeigler, K.E., Heckert, A.B. and Lucas, S.G., 2002, A new species of *Desmatosuchus* (Archosauria: Aetosauria) from the Upper Triassic of the Chama Basin, north-central New Mexico: New Mexico Museum of Natural History and Science, Bulletin 21, p. 215-219.

Zhang, G.-R., Wang, S.-T., Wang, J.-Q., Wang, N.-Z. and Zhu, M., 2010, A basal antiarch (placoderm fish) from the Silurian of Qujing, Yunnan, China: Palaeoworld, 19, 129–135.

Zhang, M., 2001, Jehol biota. Shanghai, Shanghai Science and Technology Publishing, 150 p.

Zhang, X., Shu, D., Han, J., Zhang, Z., Liu, J. and Fu, D., 2014, Triggers for the Cambrian explosion: Hypotheses and problems: Gondwana Research, v. 25, p. 896–909.

Zhang, Y., Zhang, D., Yang, Y. and Wu, X., 2020, Pollen and lipid analysis of coprolites from Yuhuicun and Houtieying, China: Implications for human habitats and diets: Journal of Archaeological Science: Reports, v. 29, 102135, doi.org/10.1016/j.jasrep.2019.102135.

Zhang, Y., van Geel, B., Gosling, W.D., McMichael, C.N.H., Jansen, B., Absalah, S., Sun, G. and Wu, X., 2019, Local vegetation patterns of a Neolithic environment at the site of Tianluoshan, China, based on coprolite analysis: Review of Palaeobotany and Palynology, v. 271, 104101, doi.org/10.1016/j.revpalbo.2019.104101.

Zhao W.-J. and Zhu, M., 2010, Siluro-Devonian vertebrate biostratigraphy and biogeography of China: Palaeoworld, v. 19, p. 4–26.

Zheng, X., Martin, L.D., Zhou, Z., Burnham, D.A., Zhang, F. and Miao, D., 2011, Fossil evidence of avian crops from the Early Cretaceous of China: Proceedings of the National Academy of Sciences, v. 108, p. 15904-15907.

Zheng, X., O'Connor, J.K., Wang, X., Pan, Y., Wang, Y., Wang, M. and Zhou, Z., 2017, Exceptional preservation of soft tissue in a new specimen of *Eoconfuciusornis* and its biological implications: National Science Review, v. 4, p. 441-452.

Zheng, X.-T., O'Connor, J.K., Wang, X.-L., Wang, Y. and Zhou, Z.-H., 2018a, Reinterpretation of a previously described Jehol bird clarifies early trophic evolution in the Ornithuromorpha: Proceedings of the Royal Society of London, Series B, Biological Sciences, v. 285, 20172494, dx.doi.org/10.1098/rspb.2017.2494.

Zheng X., O'Connor, J.K., Huchzermeyer, F., Wang, X., Wang, Y., Zhang, X. and Zhou, Z., 2014, New specimens of *Yanornis* indicate a piscivorous diet and modern alimentary canal: PLoS ONE, v. 9(4): e95036, doi: 10.1371/journal.pone.0095036.

Zheng, X., Wang, X., Sullivan, C., Zhang, X., Zhang, F., Wang, Y., Li, F. and Xu, X., 2018b, Exceptional dinosaur fossils reveal early origin of avian-style digestion: Scientific Reports, v. 8, 14217, doi.org/10.1038/s41598-018-32202-x.

Zhou, Z. and Wang, X., 2000, A new species of *Caudipteryx* from the Yixian Formation of Liaoning, northeast China: Vertebrata PalAsiatica, v. 38, p. 111-127.

Zhou, Z. and Zhang, F., 2002, A long-tailed, seed-eating bird from the Early Cretaceous of China: Nature, v. 418, p. 405–409.

Zhou, Z. and Zhang, F., 2003, Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China: Canadian Journal of Earth Sciences, v. 40, p. 731-747.

Zhou, Z. and Zhang, F., 2006, A beaked basal ornithurine bird (Aves, Ornithurae) from the Lower Cretaceous of China: Zoological Scripta, v. 35, p. 363-373.

Zhou, S., Zhou, Z. and O'Connor, J. K., 2013, Anatomy of the Early Cretaceous *Archaeorhynchus spatula*: Journal of Vertebrate Paleontology, v. 33, p. 141-152.

Zhou, S., Zhou, Z.-H. and O'Connor, J.K., 2014, A new piscivorous ornithuromorph from the Jehol Biota: Historical Biology, v. 26, p. 608–618.

Zhou, Z., Clarke, J., Zhang, F. and Wings, O., 2004, Gastroliths in *Yanornis*: An indication of the earliest radical diet-switching and gizzard plasticity in the lineage leading to living birds?: Naturwissenschaften, v. 91, p. 571–574.

Zhou, Z.-H., Wang, X.-L., Zhang, F.-C. and Xu, X., 2000, Important features of *Caudipteryx* – evidence from two nearly complete new specimens: Vertebrata PalAsiatica, v. 38, p. 241-254.

Zhu, M., Yu, X. and Janvier, P., 1999, A primitive fossil fish sheds light on the origin of bony fishes: Nature, v. 397, p. 607–610.

Zhu, M., Zhao, W., Jia, L., Lu, J., Qiao, T. and Qu, Q., 2009, The oldest articulated osteichthyan reveals mosaic gnathostome characters: Nature, v. 458, p. 469–474.

Zhuravlev, K. N., 1943a, [The remains of Upper Jurassic sea reptiles at the Saveljevka Shale Mine site]: Bulletin de l'Académie de Sciences de l'URSS, Classe des Sciences Biologique, v. 5, p. 293-306. [In Russian]

Zhuravlev, K. I., 1943b, Nakhodki ostatkov verkhneorskikh reptilii v savelevskom slantysevom rudniki [Finds of the remains of the upper orian reptile in the Savelievsky schantose mines]: Izvestiya Akad Nauk Sooza SSR Otdelenie Biologich Nauk, v. 5, p. 293-306. [In Russian]

Zidek, J., 1980, *Acanthodes lundi*, new species (Acanthodii) and associated coprolites from uppermost Mississippian Heath Formation of central Montana: Annals of Carnegie Museum, v. 49, p. 49-78.

Zijlstra, M. and Van Eerden, M.R., 1995, Pellet production and the use of otoliths in determining the diet of cormorants *Phalacrocorax carbo sinensis*: Trials with captive birds: Ardea, v. 83, p. 123–131.

Zinsmeister, W.J., 1980, Observations on the predation of the clypeastroid echinoid, *Monophoraster darwini*, from the upper Miocene Entrerrios Formation, Patagonia, Argentina: Journal of Paleontology, v. 54, p. 910-912.

Zotz, L., 1928, Die Fische der typischen Fischschiefer aus den Schächten der Kaliwerke Buggingen: Mitteilungen der Badischen Geologische Landesanstalt zu Heidelberg, v. 10, p. 145-174.

Zug, G. R., 1971, Buoyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtles: University of Michigan Museum of Zoology, Miscellaneous

Publications, v. 141, p. 1-98.

Zuschin, M., Stachowitsch, M. and Stanton, R. J., Jr., 2003, Patterns and processes of shell fragmentation in modern and ancient marine environments: Earth Science Reviews, v. 63, p. 33-82.

Zverkov, N.G., Arkhangelsky, M.S. and Stenshin, I.M., 2015, A review of Russian Upper Jurassic ichthyosaurs with an intermedium/humeral contact. Reassessing *Grendelius* McGowan, 1976: Proceedings of the Zoological Institute RAS, v. 319, p. 558–588.

Note Added in Proof

Zonneveld et al. (2021) described *Nihilichnus nihilicus* and cf. *Nihilichnus* isp. on a left front peripheral of a tortoise (Testudininei indeterminate) from the early Miocene Moghra Formation of Egypt. They attribute these traces to the bites of an unidentified mammalian carnivore during predation or scavenging.

Reference

Zonneveld, J.P., AbdelGawad, M.K. and Miller, E.R., 2021, Ectoparasite borings, mesoparasite borings, and scavenging traces in early Miocene turtle and tortoise shell: Moghra Formation, Wadi Moghra, Egypt: Journal of Paleontology, p.1-19, doi: 10.1017/jpa.2021.92.

APPENDIX A

Fossil Record of Vertebrate Dentalites and Consumulites (tables)

TABLE A.1. Mesozoic marine dentalites on bony substrate.

Mesozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Chondrichthyes	*Cretoxyrhina mantelli*	Late Cretaceous	Italy	Amalfitano et al. (2019)	
	Cretoxyrhina mantelli	Late Cretaceous	USA	Shimada (1997)	*Squalicorax falcatus*, tooth in dentalite
	Eumylodus laqueatus	Late Cretaceous	USA	Cicimurri et al. (2008)	*Squalicorax* sp.
Osteichthyes	*Leedsichthys* sp.	Middle Jurassic	UK	Martill (1985b)	*Metriorhynchus* tooth in dentalite
	Xiphactinus audax	Late Cretaceous	USA	Shimada and Everhart (2004)	embedded *Cretoxyrhina mantelli* tooth
	Enchodus sp.	Late Cretaceous	USA	Konuki (2008)	*Squalicorax*
	plethodid *Martinichthys* sp.	Late Cretaceous	USA	Everhart and Everhart (1994)	
	Martinicthys sp.	Late Cretaceous	USA	Konuki (2008)	
	Protosphyraena nitida	Late Cretaceous	USA	Schwimmer et al. (1997)	2 specs *Squalicorax*
	Protosphyraena spp.	Late Cretaceous	USA	Schwimmer et al. (1997)	10 specs Squalicorax
	Pachyrhizodus caninus	Late Cretaceous	USA	Schwimmer et al. (1997)	*Squalicorax*
	Cooyoo australis	Early Cretaceous	Australia	Wretman and Kear (2014)	perhaps a polycotylid plesiosaurian, ornithocheiroid pterosaur, ichthyosaurian *Platypterygius australis*
Testudines	Large chelonioid	Late Cretaceous	Italy	Amalfitano et al. (2017)	shark lamniform *Cretodus* sp. in consumulite
	Protostega gigas	Late Cretaceous	USA	Shimada and Hooks (2004); Everhart (2017)	2 specimens *Cretoxyrhina mantelli*
	Protostega gigas	Late Cretaceous	USA	Everhart (2013, 2017)	mosasaur ?*Tylosaurus*
	Protostega sp.	Late Cretaceous	Angola	Mateus et al. (2012)	shark
	Protostega sp.	Late Cretaceous	USA	Konuki (2008)	*Squalicorax* dentalites and tooth in dentalite
	Chelospargus advena	Late Cretaceous	USA	Schwimmer (2010)	crocodilian
	Plesiochelys sp. and Plesiochelyidae indet.	Late Jurassic	Switzerland	Meyer (1991)	*Machimosaurus*

Mesozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Testudines	*Bothremys barberi*	Late Cretaceous	USA	Schwimmer et al. (1997)	*Squalicorax kaupi*
	Toxochelys latiremis	Late Cretaceous	USA	Konuki (2008)	*Squalicorax* and *Xiphactnus, Cretoxyrhina*
	Toxochelys? sp.	Late Cretaceous	USA	Schwimmer et al. (1997)	*Squalicorax*
	Desmatochelys lowii	Late Cretaceous	USA	Schwimmer et al. (1997)	*Squalicorax*
	Osteopygis sp.	Late Cretaceous	USA	Grandstaff (1998)	*Mosasaurus maximus*
	Protostega dixie (=gigas)	Late Cretaceous	USA	Schwimmer et al. (1997)	shark
	Gigantatypus salahi	Late Cretaceous	Jordan	Kaddumi (2006)	*Squalicorax*?
	Allopleuron hofmanni	Late Cretaceous	Netherlands	Mulder (2003a)	?mosasaur
	Allopleuron hofmanni	Late Cretaceous	Netherlands	Jagt et al. (2020)	*Machichnus* isp., possibly produced by enchodontid fish
	Chedighaii (Bothremys) barberi	Late Cretaceous	USA	Schwimmer (2010)	*Deinosuchus*
	Ctenochelys tenuitesta	Late Cretaceous	USA	Zangerl (1953)	?mosasaur
	Catapleura repanda or cf. *Bothremys* sp.	Late Cretaceous/ Paleogene	USA	Boles (2016)	*Cretolamna appendiculata*
	indeterminate	Late Cretaceous/ Paleogene	USA	Boles (2016)	hexanchid
	indeterminate	Late Cretaceous/ Paleogene	USA	Boles (2016)	shark
	indeterminate	Late Cretaceous/ Paleogene	USA	Boles (2016)	*Bottosaurus harlani* or a mosasaur
	indeterminate	Late Cretaceous	USA	Becker et al. (2006)	shark
Mosasauroidea	*Tylosaurus* sp.	Late Cretaceous	Germany	Massare (1987)	
	Tylosaurus kansasensis	Late Cretaceous	USA	Everhart (2005g)	mosasaur
	Tylosaurus sp.	Late Cretaceous	USA	Everhart (2005g)	tips of three *Cretoxyrhina* teeth embedded in the skull and lower jaws
	Tylosaurus nepaeolicus	Late Cretaceous	USA	Schumacher (1993); Everhart (2002)	mosasaur
	Platecarpus tympaniticus	Late Cretaceous	USA	Everhart (2008)	mosasaur
	Tylosaurus nepaeolicus	Late Cretaceous	USA	Rothschild and Martin (1993)	head biting

Mesozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Mosasauroidea	*Tylosaurus nepaeolicus*	Late Cretaceous	USA	Everhart (2008)	two partially healed puncture wounds on the left-lateral side of the premaxilla, consistent with the "head biting" scenario
	Clidastes propython	Late Cretaceous	USA	Everhart (2008)	skull partially healed puncture wounds on the frontal, right prefrontal and right articular from mosasaur
	Clidastes sp.	Late Cretaceous	Germany	Hans-Volker and Nyhuis (2012)	
	Clidastes sp.	Late Cretaceous	USA	Rothschild Martin (1993)	*Squalicorax*, dentalite and tooth in dentalite
	Clidastes sp.	Late Cretaceous	USA	Konuki (2008)	*Squalicorax*
	Prognathodon saturator	Late Cretaceous	Netherlands	Dortangs et al. (2002); Rothschild et al. (2005)	shark, associated teeth of *Squalicorax* and *Plicatoscyillium*
	Prognathodon kianda	Late Cretaceous	Angola	Strganac et al. (2015)	*Squalicorax pristodontus*
	cf. Ectenosaurus clidastoides	Late Cretaceous	USA	Everhart (2004c)	*Cretoxyrhina mantelli* and *Squalicorax falcatus*, dentalites and tooth in dentalite
	Mosasaurus conodon	Late Cretaceous	?	Bell and Martin (1995)	mosasaur
	Mosasaurus hoffmanni	Late Cretaceous	Netherlands	Lingham-Soliar (2004)	dentary mosasaur?
	Platecarpus ictericus	Late Cretaceous	USA	Lingham-Soliar (2004)	dentary – mosasaur?
	Platecarpus sp.	Late Cretaceous	USA	Everhart (1999)	unhealed *Cretoxyrhina* bite marks on the skull and dorsal vertebrae
	Platecarpus sp.	Late Cretaceous	USA	Rothschild and Martin (1993)	*Squalicorax*
	?*Platecarpus* sp.	Late Cretaceous	USA	Shimada (1997); Rothschild et al. (2005)	one of several punctures includes *Cretoxyrhina* tooth
	Plioplatecarpus sp.	Late Cretaceous	USA	Bell and Martin (1995)	mosasaur
	Plioplatecarpus marshi	Late Cretaceous	Belgium	Bardet, et al. (1998)	shark
	Plioplatecarpus marshi	Late Cretaceous	The Netherlands	Jagt et al. (2020)	*Linichnus* cf. *serratus*

Mesozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Mosasauroidea	plioplatecarpine	Late Cretaceous	USA	Carr et al. (2020)	plioplatecarpine mosasaur head biting
	Platecarpus ictericus	Late Cretaceous	USA	Schwimmer et al., (1997); Jacobsen and Bromley (2009)	shark with serrations, *Knethichnus parallelum*
	Platecarpus ictericus	Late Cretaceous	USA	Konuki (2008)	one is tooth in dentalite, *Squalicorax*
	Platecarpus coryphaeus	Late Cretaceous	USA	Konuki (2008)	*Squalicorax*
	Platecarpus sp	Late Cretaceous	USA	Schwimmer et al. (1997)	*Squalicorax*
	Platecarpus sp	Late Cretaceous	USA	Schwimmer et al. (1997)	serrated shark
	Platecarpus sp.	Late Cretaceous	USA	Konuki (2008)	*Squalicorax*
	Tylosaurus proriger	Late Cretaceous	USA	Schwimmer et al. (1997)	serrated shark
	Tylosaurus proriger	Late Cretaceous	USA	Everhart (2005b)	*Squalicorax falcatus*
	Tylosaurus kansasensis	Late Cretaceous	USA	Everhart (2002)	tooth in dentalite, *Cretoxyrhina*
	Tylosaurus sp.	Late Cretaceous	USA	Schumacher (1993)	mosasaur
	Tylosaurus sp.	Late Cretaceous	USA	Konuki (2008)	*Squalicorax, Cretoxyrhina, Squalicorax* and *Cretoxyrhina*
	tylosaurine	Late Cretaceous	USA	Hamm and Shimada (2007)	*Pseudocorax laevis* and *Squalicorax pristodontus*
	indeterminate	Late Cretaceous	Spain	Corral et al. (2004)	shark, maybe *Squalicorax kaupi* (Agassiz, 1843) or *Cretolamna appendiculata*, both from same unit
	indeterminate	Late Cretaceous	USA	Everhart et al. (1995); Shimada (1997)	*Cretoxyrhina*
	indeterminate	Late Cretaceous	USA	Everhart (1999); Rothschild and Everhart (2015)	shark bite on the tail, 2 age sets of bites
	indeterminate	Late Cretaceous	USA	Schwimmer et al. (1997)	striated shark
	indeterminate	Late Cretaceous	USA	Schwimmer et al. (1997)	striated shark
	indeterminate	Late Cretaceous	USA	Welton and Farish (1993); Schwimmer et al. (1997)	*Squalicorax*

Mesozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Mosasauroidea	mosasaur	Late Cretaceous	USA	Konuki (2008)	*Squalicorax, Squalicorax* and *Cretoxyrina*
Plesiosauria	cf. *Cryproclidus* sp.	Middle Jurassic	UK	Martill et al. (1994)	propodeal bitten by pliosaur
	cf. *Dolichorhynchops osborni*	Late Cretaceous	USA	Everhart (2003)	
	polycotylid	Late Cretaceous	Sweden	Einarsson et al. (2010)	mosasaur
	Dolichorhynchops sp	Late Cretaceous	USA	Schwimmer et al. (1997)	*Squalicorax*
	Trinacromerum willistoni	Late Cretaceous	USA	Schwimmer et al. (1997)	shark
	Trinacromerum willistoni	Late Cretaceous	USA	Riggs, 1944	?shark
	Brachauchenius lucasi	Late Cretaceous	USA	Schwimmer et al. (1997)	*Squalicorax*
	Ogmodirus martini	Late Cretaceous	USA	Williston and Moodie (1917); Everhart (2006)	bite marks were serrated, scavenging by *Squalicora*x
	Albertonectes vanderveldei	Late Cretaceous	Japan	Kubo et al. (2012)	shark
	Futabasaurus suzukii	Late Cretaceous	Japan	Sato et al. (2006); Shimada et al. (2010)	shark – teeth in dentatlites
	Eromangasaurus carinognathus	Early Cretaceous	Australia	Thulborn and Turner (1993); Kear (2005); McHenry (2009)	pliosaur - *Kronosaurus*
	indeterminate elasmosaur	Late Cretaceous	Chile	Otero et al. (2014)	
	indeterminate elasmosaur	Late Cretaceous	USA	Everhart (2005a)	*Cretoxyrhina mantelli*
	indeterminate elasmosaur	Late Cretaceous	Angola	Araújo et al. (2015)	*Squalicorax pristodontus*
	indeterminate elasmosaur	Late Cretaceous	New Zealand	Barnes and Hiller (2010)	mosasaur *Prognathodon waiparaensis* and shark, similar to or smaller than *Cretoxyrhina mantelli*
	cf. *Cryptoclidus* sp.	Middle Jurassic	UK	Martill et al. (1994)	pliosaur
	Cryptoclidus sp.	Middle/Late Jurassic	UK	Forrest (2000)	75% of sample have bite marks of pliosaur
	Cryptoclidus sp.	Middle Jurassic	UK	Forrest (2003)	marine crocodile *Metriorhynchus*

Mesozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Plesiosauria		Late Cretaceous	USA	Konuki (2008)	*Tylosaurus, Squalicorax falcatus, Pseudocorax laevis*
	Cryptoclidus eurymerus	Middle Jurassic	England	Rothschild et al. (2018)	*Peloneustes* (a small pliosaur, healed)
	cf. *Cryproclidus*	Late Jurassic	England	Martill et al. (1994)	
	indeterminate	Late Jurassic	USA	Wahl (2006)	? juvenile propodial
	Pliosaurus sp.	Early Jurassic	England	Grange et al. (1996)	
	Kronosaurus sp.	Early Cretaceous	Australia	McHenry (2009)	*Kronosaurus*
	Kronosaurus queenslandicus	Early Cretaceous	Australia	Holland (2018)	cretoxyrhinid lamniform
	indeterminate	Late Jurassic	Mexico	Buchy (2007)	pliosaur + indeterminate
Ichthyosauria	*Leptonectes cf. tenuirostris*	Early Jurassic	England	Maisch and Matzke (2003)	?angular, healed
	Temnodontosaurus sp.	Early Jurassic	Germany	Pardo-Pérez et al. (2018)	5 specimens, possibly *Temnodontosaurus,* crocodylomorph or *Steneosaurus*
	Dearcmhara shawcrossi	Middle Jurassic	Scotland	Brusatte et al. (2015)	humerus
	indeterminate	Middle Jurassic	England	Martill (1996)	pliosaur *Liopleurodon*
	Platypterygiinae gen. et sp. indet.	Late Jurassic	Russia	Zverkov et al. (2015)	medium-sized pliosaur.
	Cryopterygius kielanae	Late Jurassic	Poland	Tyborowski (2016)	
	?ophalmosaurid	Late Jurassic	Norway	Druckenmiller et al. (2012); Novis (2012)	pelvic area
	Platypterygius australis	Late Cretaceous	Australia	Zammit, (2011); Zammit and Kear (2011)	*Platypterygius australis*
Marine reptiles?	marine reptiles?	Late Cretaceous	USA	McKean and Gillette (2015)	
Crocodyliformes	*Geosaurus saltillense*	Late Jurassic	Mexico	Buchy et al. (2006)	crocodilian
	Geosaurus vignaudi	Late Jurassic	Mexico	Frey et al. (2002)	
	Pachycheilosuchus trinquei	Early Cretaceous	USA	Rogers (2003)	large predator
	? Rhabdognathus keiniensis	Late Cretaceous	Mali	Hill et al. (2015)	neoselachian - *Linichnus serratus,* serrate-toothed - *Knethichnus parallelum*

Mesozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Crocodyliformes	*Oceanosuchus boecensis*	Late Cretaceous	France	Hua et al. (2007)	
	Neosuchian crocodylomorph	Late Cretaceous	Netherlands	Mulder et al. (2016)	femur, *Linichnus* isp.
	Thoracosaurus neocesariensis	Late Cretaceous/ Paleocene	USA	Boles and Lacovara(2013)	*Squalicorax*
Pterosauria	*Pteranodon* cf. *P. longiceps*	Late Cretaceous	USA	Ehret and Harrell (2018)	*Squalicorax kaupi*, and a small to moderate-sized saurodontid fish, such as *Saurodon* or *Saurocephalus*
	Pteranodon sp.	Late Cretaceous	USA	Konuki (2008); Hone et al. (2018b)	*Cretoxyrhina mantelli* tooth and possibly missing, damaged neural spines
		Late Cretaceous	USA	Bennett in Witton (2018)	tooth gouges made by the serrated teeth of *Squalicorax*
	Anhanguera sp.	Early Cretaceous	Brazil	Buffetaut et al. (2004); Kellner (2004)	dentalite infilled by spinosaur tooth
Hadrosauroidea	indeterminate	Late Cretaceous	USA	Schein and Poole (2014)	*Cretalamna appendiculata* or *Odontaspis cuspidata*, and possibly secondarily by *Hexanchus* sp.
	indeterminate	Late Cretaceous	USA	Everhart and Ewell (2006)	no serrations *Cretoxyrhina mantelli*
	indeterminate	Late Cretaceous	USA	Schwimmer et al. (1997)	*Squalicorax*, tooth in dentalite
	Indeterminate ?lambeosaur	Late Cretaceous	USA	Brownstein and Bissell (2021)	shark without serrated dentition, possibly *Cretalamna*
Nodosauridae	*Niobrarasaurus coleii*	Late Cretaceous	USA	Everhart and (Hamm, 2005)	*Cretoxyrhina mantelli*
Theropoda	ornithominimosaur	Late Cretaceous	USA	Brownstein (2018)	shark, on femur
	theropod	Late Cretaceous	USA	Brownstein (2018)	crocodile, on tibia
Aves	*Hesperornis* sp	Late Cretaceous	USA	Martin et el. (2016)	polycotylid plesiosaur

Mesozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
	bird	Late Cretaceous	USA	Hanks and Shimada (2002)	*Squalicorax*

TABLE A.2. Mesozoic nonmarine dentalites on bony substrate.

Mesozoic nonmarine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Temnospondyli	*Broomistega putterilli*	Early Triassic	South Africa	Fernandez et al. (2013)	two punctures above left orbit may be dentalites
	Koskinonodon perfectum	Late Triassic	USA	Rinehart et al. (2006)	*Heterodontichnites hunti*; phytosaur
Testudines	*Foxemys trabanti*	Late Cretaceous	Hungary	Botfalvai et al. (2014)	crocodilian
	Plesiochelys solodurensis	Late Jurassic	Germany	Karl (2012)	machimosaurid, velociraptorine, dromaeosaurid, survived both
	turtle	Early Cretaceous	France	Rozada et al. (2021)	Goniopholididae
	Eurysternum wagleri	Late Cretaceous	Germany	McCoy et al. (2012)	*Goniopholis*
	Rionegrochelys caldieroi	Late Cretaceous	Argentina	de Valais et al. (2020)	crocodyliform
	turtle	Late Jurassic	Germany	Karl and Tichy (2004)	crocodile
	turtle	Late Cretaceous	USA	Noto et al. (2012)	crocodyliform
	turtle	Late Cretaceous	USA	Carpenter and Lindsey (1980)	*Brachychampsa*
	Solnhofia parsonsi	Late Jurassic	Germany	Joyce (2000)	broad nosed crocodilian
	Pleurosternon bullockii	Early Cretaceous	France	Gônet et al. (2019)	Crocodile
	turtle, crocodyliform and dinosaur	Late Cretaceous	Romania	Augustin et al. (2019)	multituberculate mammals, (4) ziphodont theropod dinosaurs or crocodyliforms
	Mongolemys elegans	Late Cretaceous	Mongolia	Szczygielski and Surmik (2020)	
Rhynchocephalia	*Clevosaurus brasiliensis*	Late Triassic	Brazil	Romo-de-Vivar-Martínez et al. (2017)	*Clevosaurus brasiliensis*
Archosauromorpha	protorosaurian	Late Triassic	Italy	Holgado et al. (2015)	large fish, perhaps *Saurichthys* or a coelacanthiform, protorosaurians
Choristodera	*Champsosaurus* sp.	Late Cretaceous	Canada	Longrich and Ryan, (2010)	?multituberculate

Mesozoic nonmarine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Serpentes	*Nidophis insularis*	Late Cretaceous	Romania	Venczel et al. (2015)	crocodyliform or a theropod
Pseudosuchia	*Revueltosaurus callenderi*	Late Triassic	USA	Hunt et al. (2005c); Hunt and Lucas (2014)	?crocodylomorph
Phytosauria	*Nicrosaurus* sp.	Late Triassic	Germany	Abel (1922a); Ruben (1990)	*Nicrosaurus*
	Pseudopalatus sp.	Late Triassic	USA	Camp (1930); Ruben (1990).	*Pseudopalatus*
Aetosauria	*Typothorax coccinarum*	Late Triassic	USA	Drymala and Bader (2012); Drymala et al. (2021)	phytosaur or paracrocodylomorph
	Desmatosuchus sp.	Late Triassic	USA	Zeigler et al. (2002)	possibly phytosaur
Paracrocrodylomorpha	paracrocodylomorphs	Late Triassic	USA	Drumheller et al. (2014)	phytosaur
	Postosuchus kirkpatricki	Late Triassic	USA	Weinbaum (2013)	
Crocodylomorpha	*Dromicosuchus grallator*	Late Triassic	USA	Sues et al. (2003)	paracrocodylomorph
Crocodyliformes	*Anteophthalmosuchus epikrator*	Early Cretaceous	England	Ristevski et al. (2018)	another goniopholid
	Goniopholis simus	Early Cretaceous	England	Andrade et al. (2011)	*Goniopholis simus*
	goniopholid	Early Cretaceous	Spain	Buscalioni et al. (2013)	*Goniopholis*
	?Brachychampsa sealeyi	Late Cretaceous	USA	Williamson (1996)	?*Brachychampsa sealeyi*
	Baurusuchus pachecoi	Late Cretaceous	Brazil	Avilla et al. (2004)	baurusuchid
	Baurusuchus salgadoensis	Late Cretaceous	Brazil	de Vasconcellos and Carvalho (2010)	baurusuchid
	Baurusuchus sp.	Late Cretaceous	Brazil	de Araújo Júnior and da Silva Marinho (2013)	small baurusuchid or theropod
	Iharkutosuchus makadii	Late Cretaceous	Hungary	Botfalvai et al. (2014)	crocodilian
	peirosaurid	Late Cretaceous	Argentina	Fiorelli (2010)	theropod
	crocodilian	Late Cretaceous	Romania	Codrea et al. (2010, 2012)	crocodilian
Theropoda	*Herrerasaurus ischigualastensis*	Late Triassic	Argentina	Sereno and Novas (1994)	parietal and splenial; *Herrerasaurus*
	Monolophosaurus jiangi	Middle Jurassic	China	Tanke and Currie (1998); Brown et al. (2021)	head; *Monolophosaurus jiangi*
	Sinraptor dongi	Late Jurassic	China	Tanke and Currie (1998)	*Sinraptor dongi*

Mesozoic nonmarine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Theropoda	*Allosaurus fragilis*	Late Jurassic	USA	Chure et al. (1998); Drumheller et al. (2020); Brown et al. (2021)	*Ceratosaurus, Torvosaurus* or *Allosaurus*
	"Labrosaurus ferox" Allosaurus?	Late Jurassic	USA	Gilmore (1920); Tanke and Currie (1998)	bitten off symphysis?
	Acrocanthosaurus atokensis	Early Cretaceous	USA	Harris (1997, 1998); Eddy and Clark (2011)	2 skeletons, skull, vertebrae and ribs
	ornithominosaur	Early Cretaceous	France	Rozada et al. (2021)	Goniopholididae
	Carcharodontosaurus saharicus	Late Cretaceous	Algeria	Tanke and Currie (1998); Brown et al. (2021a)	skull; *Carcharodontosaurus saharicus*
	Albertosaurus sarcophagus	Late Cretaceous	Canada	Bell (2010); Brown et al. (2021a)	dentary; *Albertosaurus*
	Albertosaurus sarcophagus	Late Cretaceous	Canada	Tanke and Currie (1998); Currie and Eberth (2010); Brown et al. (2021a)	numerous skull elements; *Albertosaurus sarcophagus*
	Gorgosaurus libratus	Late Cretaceous	Canada	Tanke and Currie (1998); Bell and Currie (2010); Brown et al. (2021a)	many specimens; *Gorgosaurus*
	Daspletosaurus torosus	Late Cretaceous	Canada	Brown et al. (2021a)	many skull elements; *Daspletosaurus*
	Daspletosaurus sp.	Late Cretaceous	Canada	Tanke and Currie (1998); Hone and Tanke (2010); Brown et al. (2021a)	many skull elements; *Daspletosaurus*
	Tarbosaurus bataar	Late Cretaceous	Mongolia	Tanke and Currie (1998)	*Tarbosaurus*
	Tyranosaurus rex	Late Cretaceous	USA	Horner and Lessem (1993); Brochu (2003)	"Sue;" tyrannosaur
	Tyrannosaurus rex	Late Cretaceous	USA/ Canada	Longrich et al. (2010)	*Tyrannosaurus rex*
	Tyrannosaurus rex	Late Cretaceous	USA	Peterson et al. (2020)	juvenile *Tyrannosaurus rex*
	Tyrannosaurus sp.	Late Cretaceous	USA	Stein (2021)	two large, sub-circular holes on the lateral anterior end of dentary
	Tyrannosaurus sp.	Late Cretaceous	USA	Larson (2001)	
	Thanatotheristes olegrootorum	Late Cretaceous	Canada	Brown et al. (2021)	*Thanatotheristes olegrootorum*

Mesozoic nonmarine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Theropoda	tyrannosaurs	Late Cretaceous	USA	Dalman and Lucas (2020)	3 specimens; tyrannosaur
	tyrannosaur	Late Cretaceous	USA	Peterson et al. (2009, 2021)	*Tyrannosaurus*
	tyrannosaur	Late Cretaceous	Canada	Bell and Currie (2010)	tyrannosaur, tooth in dentalite
	tyrannosaur	Late Cretaceous	USA	McLain (2016); McLain et al. (2018)	*Tyrannosaurus rex*; *Knethichnus parallelum*; *Linichnus serratus*
	tyrannosaurids	Late Cretaceous	Canada	Jacobsen (1995, 1998); Jacobsen and Bromley (2009)	theropod
	six genera of tyrannosaurs	Late Cretaceous	USA/ Canada	Rothschild and Molnar (2008)	theropods
	Deinocheirus sp.	Late Cretaceous	Mongolia	Bell et al. (2012)	*Tarbosaurus bataar*
	Vitakridrinda sulaimani	Late Cretaceous	Pakistan	Malkani (2006, 2009, 2010)	*Vitakridrinda*
	Majungasaurus crenatissimus	Late Cretaceous	Madagascar	Rogers et al. (2004); Gutherz et al. (20220)	3 specimens; *Majungasaurus*
	Aniksosaurus darwini	Late Cretaceous	Argentina	Ibiricuet al. (2013)	vertebrate
	Buitreraptor gonzalezorum	Late Cretaceous	Argentina	Gianechini and de Valais (2016)	mammal
	Saurornitholestes langstoni	Late Cretaceous	Canada	Jacobsen and Bromley (2009)	tyrannosaur
	Saurornitholestes langstoni	Late Cretaceous	Canada	Tanke and Currie (1998); Jacobsen (2001)	small tyrannosaur, *Saurornitholestes*
	Stenonychosaurus inequalis	Late Cretaceous	Canada	Currie (1985); Tanke and Currie (1998)	
	ornithomimosaur	Early Cretaceous	France	Gônet et al. (2019)	crocodile
	theropod	Early Jurassic	Antarctica	Hammer and Hickerson (1993)	small theropod
	Gobiraptor minutus	Late Cretaceous	Mongolia	Lee et al. (2019)	
	Velociraptor mongoliensis	Late Cretaceous	Mongolia	Saneyoshi et al. (2011)	mammal
	Velociraptor mongoliensis	Late Cretaceous	Mongolia	Norell et al. (1995)	multiple dentalites on dorsal braincase; *Velociraptor*?
	Tetanurae	Early Cretaceous	Australia	Poropat et al. (2019)	small theropod
	theropod	Late Cretaceous	USA	Schwimmer (2010)	*Deinosuchus*

Mesozoic nonmarine dentalites on bony substrate

Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Sauropoda	*Lufengosaurus huenei*	Early Jurassic	China	Xing et al. (2018)	?*Sinosaurus*; osteomyalitis
	Cetiosauriscus greppini	Late Jurassic	Switzerland	Meyer and Thüring (2003)	femur; *Machimosaurus*
	Titanosauriform	Early Cretaceous	Spain	Alonso et al. (2017)	theropod
	Apatosaurus sp.	Late Jurassic	USA	Osborn (1904)	*Allosaurus*
	Camarasaurus supremus	Late Jurassic	USA	Chure et al. (1998)	*Allosaurus*
	Camarasaurus supremus	Late Jurassic	USA	Jacobsen (1998)	theropod
	Camarasaurus lewisi	Late Jurassic	USA	Jensen (1988); Hunt et al. (1994)	*Torvosaurus* or *Allosaurus*
	three *Camarasaurus*, a partial diplodocid skeleton, left pes and right manus of a brachiosaur	Late Jurassic	USA	Bader et al. (2009)	theropod or crocodilian
	Camarasaurus sp.	Late Jurassic	USA	Jennings and Hasiotis (2006)	*Allosaurus*
	Apatosaurus sp.	Late Jurassic	USA	Kirkland et al. (2005)	theropod
	Apatosaurus sp.	Late Jurassic	USA	Matthew (1908)	*Allosaurus*
	Diplodocus sp.	Late Jurassic	USA	Myers (2004); Myers and Storrs (2007); Storrs et al. (2013)	
	sauropods, theropods, ankylosaur, other	Late Jurassic	USA	Drumheller et al. (2020)	of 2368 vertebrate fossils, 28.885% preserve at least one theropod bite mark; *Allosaurus, Torvosaurus, Saurophaganax*
	mamenchisaurid	Late Jurassic	China	Augustin et al. (2020b)	mammal
	diplodocoid	Late Jurassic	USA	Hone and Chure (2018)	young diplodocoid; large theropod ?*Allosaurus*
	Europasaurus holgeri	Late Jurassic	Germany	Slodownik and Wings (2015); Wings (2015)	small crocodilians or, less likely, sharks
	Dongbeititan dongi	Early Cretaceous	China	Xing et al. (2012)	small theropod tooth in dentalite
	Rapetosaurus sp.	Late Cretaceous	Madagascar	Rogers and Krause (2007)	*Majungatholus atopus*
	Brasilotitan nemophagus	Late Cretaceous	Brazil	Machado et al. (2013)	
	sauropod	Early Cretaceous	Korea	Paik et al. (2011)	small and large theropod

Mesozoic nonmarine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Sauropoda	*Opisthocoelicaudia skarzynskii*	Late Cretaceous	Mongolia	Borsuk-Bialynicka (1977)	anterior border of iliac blade “strongly damaged by predators”
	sauropod	Late Cretaceous	Mongolia	Currie et al. (2018)	caudal vertebra
	titanosaur	Late Cretaceous	Brazil	da Silva Marinho et al. (2011)	osteoderm; large crocodyliform or theropod dinosaur
	titanosaur	Late Cretaceous	Brazil	Paes Neto et al. (2018)	theropod or crocodilian
	sauropod	Late Jurassic	USA	Hasiotis (2004)	*Allosaurus*
	sauropods	Late Cretaceous	Madagascar	Rogers et al. (2004)	*Majungasaurus*
	sauropods	Late Jurassic	USA	Hunt et al. (1994)	theropods
	Mamenschisauridae indet	Late Jurassic	China	Augustin et al. (2020a)	large theropod, probably metriacanthosaurid
Ankylosauria	*Mymoorapelta maysi*	Late Jurassic	USA	Kirkland et al. (2005)	theropod
	Tarchia sp.	Late Cretaceous	Mongolia	Tumanova et al. (1998); Gallagher et al. (1998)	*Tarbosaurus*
Hypsilophontidae	hypsilophodontid	Late Cretaceous	USA	Drumheller and Boyd (2011); Boyd et al. (2013)	crocodyliform feeding on juvenile
Ankylopollexia	*Camptosaurus* sp.	Early Cretaceous	Romania	Grigorescu (1992)	
Parkosauridae	*Thescelosaurus neglectus*	Late Cretaceous	USA	Longrich et al. (2010)	*Tyrannosaurus rex*
Iguanodontia	*Tenontosaurus tilletti*	Early Cretaceous	USA	Gignac et al. (2010)	*Deinonychus antirrhopus*
	Lurdusaurus arenatus	Early Cretaceous	Niger	Taquet and Russell (1999)	left prepubis with two tooth punctures?
	iguanodont	Early Cretaceous	Romania	Posmoşanu (2003)	
	Thescelosaurus neglectus	Late Cretaceous	USA	Longrich et al. (2010)	*Tyrannosaurus rex*
Hadrosauroidea	*Hypacrosaurus* sp.	Late Cretaceous	USA	Chin (1997)	fibula with a tooth embedded in it, *Tyrannosaurus*
	Kritosaurus notabilis	Late Cretaceous	Canada	Pinna (1979)	theropod
	Naashoibitosaurus ostromi	Late Cretaceous	USA	Horner (1992), Tanke and Rothschild (2002); this paper	compression fractured gouge on the dorsal aspect of the left squamosal; “healed remnants of a predator’s bite?”

Mesozoic nonmarine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Hadrosauroidea	*Edmontosaurus regalis*	Late Cretaceous	USA	Bell and Campione (2014)	*Dromaeosaurus albertensis* or juvenile tyrannosaurs
	Edmontosaurus annectens	Late Cretaceous	USA	Ullman et al. (2017)	dromaeosaur
	Edmontosaurus annectens, *Triceratops horridus*	Late Cretaceous	USA	McLain (2016)	tyrannosaur, crocodilians and theropods
	Edmontosaurus sp.	Late Cretaceous	USA	Carpenter (1998); Tanke and Rothschild (2014)	*Tyrannosaurus rex*; osteomyelitis resulting from an infection of a wound, but see Tanke and Rothschild (2014) for alernative hypothesis of damage caused by trampling
	Edmontosaurus sp.	Late Cretaceous	USA	Longrich et al. (2010)	*Tyrannosaurus rex*
	Edmontosaurus sp.	Late Cretaceous	USA	Erickson and Olson (1996)	
	Edmontosaurus sp.	Late Cretaceous	USA	Peterson et al. (2020)	juvenile *Tyrannosaurus rex*
	Edmontosaurus sp.	Late Cretaceous	USA	Gangloff et al. (1999); Gangloff and Fiorillo (2010)	
	Edmontosaurus sp.	Late Cretaceous	USA	Stein (2021)	
	Telmatosaurus transylvanicus	Late Cretaceous	Romania	Codrea et al. (2010); Codrea and Solomon (2012)	crocodilian
	Amurosaurus riabinini	Late Cretaceous	Russia	Lauters et al. (2008)	theropod
	Brachylophosaurus sp.	Late Cretaceous	USA	Murphy et al. (2006)	tyrannosaur
	Brachylophosaurus sp.	Late Cretaceous	USA	Murphy et al. (2013)	tyrannosaur tail
	Brachylophosaurus sp.	Late Cretaceous	USA	LaRock (2000)	
	Gryposaurus sp.	Late Cretaceous	USA	Dinter (2013)	crocodyliform
	Saurolophus sp.	Late Cretaceous	Mongolia	Hone and Watabe (2010)	*Tarbosaurus*
	?Velafrons coahuilensis	Late Cretaceous	Mexico	Rybakiewicz et al. (2019)	crocodilian
	lambeosaurine	Late Cretaceous	Canada	Holland et al. (2021)	possibly smaller tyrannosaurid

Mesozoic nonmarine dentalites on bony substrate

Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Hadrosauroidea	hadrosaur	Late Cretaceous	Canada	Brown et al. (2021)	pedal ungual with multiple bites from adult-sized dromaeosaurid, or a very young tyrannosaurid in late-stage carcass consumption
	hadrosaur	Late Cretaceous	Canada	Brown et al. (2021)	three unguals
	hadrosaur	Late Cretaceous	USA	Rothschild and DePalma (2013)	hadrosaurid skin associated with a skull, showing healed bone around tooth score traces; tyrannosaurid
	hadrosaur	Late Cretaceous	USA	Campagna (2000)	on dentaries
	hadrosaur	Late Cretaceous	USA	Fiorillo (1991a, b)	large theropod
	hadrosaur	Late Cretaceous	Mexico	Rivera-Sylva et al. (2009, 2011)	*Deinosuchus*
	hadrosaur	Late Cretaceous	Mexico	Rivera-Sylva et al. (2012)	tibia; tyrannosaurine
	hadrosaur	Late Cretaceous	Mexico	Serrano-Brañas and Espinosa-Chavez (2017)	crocodilian
	hadrosaur	Late Cretaceous	Spain	Canudo et al. (2005)	osteomyelitis resulting from an infection of a wound
	hadrosaur	Late Cretaceous	USA	DePalma et al. (2013)	*Tyrannosaurus rex* tooth in dentalite in fused caudal centra
	hadrosaur	Late Cretaceous	USA	Gangloff and Fiorillo (2010); Fiorillo et al. (2010)	theropod
	hadrosaurine	Late Cretaceous	USA	Robinson et al. (2015)	theropod
	hadrosaur	Late Cretaceous	USA	Peterson and Daus (2019)	*Tyrannosaurus rex*
	hadrosaurs	Late Cretaceous	USA	Schwimmer (2010)	*Deinosuchus*
	hadrosaurs	Late Cretaceous	USA	Varricchio (1995a, b)	theropod
	hadrosaurs	Late Cretaceous	Canada	Jacobsen (1995, 1998); Jacobsen and Bromley (2009)	theropod
	hadrosaurs	Late Cretaceous	USA	Longrich et al. (2010)	*Tyrannosaurus rex*
	hadrosaur	Late Cretaceous	USA	Lewis (2011)	crocodilian

Mesozoic nonmarine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Ornithischia	ornithopod	Late Cretaceous	USA	Noto et al. (2012)	crocodyliform
	ornithopod	Late Cretaceous	Romania	Benton et al. (2006)	phalanges and vertebrae; theropods
	ornithischian	Late Cretaceous	Canada	Longrich et al. (2010)	*Tyrannosaurus rex*
Stegosauria	*Stegosaurus* sp.	Late Jurassic	USA	Carpenter et al. (2005)	*Allosaurus*
Pachycephalosauridae	*Prenocephale edmontonensis*	Late Cretaceous	Canada	Sullivan (2000)	*Albertosaurus* or *Daspletosaurus*
Ceratopsia	*Psittacosaurus* sp.	Lower Cretaceous	Thailand	Buffetaut et al. (2007)	
	Protoceratops sp.	Late Cretaceous	Mongolia	Saneyoshi et al. (2011)	mammal
	Bagaceratops sp.	Late Cretaceous	Mongolia	Saneyoshi et al. (2011)	mammal
	Brachyceratops sp.	Late Cretaceous	USA	Sampson in Rogers (1990)	
	Pachyrhinosaurus lakustai	Late Cretaceous	USA	Fanti et al. (2015)	small theropod
	small *Centrosaurus* sp.	Late Cretaceous	Canada	Hone et al. (2018)	dromaeosaurid or young tyrannosaur
	Styracosaurus sp.	Late Cretaceous	USA	Rogers (1990)	*Albertosaurus*
	chasmosaurine	Late Cretaceous	USA	Dalman and Lucas (2018)	tyrannosaur
	Eotriceratops xerinsularis	Late Cretaceous	Canada	Wu et al. (2007)	
	Triceratops sp.	Late Cretaceous	USA	Gignac and Erickson (2017)	*Tyrannosaurus rex,* repetitive localized biting
	Triceratops sp.	Late Cretaceous	USA	Erickson and Olson (1996)	*Tyrannosaurus rex*
	Triceratops sp.	Late Cretaceous	USA	Erickson et al. (1996)	*Tyrannosaurus rex*
	Triceratops sp.	Late Cretaceous	USA	Longrich et al. (2010)	*Tyrannosaurus rex*
	Triceratops sp.	Late Cretaceous	USA	Rothschild (2015)	occipital condyles, not bites for feeding, but play; tyrannosaurid
	Triceratops sp.	Late Cretaceous	USA	Happ (2008)	*Tyrannosaurus rex*
	Triceratops sp.	Late Cretaceous	USA	de Rooij (2020)	crocodilian
	ceratopsids	Late Cretaceous	USA/ Canada	Longrich et al. (2010)	*Tyrannosaurus rex*
	ceratopsian	Late Cretaceous	USA	Fowler and Sullivan (2006)	*Daspletosaurus*

Mesozoic nonmarine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Ceratopsia	ceratopsian	Late Cretaceous	Canada	Jacobsen and Bromley (2009)	*Linichnus serratus* matching denticles of *Troodon*
	ceratopsians	Late Cretaceous	Canada	Jacobsen (1995, 1998)	Theropod
	ceratopsian	Late Cretaceous	Canada	Jacobsen and Bromley (2009)	Tyrannosaur
Dinosauria	ornithischians	Late Cretaceous	Canada	Longrich and Ryan (2010)	?multituberculate
	sphenodontids, crocodyliforms and theropod dinosaurs	Late Cretaceous	Argentina	de Valais et al. (2012)	mainly mammals were scavenging on the carcasses; non-mammalian marks also found on the skeletons possibly made by crocodyliforms, dromaeosaurids and snakes
Pterosauria	ornithocheiroid	Early Cretaceous	Australia	Kellner et al. (2010)	wing metacarpal with small depressions
	azhdarchid pterosaur	Late Cretaceous	Canada	Currie and Jacobsen (1995)	*Saurornitholestes langstoni* tooth in dentalite
	Eurazhdarcho langendorfensis	Late Cretaceous	Romania	Vremir et al. (2013)	bite marks on cervical vertebrae and distal metacarpal IV (possibly made by Crocodyliformes)
	Quetzalcoatlus sp	Late Cretaceous	USA	Kellner and Langston (1996)	three openings in the quadrate may be punctures
	pterosaur vertebra	Early Cretaceous	?Brazil	Buffetaut et al. (2004)	spinosaurid tooth in dentalite
Dicynodontia	*Lystrosaurus* sp.	Early Triassic	South Africa	Modesto and Botha-Brink (2010)	
	dicynodont	Middle Triassic	Tanzania	Cruickshank (1986)	*Mandaodontites coxi*; archosaur
	cf. *Ischigualastia* sp.	Late Triassic	USA	Lucas and Hunt (1993); Hunt and Lucas (2014)	phytosaur - *Heterodontichnites hunti*
	dicynodont	Late Triassic	Poland	Budziszewska-Karwowska et al. (2010)	tibia; multiple dentalites
	dicynodont	Late Triassic	Poland	Dzik et al. (2008); Niedźwiedzki et al. (2010)	*Linichnus serratus, Knethichnus parallelum* and *Nihilichnus nihilicus;* attributed to theropod dinosaurs
	Jachaleria candelariensis	Late Triassic	Brazil	Braunn et al. (2001)	

Mesozoic nonmarine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Dicynodontia	dicynodonts	Late Triassic	Brazil	Vega-Dias and Schultz (2007)	archosauriform
Cynodontia	*Exaeretodon* sp.	Late Triassic	Brazil	Müller et al. (2015)	ecteniniid cynodont
Mammalia	*Eodelphis* sp.	Late Cretaceous	Canada	Longrich and Ryan (2010)	?multituberculate

TABLE A.3. Cenozoic marine dentalites on bony substrate.

Cenozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Chondrichthyes	*Anoxypristis*?	Pliocene	Italy	Collareta et al. (2017a)	
	Pristis sp.	Pliocene	USA	Purdy et al. (2001), but see Collareta et al. (2017a)	
	Carcharhinus sp.	Miocene	USA	Godfrey (2003)	*Carcharhinus* tooth in dentalite
	Carcarodon megalodon	Pliocene	USA	Purdy et al. (2001)	shark; tooth on tooth
Osteichthyes	fossil tuna, *Thunnus*	Pliocene	USA	Schneider and Fierstine (2004)	istiophorid billfishes
Testudines	Cheloniidae	Paleocene	Denmark	Myrvold et al. (2018)	crocodilian and shark, carapace fragment
	Ctenochelys cf. *stenoporus*	Paleocene	Denmark	Myrvold et al. (2018)	crocodilian, hypoplasstron
	Chelonioidea indeterminate	Paleocene	Denmark	Milàn et al. (2011)	shark; *Machichnus bohemicus*, others - sharks or fish
Crocodyliformes	dyrosaurid	Paleocene	Niger	Martin (2013)	crocodilian
Protocetidae	*Aegyptocetus tarfa*	Eocene	Egypt	Bianucci and Gingerich (2011)	dentalites on ribs, large shark
Basilosauridae	*Dorudon atrox*	Eocene	Egypt	Fahlke (2012)	*Basilosaurus isis* (both Cetacea, Basilosauridae)
	Dorudon atrox	Eocene	Egypt	Uhen (2004)	*Basilosaurus isis*
	Dorudon atrox	Eocene	Egypt	Voss et al. (2019)	*Basilosaurus isis*
Cetiotheriidae	*Piscobalaena nana*	Miocene	Peru	Collareta et al. (2017b)	*Carcharocles megalodon*
	Cetotherium capellinii	Pliocene	Italy	Freschi (2017)	*Carcharodon carcharias*
	cetothere cetacean	Miocene	USA	Godfrey and Altman (2005)	*Carcharodon megalodon*
	cetotheriid whale	Pliocene	USA	Deméré and Cerutti (1982); Jacobsen and Bromley (2009)	*Carcharodon, Knethichnus parallelum*
Balaenopteridae	*Fragilicetus velponi*	Pliocene	Belgium	Bisconti and Bosselaers (2016)	shark

Cenozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Balaenopteridae	"*Megaptera*" *hubachi*	Pliocene	Chile	Bisconti (2010)	shark
	balaenopterid	Miocene	Argentina	Noriega et al. (2007)	*Isurus xiphodon*
	balaenopterid	Miocene	Peru	Takakuwa (2014)	*"Isurus" hastalis*
	balaenopterid	Early Pliocene	Spain	Muñiz et al. (2009)	*Notorhynchus, Linichnus* isp.
	balaenopterid mysticete	Pliocene	Panama	Cortés et al. (2019)	*Carcharodon carcharias*
Escrichtiidae	*Eschrichtius* cf. *E. robustus*	Pleistocene	USA	Barnes (1976); Barnes and McLeod (1984)	shark bites on snout
Mysticeti	baleen whale	Miocene	USA	Godrey (2021)	distal portion ulna, shark dentalites; *Linichnus bromleyi*
	mysticete	Pliocene	Italy	Portis (1883); Bianucci et al. (2002)	*Carcharodon carcharias*
	mysticete	Pliocene	Peru	Ehret et al. (2009)	tooth in dentalite *Carcharodon* sp.
	mysticete	Pliocene	Spain	Esperante et al. (2009)	shark
	mysticete	Pliocene	Italy	Dominici et al. (2009)	shark
	mysticete	Pliocene	Spain	Muñiz et al., 2020	dentary and rib. *Linichnus bromleyi*. Shark
	baleen whale	Pliocene	USA	Cicimurri and Knight (2009)	*Galeocerdo cuvier, Carcharhinus falciformis, C. longimanus, C. obscurus, C. plumbeus*
	baleen whale	Pleistocene/ Holocene	USA	Cicimurri and Knight (2009)	*Galeocerdo cuvier, Carcharhinus falciformis, C. longimanus, C. obscurus, C. plumbeus*
Odontoceti	*Albertocetus meffordorum*	Early Oligocene	USA	Boessenecker et al. (2017)	vertebrae and chevron; shark, ray, skate or fish; *Linichnus* isp.
	Inticetus vertizi	Miocene	Peru	Lambert et al. (2018)	shark, no serrations
	odontocete	Miocene	USA	Godrey et al. (2018)	three caudal vertebrae. *Carcharocles megalodon* or *Carcharocles chubutensis*
	Physeteroidea	Miocene or Pliocene	USA	Godfrey et al. (2021)	tooth shows three gouges, one of which preserves raking bite traces of *Otodus chubutensis* or *Otodus megalodon*

Cenozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Kogiidae	*Pliokogia apenninica*	Pliocene	Italy	Collareta et al. (2019a)	long, unserrated dentalites, *Cosmopolitodus plicatilis*
Squalodontidae	squalodontid	Miocene	Argentina	Frenguelli (1928)	shark
Eurhinodelphinidae	*Eurhinodelphis* sp.	Miocene	USA	Godfrey (2003)	shark
	eurhinodelphinid-size	Miocene	USA	Godfrey et al. (2018)	two peduncular caudal vertebrae with dentalites of *Carcharocles* spp.
Eurhinodelphinidae	eurhinodelphinid-size	Pliocene	USA	Godfrey et al. (2018)	peduncular caudal vertebra with dentalites of *Carcharocles* spp.
Monodontidae	monodontid	Pliocene	Belgium	Lambert and Gigase (2007)	*Cosmopolitodus hastalis*
Delphinidae	cetacean (dolphin)	Pliocene	Italy	Cigala-Fulgosi (1990); Jacobsen and Bromley (2009)	*Carcharodon carcharias*, *Knethichnus parallelum*
	Hadrodelphis calvertense	Miocene	USA	Dawson and Gottfried (2002); Godfrey (2003)	shark, and tooth in dentalite
	Halitherium schinzii	Oligocene	Austria	Pervesler et al. (1995)	shark
	Astadelphis gastaldii	Pliocene	Italy	Portis, (1883); Bianucci et al. (2002)	*Cosmopolitodus hastalis*
	Hemisyntrachelus cortessi	Pliocene	Italy	Bianucci et al. (2002)	*Carcharodon carcharias*
Cetacea	mysticetes	Miocene	Peru	Bosio et al. (2021)	7 specimens, 4 cetotheriids, 3 indeterminate, *Carcharhinus* cf. *C. leucas* or *Galeocerdo aduncus* and *Cosmopolitodus hastalis* or *C. plicatilis*
	ondontocetes	Miocene	Peru	Bosio et al. (2021)	3 specimens, 1 phocoenid, 2 indetermintae delphinidans; *Cosmopolitodus hastalis* or *C. plicatilis*
	cetaceans	Miocene	Peru	Bosio et al. (2021)	3 indeterminate specimens
	cetacean	Miocene	Venezuela	Aguilera and de Aguilera (2004); Aguilera et al. (2008)	ribs with shark dentalites
	whale	Miocene	USA	Godfrey (2003)	shark
	cetacean	Miocene	Peru	Collareta et al. (2017b)	*Carcharocles megalodon*

Cenozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Cetacea	cetaceans	Miocene	Peru	Bianucci et al. (2018); Basio et al. (2021)	sharks, from Chilcatay Formation and dentalites more common than in underlying Pisco Formation
	cetacean	?Miocene	USA	Mierzwiak and Godfrey (2019)	partial rib with dentalites on both sides of *Carcharocles megalodon*
	cetaceans	Mio-Pliocene	Peru	Esperante et al. (2002, 2015)	3 specimens, shark tooth in dentalite and dentalites
	Cetacea indeterminate	Pliocene	South Africa	Govender (2019)	white shark (*Carcharodon carcharias*) and *Isurus oxyrinchus* or *Cosmopolitodus hastalis*
	cetacean	Pliocene	Italy	Bianucci et al. (2010)	shark
	cetaceans	Pliocene	South Africa	Govender (2015)	*Carcharodon carcharias*
	cetacean	Pliocene	South Africa	Govender and Chinsamy, (2013)	maybe white (*Carcharodon* spp.), Zambezi (bull) (*Carcharhinus leucas*), tiger (*Galeocerdo* sp.) and mako (*Isurus* sp.) sharks
	cetacean	Pliocene	USA	Kallal et al. (2012)	shark or physeterids
	cetacean	Pliocene	Venezuela	Aguilera et al. (2008)	lumbar vertebra with an embedded tooth of a *Carcharocles megalodon*
	cetacean	Pliocene	USA	Purdy (1996)	*Carcharodon carcharias*
	cetacean	Plio-Pleistocene	USA	Deméré and Cerutti (1982); Jacobsen and Bromley (2009)	*Carcharodon, Knethichnus parallelum*
Pinnipedia	Otariidae	Miocene and Pliocene	USA	Boessenecker and Perry (2011)	mammal, 2 specimens; pilot whale or beluga-like cetacean, a terrestrial carnivore, a dusignathine or odobenine walrus, or a case of infanticide by a conspecific otariid
	pinniped	Miocene	USA	Bigelow (1994)	shark
	pinniped	Miocene	Peru	Collareta et al. (2017b)	*Carcharocles megalodon*
	Monachinae	Pliocene	Spain	Muñiz et al. (2008)	

Cenozoic marine dentalites on bony substrate					
Higher level taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Pinnipedia	*Homiphoca* sp.	Pliocene	Spain	Muñiz et al., 2020	pelvic bone; *Linichnus bromleyi*. shark
	Homiphoca sp.	Pliocene	Spain	Rahmat et al. (2018)	bony fish and/ or small sharks; *Linichnus*
	Eumetopias jubatus	Pleistocene	Canada	Harington et al. (2004)	bull *Eumetopias jubatus*
Sirenia	*Halitherium schinzii*	Oligocene	Germany	Diedrich (2008)	*Isurus*
Sirenia	dugongids	Miocene	Venezuela	Aguilera and de Aguilera (2004); Cozzuol and Aguilera (2008)	shark
Sphenisciformes	*Palaeeudyptes klekowskii*	Eocene	Antarctica	Hospitaleche (2016)	small fish
	Tereingaomis moisleyi	Pliocene	New Zealand	McKee (1987)	dolphin
	penguin	Miocene	Argentina	Cione et al. (2010)	carcharhiniform *Galeocerdo aduncus*
	cf. *Spheniscus* sp.	Miocene	Argentina	Walsh and Hume (2001)	similar to *Carcharhinus*
Charadriiformes	?charadiiform	Pliocene	Spain	Muñiz et al. (2008)	shark
Vertebrata	vertebrates	Miocene	USA	Prothero et al. (2008)	sharks
	marine vertebrates	Miocene	Peru	Bianucci et al. (2018)	shark

TABLE A.4. Cenozoic nonmarine dentalites on bony substrate.

Cenozoic nonmarine dentalites on bony substrate					
Higher taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Squamata	*Varanus* sp.	Miocene	Greece	Georgalis et al. (2018)	hyaenid *Protictitherium*
Testudines	turtles	Paleocene	USA	Erickson (1984)	*Leidyosuchus formidabilis*
	pelomedusoid turtle	Paleocene	Columbia	Hastings et al. (2015)	*Anthracosuchus balrogus*
	pelomedusoid turtles	Paleocene	Columbia	Cadena et al. (2012)	crocodile
	Notochelys aff. *N. salmanticensish*	Eocene	Spain	Fuentes (2003)	*Asiatosuchus* sp.
	Echmatemys uintensis	Eocene	USA	Sandau (2005)	crocodilians or large terrestrial carnivores
	Baena arenosa	Eocene	USA	Smith et al. (2017)	carnivore
	Apalone sp.	Eocene	USA	Sandau (2005)	rodent
	turtle	Eocene	USA	Hutchison and Frye (2001)	
	turtle	Eocene	USA	Brand et al. (2000)	rodent gnawing, other predator
	turtle	Oligocene	Vietnam	Böhme et al. (2011)	crocodilian
	tortoise	Oligocene	USA	LaGarry (2004)	

Cenozoic nonmarine dentalites on bony substrate					
Higher taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Testudines	cf. *Acanthochelys;* cf. *Chelonoidis*	Miocene	Bolivia	Cadena et al. (2015)	possible but doubted because no crocodilians in fauna
	turtle	Miocene	USA	Albright (1994)	alligator
	turtle	Miocene	Hungary	Mikuláš et al. (2006)	*Machichnus multilineatus, Machichnus regularis*
	Aldabrachelys gigantea	Pleistocene	Aldabra	Scheyer et al. (2018)	crocodilian
	Chelonoidis sp.	?Pleistocene	Bahamas	Steadman et al. (2007)	*Crocodylus rhombifer*
	Chelonoidis alburyorum	?Pleistocene	Bahamas	Morgan and Albury (2013)	*Crocodylus rhombifer*
	Cheloniidae (marine)	?Pleistocene	Bahamas	Morgan and Albury (2013)	*Crocodylus rhombifer*
Crocodyliformes	*Leidyosuchus formidabilis*	Paleocene	USA	Sawyer and Erickson (1998)	*Leidyosuchus formidabilis,*
	Tilemsisuchus lavocati	Eocene	Mali	Buffetaut (1983)	*Tilemsisuchus lavocati*
	crocodilian cf. *Pallimnarchus* sp.	Pliocene	Australia	Mackness et al. (2010)	crocodilian
	cf. *Asiatosuchus* sp.	Eocene	Pakistan	Angielczyk and Gingerich (1998)	bite
	Toyotamaphimeis machikanensis	Pleistocene	Japan	Katsura (2004)	*Toyotamaphimeis machikanensis*
	crocodile	Pleistocene	Tanzania	Njau (2006)	crocodile
Marsupialia	*Macropus giganteus* other marsupials	Pleistocene	Australia	Camens and Carey (2013)	cf. *Thylacoleo,* rodent gnawing, dasyurid bite, cf. *Sarcophilus*
	Diprotodon optatum	Pleistocene	Australia	Runnegar (1983)	*Thylacoleo carnifex*
	Macropus giganteus titan	Pleistocene	Australia	Horton and Wright (1981); Dortch et al. (2016)	*Thylacoleo carnifex*
"Metacheiromyidae"	*Mylanodon rosei*	Paleocene	USA	Secord et al. (2002)	
Coryphondontidae	*Coryphodon* sp.	Eocene	USA	Lucas and Schoch (1987)	*Coryphodon*
Apheliscidae	*Apheliscus chydaeus*	Eocene	USA	Gingerich (1994)	
Chalicotheriidae	*Litolophus gobiensis*	Eocene	China	Bai et al. (2011)	
Brontotheriidae	*Titanotherium*	Oligocene	USA	Scott and Jepsen (1936)	rodent
Rhinocerotidae	*Chilotherium wimani*	Miocene	China	Deng and Tseng (2010)	female skull; giant percrocutid, *Dinocrocuta gigantea*
	Iberotherium rexmanueli zbyszewskii	Miocene	China	Antunes et al. (2006a)	bear-dog (*Amphicyon giganteus*)

Cenozoic nonmarine dentalites on bony substrate					
Higher taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Rhinocerotidae	*Coelodonta antiquitatis*	Pleistocene	Germany	Diedrich (2006)	*Crocuta crocuta spelaea*
	Coelodonta antiquitatis	Pleistocene	Germany	Diedrich (2011)	*Crocuta crocuta spelaea*
Equidae	*Equus* sp.	Pleistocene	Brazil	Avilla et al. (2018)	ursid
	horse	Miocene	USA	Diffendal (2003)	
Perissodactyla	perissodactyl	Eocene	USA	Alexander and Burger (2001)	within gut of *Pristichampsus vorax*
Entelodontidae	*Archaeotherium walassi; A. scotti*	Oligocene	USA	Sinclair (1922); Effinger (1998)	*Archaeotherium*
Bovidae	*Bison antiquus taylori*	Pleistocene	USA	West and Hasiotis (2007)	rodents
	Bos primigenius	Pleistocene	Czech Republic	Diedrich (2012a)	*Crocuta crocuta spelaea*
	Bos cf. *priscus*	Pleistocene	UK	Buckland (1824)	*Crocuta crocuta spelaea*
	Hippotragus sp.	Pleistocene	South Africa	van Zyl et al. (2016)	carnivore
Tragulidae	*Siamotragulus songhorensis*	Miocene	Uganda	Sánchez et al. (2015)	carnivore
Merycoidodontoidae	oreodonts	Oligocene	USA	Tanke et al. (1992); Tanke and Currie (1998)	carnivore
Climacoceratidae	climacoceratid	Miocene	South Africa	Pickford (1996)	crocodilian
Cervidae	*Euprox furcatus*	Miocene	Austria	Havlik et al. (2014)	medium-sized carnivore
	Megaloceros giganteus	Pleistocene	Czech Republic	Diedrich (2012a)	*Crocuta crocuta spelaea*
	Rangifer tarandus	Pleistocene	Czech Republic	Diedrich (2012a)	*Crocuta crocuta spelaea*
	deer and other mammals	Pleistocene	USA	Glowiak (2007)	*Canis dirus*
Camelidae	*Poebrotherium* sp.	Miocene	USA	Sundell (1999); Benton et al. (2015)	multiple skeletons and dentalites, *Archeotherium* meat cache
	Michenia sp.	Miocene	USA	Morgan and Williamson (2000)	carnivore, rodent gnawing
	camel	Miocene	USA	Winkler (1987)	coyote-sized carnivore
Ungulata	ruminant	Miocene	Austria	Havlik et al. (2014)	femur; undescribed carnivore
	ungulate	Pliocene	Italy	Mazza et al. (2004); Mazza (2006)	*Pachycrocuta brevirostris*
Chlamyphoridae	cf. *Eosclerocalyptus lineatus*	Pliocene	Argentina	de los Reyes et al. (2013)	procyonid *Chapalmalania*

Cenozoic nonmarine dentalites on bony substrate					
Higher taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Mylodontidae	*Glyptotherium* sp.	Pleistocene-Holocene	Brazil	de Araújo-Júnior et al. (2017)	*Machichnus fatimae, Machichnus bohemicus* - *Protocyon troglodytes*
	Pseudoprepotherium sp.	Miocene	Peru	Pujos and Salas-Gismondi (2020)	*Purussaurus,* young or subadult
Megatheriidae	*Eremotherium laurillardi*	Pleistocene-Holocene	Brazil	de Araújo-Júnior et al. (2011, 2017)	*Machichnus bohemicus;* a juvenile individual of *Protocyon troglodytes* or an adult of *Cerdocyon thous*
Proboscidea	*Deinotherium leviusvel giganteum*	Miocene	Austria	Havlik et al. (2014)	larger carnivore
	Mammuthus columbi	Pleistocene	USA	Wiest et al. (2016)	*Machichnus bohemicus* – small carnivore *Nihilichnus nihilicus* – large carnivore *Machichnus regularis* – rodent, large cat
	mammoth	Pleistocene	Germany	Diedrich (2011)	*Crocuta crocuta spelaea*
	gomphothere	Pleistocene	Chile	Labarca et al. (2014)	large felid
	Haplomastodon waringi	Pleistocene	Brazil	Dominato et al. (2011); de Araújo-Júnior et al. (2017)	*Machichnus bohemicus*
	mastodon	Pliocene	USA	Harington (1996)	beaver gnawed molars
	proboscidean	Pleistocene	El Salvador	Cisneros (2005)	rib; *Crocodylus acutus*
Viverravidae	*Viverravus*	Eocene	USA	Gingerich (1987)	mammal
Nimravidae	*Nimravus brachyops*	Oligocene	USA	Scott and Jepsen (1936)	left frontal; *Nimvarus*
	Nimvarids	Oligocene	USA	Boyd et al. (2013)	five crania; mainly nimravids
Ursidae	*Ursus spelaeus*	Pleistocene	Spain	Pinto Llona and Andrews (2004)	*Ursus spelaeus*
	Ursus spelaeus	Pleistocene	Spain	Rabal-Garcés et al. (2012)	*Ursus spelaeus*
	Ursus spelaeus	Pleistocene	Germany	Diedrich (2013)	*Panthera leo spelaea, Crocuta crocuta spelaea*
	Ursus spelaeus	Pleistocene	Spain	Capasso (1998)	*Ursus spelaeus* or *Panthera leo spelaea*
Amphicyonidae	*Daphoenodon superbus*	Miocene	USA	Hunt et al. (1983); Hunt (1984)	carnivorous mammal
Canidae	*Canis lupus*	Pleistocene	USA	Courville (1953)	intraspecific

Cenozoic nonmarine dentalites on bony substrate					
Higher taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Felidae	*Smilodon fatalis*	Pleistocene	USA	Miller (1980); Akersten (1985); Rothschild and Martin (1993)	intraspecific
	Smilodon populator	Pleistocene-Holocene	Brazil	de Araújo-Júnior et al. (2017)	*Machichnus bohemicus* - a juvenile individual of *Protocyon troglodytes* or an adult of *Cerdocyon thous*
	Panthera leo spelaea	Pleistocene	Germany	Diedrich (2011)	*Crocuta crocuta spelaea*
Hyaenidae	*Crocuta crocuta spelaea*	Pleistocene	Czech Republic	Diedrich (2012a)	*Crocuta crocuta spelaea*
Carnivora	*Canis*, Lynx	Pleistocene	Italy	Sardella et al. (2018)	*Acinonyx pardinensis*, crania
Rodentia	*Isoptychus* sp., *Thalerimys fordi*	Eocene	UK	Vasileiadou et al. (2007, 2009)	*Cynodictis* cf. *lacustris*
	Xerus daamsi	Pliocene	Chad	Denys et al. (2003)	mammalian carnivore
Lemuriformes	lemurs	Pleistocene	Madagascar	Meador (2017)	crocodiles, raptors, mammalian carnivores
Notharctidae	*Notharctus* sp.	Eocene	USA	Alexander (1992)	*Vulpavus*
	Notharctus, Omomys	Eocene	USA	Alexander and Burger (2001)	raptor dentalites
	Notharctus sp.	Eocene	USA	Alexander and Burger (2001)	?*Vulpavus*
Adapidae	*Europolemur* sp.	Eocene	Germany	Franzen and Frey (1993); Franzen (2001)	small crocodilian
Propliopthecidae	*Aegyptopithecus* and *Propliopithecus*	Oligocene	Egypt	Gebo and Simons (1984)	crocodile or creodont
Cercopithecidae	*Mesopithecus pentelicus*	Miocene	Greece	Zapfe (1981)	felid
	Theropithecus oswaldi leakeyi	Pleistocene	Tanzania	Frost et al. (2017)	felid
Homininae	*Orrorin tugenensis*	Miocene	Kenya	Gommery et al. (2007)	proximal femur
	Australopithecus anamensis Australopithecus afarensis	Pliocene	Ethiopia	Sahle et al. (2017)	crocodilian
	Australopithecus africanus, Paranthropus robustus (and cercopithecoids)	Pleistocene	South Africa	Brain (1970, 1978, 1981)	leopard, felids
	Australopithecus africanus (and cercopithecoids)	Pleistocene	South Africa	Berger and Clarke (1995); Sanders et al. (2003)	raptor, Taung child

Cenozoic nonmarine dentalites on bony substrate

Higher taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Homininae	*Homo erectus*	Pleistocene	China	Boaz et al. (2004)	*Pachycrocuta brevirostris*
	Homo erectus	Pleistocene	Georgia	Wong (2003)	felid
	Homo habilis	Pleistocene	Tanzania	Davidson and Soloman (1990); Njau (2006); Njau and Blumenschine (2006); Brochu et al. (2010)	*Crocodylus anthropophagus*
	Homo sp.	Pleistocene	Morocco	Daujeard et al. (2016)	*Crocuta crocuta* or *Hyaena hyaena*
	Homo neanderthalis	Pleistocene	Spain	Camarós et al. (2015)	large felid
	Homo neanderthalis	Pleistocene	Croatia, Portugal, Germany, Spain, France, Italy	Diedrich (2014)	*Crocuta crocuta spelaea* and other carnivores
Mammalia	mammal	Paleocene	USA	Longrich and Ryan (2010)	multituberculate gnawing
	multiple mammals, including *Ignacius* sp.	Paleocene	USA	Gingerich (1987); Bloch and Boyer (2001)	mammal
	mammals	Paleocene	USA	Sinclair and Granger (1914); Simpson and Elftman (1928)	*Eucosmodon*
	early equids, and the tapir-like perissodactyl *Lophiodon,* and turtle shells	Eocene	Germany	Falk et al. (2019)	crocodilians
	mammals	Eocene	France	Laudet and Fosse (2001)	rodents, possibly *Archaeomys*
	mammals	Oligocene	USA	Longrich and Ryan (2010)	gnawing
	mammals	Oligocene	USA	LaGarry (2004)	*Hesperocyon, Mesocyon, Daphoenus hartshornianus, Daphoenus vetus,* and rodents
	ungulates, small mammals and carnivores	Miocene	Hungary	Mikuláš et al. (2006); Ekrt et al. (2016)	*Nihilichnus nihilicus, Nihilichnus mortalis, Machichnus regularis, Machichnus multilineatus, Machichnus bohemicus, Brutalichnus brutalis*, - squirrels, carnivore *Amphicyon* sp. and crocodilians
	mammals	Miocene	China	Andersson and Kaakinen (2004)	
	mammals	Miocene	USA	Bartley (2005)	carnivores

Cenozoic nonmarine dentalites on bony substrate					
Higher taxon of substrate	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Mammalia	mammals	Miocene	Uganda	Morales (2016)	gnawing marks due to carnivore activity, parallel gnawing traces made by rodents.
	alcelaphine bovid, ungulate, bovid, equid	Pliocene	Ethiopia	Sahle et al. (2017)	crocodilian
	large mammals	Pliocene	Tanzania	Su and Harrison (2008)	carnivores
	bovids, mammals	Pleistocene	South Africa	Brain (1970, 1978, 1981); Pickering et al. (2004)	leopards, hyenas, other carnivores
	mammals (bovid, suid, *Parmularius*, Tragelaphini, Alcelaphini, Antilopini, equid)	Pleistocene	Tanzania	Bunn et al. (1986); Njau (2006); Njau and Blumenschine (2006)	carnivores, rodents
	Bison, *Mammuthus*, *Alces*, *Equus*, *Cervus*, and *Rangifer*	Pleistocene	USA	Haynes (1980)	canid, felid, ursid gnawing
	Stephanorhinus etruscus, Equus altidens, Megaloceros (*Megaceroides*) *solilhacus*	Pleistocene	Spain	Palmquist et al. (1996); Palmqvist and Arribas (2001)	*Pachycrocuta brevirostris* and other carnivores
	mammals	Pleistocene	South Africa	Kandel and Conrad (2012)	>200 bones with bites or rodent gnawing
	mammals	Pleistocene	Australia	Westaway et al. (2011)	*Pallimnarchus*
	mammals	Pleistocene	Pakistan	Dennell et al. (2008)	*Pachycrocuta brevirostris*
	mammals	Pleistocene	Brazil	Araújo-Júnior et al. (2011, 2017)	*Machichnus bohemicus*
Aves	penguin	Miocene	Argentina	Cione et al. (2010)	didelphid or borhyaenid marsupials, didelphid or hathliacyniid sparassodont marsupials
	Cayaoa bruneti	Miocene	Argentina	De Mendoza and Haidr (2018)	Hathliacynidae
	Geronticus cf. *calvus*	Pliocene	South Africa	Pavia et al. (2017)	
	Moa	Holocene	New Zealand	Farlow and Holtz (2002)	*Harpagornis*

TABLE A.5. Dentalites on invertebrate substrate.

Vertebrate dentalites on invertebrate substrate						
Ecology	**Higher level taxon of substrate**	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
Sessile	rugose coral	*Calceola sandalina*	Middle Devonian	Czech Republic	Galle and Mikulas (2003)	fish-like animals capable of durophagy (placoderms and chondrichthyans)
	hermatypic coral	*Acropora cervicornis*	Late Pleistocene	Jamaica	Kaufman (1981)	three spot damselfish, *Eupomacentrus planifrons* - gall-like growths called "chimneys," in response to damage by the threespot
	crinoid		Middle Devonian	Poland	Gorzelak et al. (2011)	Coccosteidae (Arthrodira), placoderm
		Holocrinus longicirrifer	Early Mississippian	USA	Gahn (2004)	
			Late Jurassic	Poland	Lach et al. (2015)	fish on ossicles
		Clypeaster spp.	Late Miocene	Spain	Santos et al. (2003)	fish
		Cupressocrinitidae	Middle Devonian	Germany	Bohatý (2008, 2009)	cephalopods, placoderms or arthropods
			Middle Triassic	Poland	Salamon and Gorzelak (2008)	fishes, arthropods, asteroids and echinoids
			Late Cretaceous	Poland	Salamon and Gorzelak (2010)	high percentage of bite-marks and aberrant growths
		Bougueticrinus hagenowii	Late Cretaceous	Poland	Jagt and Salamon (2007)	?bite marks
		Semiometra saskiae	Late Cretaceous		Jagt et al. (2018)	fish or decapod
	echinoid		Middle Jurassic	Israel	Wilson et al. (2014)	fish bites on spines, *Machichnus bohemicus, Nihilichnus nihilicus*
		Echinocorys ovata	Late Cretaceous	Germany	Neumann and Hampe (2018)	globidensine mosasaur, probably *Prognathodon*
		Echinocorys sp.	Late Cretaceous	Netherlands	Jagt et al. (2018)	teleost fish and/or neoselachian

Vertebrate dentalites on invertebrate substrate						
Ecology	**Higher level taxon of substrate**	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
	echinoid	*Hemipneustes striatoradiatus*	Late Cretaceous	Netherlands	Donovan et al. (2008)	bony fish or small mosasaur, but see Neumann and Hampe (2018)
		Ananchytes ovata	Late Cretaceous	Germany	Gripp (1929)	
		Echinocorys sovata	Late Cretaceous	Germany	Thies (1985)	pock-marked test from teleost or shark
		Recurvaster polyplacus	Late Cretaceous	Germany	Neumann (2003)	fishes
		Pycinaster magnificus	Late Cretaceous	Germany	Neumann (2003)	galeoid shark *Squalicorax*
			Late Cretaceous	Germany	Schormann (1987)	fish
		Echinocorys sp.	Late Cretaceous	Germany	Frerichs (2012)	fish
			Late Cretaceous	Germany	Girod and Rösner (2013)	fish
			Late Cretaceous	Netherlands	Dortangs (1998)	fish
		Parascutella höbarthi	early Miocene	Austria	Nebelsick (1999); Kowalewski and Nebelsick (2003)	hollowed-out central area and paired grooves leading to the wound, similar to Recent triggerfish
		Monophoraster darwini	late Miocene	Argentina	Zinsmeister (1980)	test margin damage produced by small fish
	conulariid	*Paraconularia magna*	Late Pennsylvanian	USA	Mapes et al. (1989)	cladodont shark
	bivalve	*Ptychopteria* sp.	Middle Devonian	USA	Nagel-Myers et al. (2009)	fish, arthropod or cephalopod
			middle Permian	USA	Boyd and Newell (1972)	high percentage have divots probably produced by sharks
		Gryphaea lituola	Middle Jurassic	UK	Phipps (2008)	*Steneosaurus durobrivensis*
		Inoceramus	Late Cretaceous	USA	Kauffman (1972)	*Ptychodus*

Vertebrate dentalites on invertebrate substrate						
Ecology	**Higher level taxon of substrate**	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
	bivalve	nonmarine bivalve	Late Triassic	Poland	Gorzelak et al. (2010)	*Ceratodus, Hybodus*
		unionid	Early Cretaceous	Australia	Kear and Godthelp (2008)	large osteichthyan or chondrichthyan fish, crocodiles, and pliosauroid plesiosaurs
		Protopleurobema numantina	Early Cretaceous	Spain	Bermúdez-Rochas et al. (2013)	crocodiles
	rudist	*Durania maixima*	Late Cretaceous	USA	Hattin (1988)	?sea turtle
	brachiopod	productid	Early Carboniferous	England	Brunton (1966)	sharks
		brachiopods	Late Mississippian	USA	Alexander (1981)	sharks, some tetrahedron shaped
		Pygope adnethenses	Early Jurassic	Hungary	Tasnadi-Kubacska (1962)	fish
		Pyope, Menzelia	Mesozoic	Europe	Tasch (1973)	fish or reptiles
	epibionts		Miocene	Argentina	Cione et al. (2010)	epibionts on penguin bones
Vagrant	asteroid	Sea stars	Middle Jurassic	Poland	Zatoń et al. (2007)	ossicles in regurgitalites, durophagous sharks or pycnodontiform fishes
		Pycinaster magnificus,	Late Cretaceous	Germany	Neumann (2000)	galeoid shark *Squalicorax*
	crab	*Raninella* sp.	Late Cretaceous	USA	Bishop (1975)	fish
Nektonic	foraminiferan	*Assilina exponens*	Eocene	India	Syed and Sengupta (2019)	scarid parrotfish
	nautiloid	multiple taxa	Early Devonian	Morocco	Klug (2007)	mainly dentalites of nautiloids but cannot be excluded that some are vertebrate in origin
		nautiloid	Early Pennsylvanian	USA	Mapes and Hansen (1983); Hansen and Mapes (1990)	*Symmorium reniforme*
		nautiloid	Early Pennsylvanian	USA	Hansen and Mapes (1990)	*Petalodus ohioensis*

Vertebrate dentalites on invertebrate substrate						
Ecology	**Higher level taxon of substrate**	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
	nautiloid	Pseudorthoceratidae	Middle Pennsylvanian	USA	Seuss et al. (2012)	shark or other fish
		Tainoceras, Neobistrialites	Pennsylvanian	USA	Mapes and Chaffin (2003)	*Symmorium reniforme*
		Eutrephoceras dekayi	Late Cretaceous	USA	Kauffman and Sawdo (2013)	*Platycarpus*, *Prognathodon* or *Mosasaurus*
		Argonautilus catarinae	Late Cretaceous	USA	Kauffman (2004)	mosasaur
		nautiloid	Late Cretaceous	Canada	Ludvigsen and Beard (1997)	mosasaur
	ammonoid	*Platyclymenia annulata, P. subnautilina, Pleuroclymenia costata*, and *Prionoceras divisum*	Late Devonian	Germany	Slotta et al. (2011)	possibly jawed, fish-like chondrichthyans
		various	Late Devonian-Recent	Various	Keupp (2006)	some large-scale, sub-lethal injuries occurring since the Late Devonian were due to attacks by durophagous vertebrates
		Anthracoceras discus, Fayettevillea bransoni, Fayettevillea friscoense, Rhadinites miseri, Richardsonites mapesi	Late Mississippian	USA	Bond and Saunders (1989)	sharks, other fishes, or cephalopods
		Gonioloboceras goniolobum	Pennsylvanian	USA	Mapes et al. (1995)	chondrichthyans and other fish, particularly the symmoriid shark *Symmorium reniforme*
		Gonioloboceras sp.	Pennsylvanian	USA	Mapes and Chaffin (2003)	*Symmorium reniforme*
		Gonioloboceras sp.	Pennsylvanian	USA	Sims et al. (1987)	

Vertebrate dentalites on invertebrate substrate						
Ecology	**Higher level taxon of substrate**	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
	ammonoid	Dactylioceratidae (*Dactylioceras*) and Hildoceratidae (*Cleviceras, Fuciniceras, Fontanelliceras, Harpoceras, Paltarpites*, and *Protogrammoceras*	Early Jurassic	Japan	Takeda and Tanabe (2014)	mainly by ammonites, but some possibly by jawed fishes and marine reptiles
		Dactylioceras sp.	Early Jurassic	Germany	Lehmann (1975)	
		Oxycerites sp.	Middle Jurassic	Germany	Hoffmann and Keup (2015)	pycnodontid bite mark on both sides
		Gymnites sp.	Early Triassic	Greece	Hoffmann and Keup (2015)	fish
		ammonoids	Early Jurassic-terminal Cretaceous	various	Klompmaker et al. (2009)	ventral bite marks are situated at the end of the body chamber, close to the phragmocone, predatory attacks on the back or blind side of ammonoids, produced by probably coleoid cephalopods (especially teuthoids) and also predatory fish
		various	Late Devonian-Cretaceous	Various	Keupp (2006)	some large-scale, sub-lethal injuries occurring since the Late Devonian were due to attacks by durophagous vertebrates
		Pinacoceras parma	Late Triassic	Austria	Tichy and Urbanek (2004)	nothosaur
		Ataxioceras hypselocyclum	Late Jurassic	Germany	Keupp (2006)	crustacean or vertebrate
		Promicroceras, *Xipheroceras*, *Cymbites*, *Arnioceras*, *Asteroceras*, *Caenisites*, *Eoderoceras* and *Paltechioceras*?	Early Jurassic	UK	Andrew et al. (2015)	

Vertebrate dentalites on invertebrate substrate						
Ecology	**Higher level taxon of substrate**	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
	ammonoid	*Kosmoceras* cf. *K. obductum*	Middle Jurassic	UK	Martill (1990)	semionotid or pycnodontid
		Kosmoceras gulielmi	Middle Jurassic	UK	Ward and Hollingworth (1990)	unknown marine reptile
		Oxycerites sp.	Middle Jurassic	Germany	Richter (2009)	Pycnodontidae
		Orthaspidoceras sp.	Late Jurassic	France	Vullo (2011)	hybodont shark *Planohybodus*; tooth in dentalite and possible dentalites
		Kachpurites, Craspedites	Late Jurassic	Russia	Mironenko (2020)	small apertural injuries, likely traces of fish bites
		Desmoceras latidorsatum	Early Cretaceous	Madagascar	Hoffmann and Keupp (2015)	semionotid fish
		Placenticeras, *Sphenodiscus* and much less common *Baculites*	Late Cretaceous	USA	Kauffman, (1990b)	more than 100
		Placenticeras sp. cf. *P. whitfieldi*	Late Cretaceous	USA	Kauffman and Kesling (1960); Kauffman (1990b)	Platecarpinae
		Placenticeras meeki	Late Cretaceous	Canada	Hewittand Westermann (1990)	mosasaur
		Placenticeras meeki	Late Cretaceous	Canada	Wahl, (2008)	mosasaur
		Placenticeras sp.	Late Cretaceous	USA	Hoffmann and Keupp (2015)	mosasaur
		Placenticeras sp.	Late Cretaceous	Canada	Kauffman (1990b)	*Mosasaurus*
		Placenticeras sp.	Late Cretaceous	Canada	Tsujita and Westermann (1998)	*Prognathodon*
		Metoicoceras sp.	Late Cretaceous	USA	Kauffman (1990b)	*Globidens*
		Sphenodiscus sp.	Late Cretaceous	USA	Bukowski and Bond (1989)	mosasaur
		Pseudaspidoceras madagascariensis	Late Cretaceous	Morocco	Gale et al. (2017)	mosasauroid, *Tethysaurus*
		Pseudaspidoceras flexuosum.	Late Cretaceous	Mexico	Ifrim (2013)	*Ptychodus*

Vertebrate dentalites on invertebrate substrate						
Ecology	**Higher level taxon of substrate**	**Taxon of substrate**	**Age**	**Location**	**References**	**Notes/biter**
	ammonoid	*Anapachydiscus peninsularis*	Late Cretaceous	Mexico	Saul (1979)	mosasaur
		ammonite	Late Cretaceous	Canada	Ludvigsen and Beard (1997)	mosasaur
	coleoid	*Plesioteuthis subovata*	Late Jurassic	Germany	Hoffmann et al. (2020)	tooth of *Rhamphorhynchus muensteri* embedded in dentalite
	"squid"	*Tusoteuthis longa*	Late Cretaceous	USA	Stewart and Carpenter (1990)	*Tylosaurus proriger*
	thylacocephalan		Late Devonian	Poland	Broda et al. (2015)	fish damaged and fragmented carapaces
	conchostracan	*Yanjiestheria* sp.	Early Cretaceous	China	Bi (1986)	growth line abnormalities supposedly caused by fish biting
Volant	odonatan insect	*Cymatophlebia longialata*	Late Jurassic	Germany	Tischlinger (2001)	removal of the posterior right wingtip; also, minor damage to the posterior margin of the right anterior wing caused by pterosaur bite
	neuropteran insect	*Archegetes neuropterum*	Late Jurassic	Germany	Tischlinger (2001)	removal of anterior left wingtip by pterosaur bite

TABLE A.6. Paleozoic marine consumulites.

Paleozoic marine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Metazoa	*Typhloesus wellsi*	conodont apparatuses, fish, and worm teeth	early Mississippian	USA	Melton (1972); Conway Morris (1976, 1990)	
Endeiolepidiformes	*Endeiolepis aneri*	gastrolite is oblong patch of fine-grained matter, phosphatized mass	Late Devonian	Canada	Stensiö (1939); Janvier (1996b); Janvier and Arsenault (2007)	present in virtually all specimens
Furcacaudiformes	*Pezopallichthys ritchie*	gastrolite is flattened, barrel-like shape, sediment infilling, intestinilite is preserved in some specimens from gastrolite to anal notch	Middle Silurian	Canada	Wilson and Caldwell (1993, 1998)	
	Cometicercus talimaaa	the posterior end of the intestinilite is preserved as a small tubular structure at the anal notch, sediment infilling	Early Devonian	Canada	Wilson and Caldwell (1998)	
	Sphenonectris turnerae	gastrolite is represented by a large rectangular endocast of sediment infilling that has ananteroventral corner immediately posterior to the branchial row, several specimens show the weathered remnants of a slender, conical, intestinilite extending from the posteroventral corner of the gastrolite to the anal notch	Early Devonian	Canada	Wilson and Caldwell (1998)	long axis of the gastrolite makes a 25 degree angle with the long axis of the body, and the posteroventral corner reaches two-thirds the distance to the anal notch
	Furcacauda heintzae	gastrolite, and posterior to it is a short, conical intestinilite, that extends to the prominent anal notch, sediment infillings	Early Devonian	Canada	Wilson and Caldwell (1998)	gastrolite begins immediately posterior to the branchial row, and has its posteroventral corner near the ventral body margin at the end of the paired “fin-flaps;” the long axis of the stomach is parallel to the branchial row

Paleozoic marine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Furcacaudiformes	*Furcacauda fredholmae*	gastrolite consists of a rectangular endocast of fine sediment, leading posteriorly into a short, conical endocast interpreted as the short intestine, which reaches the anal opening at the anal notch	Early Devonian	Canada	Wilson and Caldwell (1998)	
Euphanerida	*Euphanerops longaevus*	gastrolite composed of oblong mass of fine-grained whitish or grayish matter	Late Devonian	Canada	Arsenault and Janvier (1991); Janvier and Arsenault (2007)	several specimens, the fine-grained sediment in the gastrolite suggests microphagous bottom feeding; in two specimens the gastrolite contents show in its center one or two rounded dark stains that suggest the presence of larger food particles but may be overprinting
Petromyzontida	gen. et sp. indet.	elongated black impression behind the branchial pouches is most probably that of the digestive tract, and in the posterior of the specimen there is a ventral dark area that may be due to the accumulation of organic matter in the cloaca	Early Carboniferous	USA	Lund and Janvier (1986)	accumulation of organic matter in the cloaca is often observed in Recent larval lampreys
Chirodipteridae	*Gogodipterus paddyensis*	gut contents	Late Devonian	Australia	Long (1992)	
Coelolepidae	*Turinia pagei*	gastrolite composed of silt-grade sediment that is much finer, and of different petrological composition than that which surrounds the body	Early Devonian	Scotland	Novitskaya and Turner (1998); Donoghue and Smith (2001)	the presence of fine-grained sediment filling the stomach and gut, but not the buccopharyngeal area, of the holotype, provides support for the interpretation of a deposit feeder

Paleozoic marine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Antiarchi	*Bothriolepis canadensis*	carbonaceous sediment	Late Devonian	Canada	Denison (1941); McAllister (1996); Upeniece (2001)	several sectioned specimens have intestinilites and enterospira – infilled valvular intestines
Antiarchi	*Asterolepis ornata*	carbonaceous and detritic-like bone material occur in several cases, as well as numerous grains of quartz; this suggests that these remains are stomach contents, with the stomach full of digested food matter at the time of death of the animal	Late Devonian	Latvia	Upeniece (2001, 2011)	occurs in >100 juveniles - not visible from the outside in adults due to the heavy armor; demonstrates mud grubber behavior of the juvenile *Astercolepis*
Arthrodira	*Coccosteus cuspidatus*	stomach contents include mostly small acanthodians and other young fish, three specimens have phosphatized material in the region of the intestine and contained scales of acanthodians, bones probably belonging to dipnoans	Middle Devonian	Scotland	Heintz, (1938); Miles and Westoll, (1968); Davidson and Trewin (2005)	gastroliths
	plourdosteid	juvenile ptyctodontid, *Ctenurella* sp.	Late Devonian	Russia	Zakharenko (2008)	
	Incisoscutum richiei	?*Incisoscutum richiei*	Late Devonian	Australia	Dennis and Miles (1981)	prey ingested head first
Symmoriiformes	*Cladoselache spp - C. brachypterygius*, *C. fyleri, C. clarki, C. desmopterygius* and *C.* sp.	about 75% contain palaeoniscoid debris and a couple of complete fish (*Kentuckia blavini*), several contain arthropods and yield four conodonts; three specimens of the crustacean *Concavicaris* cf. *bradleyi* were swallowed tail first	Late Devonian	USA	Williams (1990)	more than 40 specimens

Paleozoic marine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Symmoriiformes	*Akmonistion zangerli*	an area of debris posterior to the branchial skeleton and pectoral girdle represents remains of stomach/foregut contents; debris includes small fragments (around 1–2 mm across) of arthropod cuticle and actinopterygian scales; a second region of preserved gut contents lies directly above the pelvic plates and ventral to the dorsal fin; this squat bolus (incorporeal pelletiite) measures about 15 mm along its longest axis; the posterior end is blunt	early Carboniferous	Scotland	Coates and Sequeira (2001); Hunt and Lucas (2021a)	*Chondripilula zideki*
Ctenacanthiformes	*Ctenacanthus compressus*	*Stenosteus glaber*	Late Devonian	USA	Williams (1990)	
Xenacanthida	*Triodus sessilis*	*Cheliderpeton latirostre* with ingested juvenile of *Acanthodes bronni*, skull of larval *Archegosaurus decheni*	Permian (lowermost)	Germany	Kriwet et al. (2008)	lacustrine; consumulite within a consumulite
	Orthacanthus sp.	*Triodus* spines in oralite	late Carboniferous	Spain	Soler-Gijón (1995)	
Eugeneodontida	*Fadenia* sp.	brachiopod shells	Permian	unstated	Moy-Thomas and Miles (1971)	
Petalodontidiformes	*Janassa bituminosa*	brachiopods, crinoid, crustacean and foraminiferans	late Permian	Germany	Malzahn (1968)	
	Janassa bituminosa	bryozoan *Acnthocladia*	late Permian	Germany	Malzahn (1972)	
	Janassa bituminosa	brachiopod *Horridonia* and bryozoan	late Permian	Germany	Schaumberg (1979)	
	Janassa sp.	brachiopod fragments	unknown	unknown	Moy-Thomas and Miles (1971)	
Chondricthyes	unidentified sharks	palaeoniscoid elements and arthropod fragments	Late Devonian	USA	Williams (1990)	13 specimens
Acanthodii	*Tegeolepis clarki*	arthrodire bones and shark spine	Late Devonian	USA	Williams (1990)	
	acanthodian		early Permian	Germany	Heidtke (2007)	
	Acanthodes	valves of conchostracans	early Permian	Germany	Kner (1868)	

Paleozoic marine consumulites

Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Acanthodii	acanthodian	small osteostracan	Early Devonian	England	Miles (1973)	
	Ptomacanthus anglicus	*Cephalaspis* head shield	Early Devonian	England	Denison(1956); Allen and Tarlo (1963); Miles (1973)	head shield etched in gut
	acanthodians, actinopterygians and placoderms	amorphous organic matter interpreted as internal organs or gut contents	Middle Devonian	Scotland	Davidson and Trewin (2005)	
	Acanthodes sulcatus	*Cryphiolepis striata*	Early Carboniferous	England	Watson (1937); Viohl (1990)	
	Lodeacanthus gaujicus	a few individuals reveal a brown coprolitic-like material in the intestine region	Late Devonian	Latvia	Upeniece (2001, 2011)	
Cheirolepiformes	*Cheirolepis* sp.	acanthodians *Mesacanthus* and *Triazeucanthus* as well as juvenile *Eusthenopteron*	Late Devonian	Canada	Janvier (1996b)	
Actinopterygii	*Gogosardina coatesi*	conodont elements	Late Devonian	Australia	Choo et al (2009)	lodged among the branchial arches, indicating dietary habits and a possible cause of death
	Mimipiscis bartrami	remains of two separate conodont animals - the complete, 15-element apparatus of *Oulodus angulatus* and a partial apparatus (13 elements) of *Icriodus brevis*	Late Devonian	Australia	Nicoll (1977); Choo (2012)	
Palaeonisciformes	*Nematoptychius* sp.	*Acanthodes*	early Carboniferous	Scotland	Traquair (1879)	prey ingested head first
	Palaeoniscoid	palaeoniscoid	Pennsylvanian	USA	Richardson and Johnson (1971); Viohl (1990)	prey ingested head first
	Palaeoniscoid	*Acanthodes marshi*	Pennsylvanian	USA	Richardson (1980)	prey ingested head first
	Pygopterus sp.	*Palaeoniscus*	late Permian	Germany	Weigelt (1928)	
	Palaeoniscus magnus	*Palaeoniscus freieslebeni*	late Permian	Germany	Weigelt (1930b)	
Actinistia	*Glyptolepis* sp.	scales and spines of *Cheiracanthus* in one specimen and a small *Glyptolepis* in another	Middle Devonian	Scotland	Ahlberg (1992)	two specimens; ingested head first

Paleozoic marine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Actinistia	cf. *Diplocercides* sp.	conodont *Ctenopolygnathus*	Late Devonian	Poland	Zatoń et al. (2017)	
	Caridosuctor populosum	complete paleostomatopod shrimp and fragments	Mississippian	USA	Lund and Lund (1984, 1985); Lund et al. (1985)	several specimens
	Rhabdoderma elegans	*Parahaptolepsis tuberculata*	Pennsylvanian	USA	Viohl (1990)	prey ingested head first
Onychodontida	*Onychodus* sp.	pharynx contains bony plates of a small arthrodire *Incisoscutum ritchiei*	Late Devonian	Australia	Long (1991, 1995); Long and Trinajstic (2010)	prey ingested tail first
Eotetrapodiformes	*Eusthenopteron foordi*	*Bothriolepis canadensis, Homalacanthus concinnus, Cheirolepis*	Late Devonian	Canada	Arsenault (1982); Janvier (1996b); Chevrinais et al. (2017)	several prey ingested head first
Fish	multiple	proportion of predators with fish prey remains relatively low compared to the number of specimens with solely amorphous organic matter or devoid of digestive contents	Late Devonian	Canada	Chevrinais et al. (2017)	n=78 with identifiable gut contents
Mesosauria	*Brazilosaurus sanpauloensis*	crustacean fragments, disrupted fragmentary carapaces of small pygocephalomorph crustaceans and bones of very young mesosaurids	early Permian	Brazil	Silva et al. (2017)	

TABLE A.7. Paleozoic nonmarine consumulites.

Paleozoic nonmarine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Euphanerida	*Cornovichthys blaauweni*	patch of dark matter	Middle Devonian	Scotland	Newman and Trewin (2001)	
Symmorriifomes	*Cobelodus aculeatus*	incorporeal pelletite (intestinelite)	Late Pennsylvanian	USA	Hunt et al., (2012); Hunt and Lucas (2021a)	*Chondripilula zideki*
Xenacanthida	*Triodus sessilis*	amphibians *Archegesaurus decheni* and *Glanochthon latirostre* (which, in turn, has ingested *Acanthodes bronni*)	early Permian	Germany	Kriwet et al. (2008)	first consumulite within a consumulite
Dvinosauria	*Isodectes* cf. *obtusum*	infilled intestines	Middle Pennsylvanian	USA	Milner (1982)	
	Isodectes obtusum	three intestinal masses from mid-body to pelvic region	Middle Pennsylvanian	USA	Godfrey (1997)	
	Bermanerpeton kinneyi	syncarid arthropods (*Uronectes* cf. *kinniensis, Aenigmacaris* cf. *minima), Acanthodes* cf. *kinneyi,* actinopterygian scales, ribs and neural arches of amphibians	Late Pennsylvanian	USA	Werneburg et al. (2021); Hunt and Lucas (2021a)	three specimens; type and referred specimen of *Werneburgichnus varius*
Branchiosauridae	*Apateon flagrifer*	conchostracans	early Permian	Germany	Werneburg (1986)	small specimen
	Apateon kontheri	stomach contents including early juveniles of the palaeoniscide Elonichthys and branchiosaurids	early Permian	Germany	Werneburg (1988)	large specimens of taxon
	Apateon gracilis	*Apateon gracilis*	early Permian	Germany	Witzmann (2009)	predator was early growth stage
	Apateon caducus	branchiosaurid prey items preserved in digestive tracts	early Permian	Germany	Boy, (1993); Boy and Sues, (2000)	skull lengths exceeding 12 mm that have branchiosaurid prey items preserved in their digestive tracts

Branchiosauridae	*Apateon caducus*	neural arches, limb bone and dentary with teeth of small branchiosaurid	early Permian	Germany	Werneburg (2020)	large branchiosaurid with skull lenth of 33 mm
	Apateon caducus	small branchiosaurid skull between left hind limb and tail	early Permian	Germany	Werneburg (2020)	large branchiosaurid with skull length of 20 mm and with possible displaced consumulite
	Melanerpeton eisfeldi	stomach contents including early juveniles of the palaeoniscid *Elonichthys* and branchiosaurids	early Permian	Germany	Werneburg (1988)	large specimens
	Melanerpeton eisfeldi	*Apateon kontheri*	early Permian	Germany	Werneburg (1988)	large predator specimen
	Micromelerpeton sp.	*Apateon pedestris*	early Permian	Germany	Boy (2003)	
	Melanerpeton sembachense	specimens of the same species in the stomach contents	early Permian	Germany	Werneburg (1989)	two large individuals
	?*Branchiosaurus*	infilled stomach and intestines	Middle Pennsylvanian	USA	Milner (1982)	larval
Amphibamidae	*Amphibamus grandiceps*	infilled stomach and intestines	Middle Pennsylvanian	USA	Milner (1982)	larval
Dissorophidae	*Milnererpeton huberi*	a linear and sinuous consumulite containing ostracods that is a gastrolite and/or intestinelite	Late Pennsylvanian	USA	Werneburg et al. (2013); Hunt and Lucas (2021a)	two specimens; type and referred specimen of *Werneburgichnus kinneyensis*
Sclerocephalidae	*Sclerocephalus* sp.	paramblypterid fish, *Micromelerpeton*, *Apateon*, *Sclerocephalus*	early Permian	Germany	Lohmann and Sachs (2001)	several specimens from four ontogenetic stages
Temnospondyli	unidentified amphibian	ostracods	Middle Pennsylvanian	USA	Godfrey (1997)	
Procolophonomorpha	*Delorhynchus priscus*	arthropod cuticle in oral region	early Permian	USA	Modesto et al. (2009); Reisz et al. (2014)	two skulls, both with oralites
	Parasaurus geinitzi (Pareiasauria)	coarse clastics with interspersed carbonized particles	late Permian	Germany	Munk and Sues (1993)	

Captorhinidae	*Romeria* sp.	smaller specimen, probably of same species;the prey lay inverted, and bones of the left foreleg can be seen in the mouth of the predator, as well as a series of seven vertebrae along the inner side of the right mandible and a skull	early Permian	USA	Case, (1911); Eaton (1964)	ingested tail first, so far that its jaws reached to the back of the predator’s head
Sphenacontidae	*Dimetrodon milleri*	*Zatrachys* bones	early Permian	USA	Romer and Price (1940)	
Gorgonopsidae	*“Aelurognathus” parringtoni.*	dicynodont mandibular symphysis of *Katumbia parringtoni*	late Permian	Tanzania	Maisch (2009)	
Archosauromorpha	*Protorosaurus speneri*	numerous ovules of the conifer *Ullmannia frumentaria*	late Permian	Germany	Munk and Sues (1993)	
	Protorosaurus speneri	57 ovules of *Ullmannia frumentaria* – among scattered bones	late Permian	Germany	Weigelt (1930a)	

TABLE A.8. Mesozoic marine consumulites.

Mesozoic marine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Hybodontiformes	*Hybodus hauffianus*	about 250 belemnites	Early Jurassic	Germany	Brown (1900); Pollard (1990); Doyle and McDonald (1993); Hoffmann and Stevens (2020)	
Lamniformes	*Cretodus* sp.	large chelonioid turtle bones with dentalites, shell, vertebrae, limbs, ovoid mass, *Cretodus* tooth	Late Cretaceous	Italy	Amalfitano et al. (2017)	location of stomach
	Squalicorax falcatus	*Toxochelys, Ichthyodectes Ctenodon,* mosasaur	Late Cretaceous	USA	Druckenmiller et al. (1993)	
	Cretolamna sp.	*Xiphactinus*	Late Cretaceous	USA	Martin and Rothschild (1989)	
	Cretoxyrhina mantelli	*Xiphactinus audax*	Late Cretaceous	USA	Sternberg (1917); Shimada, (1997)	scattered along length
	Cretoxyrhina mantelli	*Elasmosaurus*	Late Cretaceous	USA	Everhart (2003)	
	Cretoxyrhina mantelli	mosasaur	Late Cretaceous	USA	Shimada (1997)	two specimens
	Cretoxyrhina sp.	plesiosaur	Late Cretaceous	USA	Shimada (1997)	
	Scapanorhynchus lewisi	teleost	Late Cretaceous	Lebanon	Viohl (1990)	prey ingested head first
Carcharhiniformes	*Scyliorhinus elongatus*	*Spaniodon*	Late Cretaceous	Lebanon	Viohl (1990)	prey ingested head first
Ginglymodi	*Lepidotes* sp.	gastrolite of small crustacean cuticle fragments indicative of shrimp-like taxa	Early Jurassic	Germany	Thies et al. (2019)	two specimens
Actinistia	*Holophagus gulo*	*Dapedius*	Jurassic	England	Huxley (1866)	prey ingested head first
	Swenzia latimerae	an incomplete, crushed, small crustacean	Late Jurassic	France	Clément (2005, 2006)	gastrolite

Mesozoic marine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Actinistia	*Axelrodichthys araripensis*	elements of an actinopterygian fish	Early Cretaceous	Brazil	Yabumoto and Brito (2013); Meunier et al. (2018)	two vertebrae, some neural and/or hemal spines, lepidotrichial hemisegments, teeth, long and thin bones that are probably myorhabdos
Gonorynchiformes	*Cearana rochae*	*Cearana*	Early Cretaceous	Brazil	Case (1982)	prey ingested head first
	Dastilbe elongatus	*Dastilbe*	Early Cretaceous	Brazil	Maisey (1994)	prey ingested head first
Birgeriformes	*Birgeria* sp.	*Birgeria* sp.	Early Triassic	Madagascar	Beltan (1977); Viohl (1990)	originally interpreted as ovivparity but probably consumulite (Viohl, 1990)
Saurichthyiformes	*Saurichthys costasquamosus*	complete individual of an early actinopterygian (cf. *Luganoia*) in the abdominal cavity just posterior to the head	Middle Triassic	Switzerland	Argyriou et al. (2016)	size of spiral intestine discussed
	Saurichthys macrocephalus	putative stomach, a short anterior intestine and part of the spiral intestine	Middle Triassic	Switzerland	Argyriou et al. (2016)	
	Saurichthys paucitrichus	post-gastric portion of the GI tract that corresponds to part of the anterior intestine, which is uncoiled, the complete spiral intestine and likely the cranial tip of the rectum	Middle Triassic	Switzerland	Argyriou et al. (2016)	
	Saurichthys yangjuanensis	undescribed stomach contents	Middle Triassic	China	Wu et al. (2015)	
Pachycormiformes	*Pachycormus sp*	stomach contains numerous hooklets that can be referred to the coleoid cephalopod *Phragmoteuthis*	Early Jurassic	Germany	Přikryl et al. (2012)	
	Saurostomus sp.	coleoid *Loligosepia*	Early Jurassic	Germany	Urlichs et al. (1994)	
	Bonnerichthys gladius	stomach contents	Late Cretaceous	USA	Everhart (2017)	

Mesozoic marine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Amiaformes	*Calamopleurus cylindricus*	conspecific	Early Cretaceous	Brazil	Mulder (2013)	
	Calamopleurus cylindricus	*Vinctifer,* arthropod material	Early Cretaceous	Brazil	Maisey (1994)	four specimens; prey ingested head first
	Enneles audax	*Aspiridorhynchus comptoni*	Late Cretaceous	Brazil	Viohl (1990)	prey ingested head first (half swallowed)
	Caturus sp.	teleost	Late Cretaceous	France	Poplin (1986)	prey directed posteriorly
Ichthyodectiformes	*Cladocyclus* sp.	*Rhacolepis* in one specimen, many disarticulated ?*Tharrhias* in another	Early Cretaceous	Brazil	Patterson and Rosen (1977)	*Rhacolepis* was swallowed tail first, most commonly swallowed head first, as with ?*Tharrhias*
	Allothrissops sp.	gut contents are frequently preserved in the form of an amorphous, phosphatic mass or ribbon	Late Jurassic	Europe	Patterson and Rosen (1977)	minute teeth and amorphous gut contents suggest was microphagous, not predatory, like other ichthyodectiforms
	Ichthyodectes ctenodon	tentative identification of *Enchodus petrosus* as stomach contents	Late Cretaceous	USA	Everhart et al. (2010)	
	Xiphactinus audax	*Gillicus arcuatus*	Late Cretaceous	USA	Bardack (1965); Schwimmer et al. (1997); Walker (2006); Everhart (2017)	four specimens: prey ingested head first
	Xiphactinus sp.	*Anogmius* sp.	Late Cretaceous	USA	Viohl (1990); Boucot and Poinar (2010)	prey ingested head first
	Xiphactinus sp.	*Enchodus*	Late Cretaceous	USA	Bardack (1965)	
	Xiphactinus sp.	unidentified fish	Late Cretaceous	USA	Bardack (1965); Everhart (2017)	four specimens
	Xiphactinus sp.	*Ananogmius*	Late Cretaceous	USA	Bardack (1965)	

Mesozoic marine consumulites

Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Crossognathiformes	*Rhacolepis* sp.	*Vinctifer*	Early Cretaceous	Brazil	Wilby and Martill (1992)	prey ingested head first
	Elopopsis microdon	three non-connected intestinilites that are about 6-8 mm thick and round in cross section, but are incomplete, phosphatic matrix	Late Cretaceous	Germany	Diedrich (2012)	
Elopiformes	*Notelops brama*	*Rhacolepis*	Early Cretaceous	Brazil	Maisey (1994, 1996)	prey ingested head first
	Notelops sp.	disarticulated arthropod	Early Cretaceous	Brazil	Wilby and Martill (1992)	
	Protostomias marocanus	*Rhinellus africanus* in one, *Paravinciguerria praecursor* in another	Late Cretaceous	Morocco	Arambourg (1954)	two specimens; prey ingested head first
	Protostomias maroccanus	skeleton of small fish is preserved in the stomach region (fish scales and beige-colored gastrolitic phosphatic material).	Late Cretaceous	Germany	Diedrich (2012)	
	Pachyrhizodus minimus	stomach and intestinal casts	Late Cretaceous	USA	Stewart (1899); Miller (1957)	two specimens
Osmeroformes	*Spaniodon* sp.	*Spaniodon blodeli* in one specimen, indeterminate in another	Late Cretaceous	Lebanon	Woodward (1901); Viohl (1990)	two specimens
Aulopiformes	*Cimolichthys nepaholica*	complete *Enchodus* skeleton	Late Cretaceous	USA	Cicimurri and Everhart (2001)	prey ingested head first
	Cimolichthys ggnephaholica	*Tusoteuthis* sp., gladius	Late Cretaceous	USA	Kauffman (1990a); Stewart and Carpenter (1990)	swallowed from rear, cause of death?
	Cimolichthys sp.	small bony fish	Late Cretaceous	USA	Konuki (2008)	
	Enchodus major	teleost	Late Cretaceous	Lebanon	Davis (1887); Viohl (1990)	prey ingested head first

Mesozoic marine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Aulopiformes	*Enchodus marchesetti*	teleost	Late Cretaceous	Lebanon	Davis (1887); Viohl (1990)	prey ingested head first
	Enchodus sp.	small bony fish	Late Cretaceous	USA	Konuki, (2008)	
Stomiiformes	*Pronotocanthus sahelalmae*	teleost	Late Cretaceous	Lebanon	Davis (1887); Woodward (1901)	prey ingested head first
Alepisauriformes	*Prionolepis cataphractus*	one to two indeterminate fish	Late Cretaceous	Lebanon	Viohl (1990)	four specimens; prey ingested head first
	Eurypholis boissieri	one, and, in one case, two fish	Late Cretaceous	Lebanon	Viohl (1990)	four specimens
	Prionolepis sp.	small osteichthyans	Late Cretaceous	Lebanon	Amalfitano et al. (2017)	high percentage of specimens
Crossognathiformes	*Goulmimichthyes* sp.	*Enchodus*	Late Cretaceous	Morocco	Cavin (1999)	prey ingested head first
Pycnodontiformes	*Brembodus* sp.	crushed shells in gut	Jurassic and Cretaceous	various	Nursall (1996)	
	Arduafrons sp.	spines of monospecific echinoderms	unspecified	unspecified	Kriwet (2001)	one specimen
	Gyrodus sp.	spines of monospecific echinoderms	unspecified	unspecified	Kriwet (2001)	two specimens
	Iemanja sp.	small actinopterygian vertebrae	unspecified	unspecified	Kriwet (2001)	one specimen
	Nursallia sp.	spines of monospecific echinoderms	unspecified	unspecified	Kriwet (2001)	two specimens
	Proscinetes sp.	shells of monospecific bivalves	unspecified	unspecified	Kriwet (2001)	one specimen
	Tepexichthys sp.	shells of monospecific bivalves	unspecified	unspecified	Kriwet (2001)	several specimens
	Pycnodus sp.	shells of monospecific bivalves	unspecified	unspecified	Kriwet (2001)	two specimens
	Neoproscinetes sp.	monospecific snails	unspecified	unspecified	Kriwet (2001)	one specimen

Mesozoic marine consumulites

Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Abuliformes	*Anogmius ornatus*	(a) four freshly swallowed fish with the head directed posteriorly, possibly *Clupavis*; (b) partly digested prey in which bones and scales are enclosed in a phosphatic bromalitic matrix (gastrolite); and (c) phosphatic bromalitic material (intestinelite) that does not contain scales or bone material	Late Cretaceous	Germany	Diedrich (2012)	
Protostegidae	cf. *Notochelone* sp.	densely packed inoceramid fragments in phosphatic matrix	Early Cretaceous	Australia	Kear (2006)	three specimens
Teleosauridae	*Steneosaurus bollensis*	black patch just above sacral region	Early Jurassic	Germany	Mateer (1974)	
Metriorhynchidae	*Metriorhynchus sp.*	cephalopod hooklets	Middle Jurassic	England	Martill (1985a)	
	Cricosaurus bambergensis	articulated crustacean	Late Jurassic	Germany	Spindler et al. (2021)	
	Dakosaurus sp.	gut contents	Late Jurassic	Germany	Spindler et al. (2021)	
Ichthyosauria	cf. *Merriamosaurus hulkei*	black hooks identified as belemnoid cephalopods and annelids	Early Triassic	Norway	Buchy et al. (2004)	annelids could have been consumed by belemnoids
	Phragmoteuthis? *ticinensis*	stomach contents composed of cephalopod hooklets	Middle Triassic	Switzerland	Rieber (1970)	
	ichthyosaurs	cephalopod hooklets	Middle Triassic	Switzerland	Brinkmann (2004)	
	Guizhouichthyosaurus tangae	fish scales and fragments of bivalves and brachiopods	Late Triassic	China	Cheng et al. (2006); Wang et al. (2008)	
	Shonisaurus popularis	vertebrate and mollusc shell fragments	Late Triassic	USA	Camp (1980)	

Mesozoic marine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Ichthyosauria	merriamosaur	a discrete mass of phosphatic residue interpreted as osteichthyan bones and scales, together with cephalopod shell fragments	Late Triassic	USA	Druckenmiller et al. (2014)	occurs in the anterior half of the rib cage
	Leptopterygius acutirostris	small ichthyosaur	Early Jurassic	Germany	Massare (1987)	
	Stenopterygius crassicostatus	cephalopod hooklets	Early Jurassic	Germany	Massare (1987)	
	Stenopterygius megalorhinus	cephalopod hooklets	Early Jurassic	Germany	Massare (1987)	
	Stenopterygius quadriscissus	fish fragments and cephalopod hooklets	Early Jurassic	Germany	Von Wurstemberger (1876)	
	Stenopterygius spp.	hooklets and rare wood fragments and fish remains	Early Jurassic	Germany	Keller (1976)	28 specimens
	Leptopterygius burgundiae	gastric mass was composed mainly of cephalopod hooklets (*Belemnitida*), and up to 200 small (10 mm or less) ichthyosaurian vertebrae, interpreted as remains of juvenile *Stenopterygius*	Early Jurassic	Germany	Böttcher (1989)	
	Stenopterygius quadriscissus	actinopterygian fish, head first	Early Jurassic	Germany	Bürgin (2000)	

Mesozoic marine consumulites

Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Ichthyosauria	*Stenopterygius quadriscissus*	small juvenile - *Dapedium* sp., Pachycormidae indet., indeterminate fish/shark remains; large juvenile - *Saurorhynchus* sp. *Dapedium* sp., *Euthynotus* sp., indeterminate fish/shark remains, belemnitid hooklets; small adult - indeterminate fish/shark remains, belemnitid hooklets, belemnoteuthid hooklets; large adult - belemnitid hooklets, belemnoteuthid hooklets, phragmoteuthid hooklets, *Stenopterygius* sp., aborted embryo	Early Jurassic	Germany	Dick et al. (2016)	43 specimens, smallest fed on small, burst-swimming fishes, with shift towards faster moving fish and cephalopods with increasing body size; larger adult specimens appear to completely reliant on cephalopods shortly after onset of sexual maturity
	Stenopterygius triscissus	juvenile - *Dapedium* sp. *Euthynotus* sp., indeterminate fish/shark remains; adult - belemnitid and phragmoteuthid hooklets	Early Jurassic	Germany	Dick et al. (2016)	15 specimens
	Stenopterygius uniter	belemnitid and belemnoteuthid hooklets	Early Jurassic	Germany	Dick et al. (2016)	5 specimens
	Ichthyosaurus communis	*Pholidophorus* scales and spines, cephalopod hooklets	Early Jurassic	England	Buckland (1858); Pollard (1968)	
	Ichthyosaurus communis	dibranchiate cephalopod hooklets	Early Jurassic	England	Pollard (1968)	
	Icthyosaurus communis	several black cephalopod hooklets preserved between the ribs	Early Jurassic	England	Lomax et al. (2019)	neonate icthyosaur
	Ichthyosaurus conybeari	dibranchiate cephalopod hooklets	Early Jurassic	England	Pollard (1968)	
	Ichthyosaurus breviceps	dibranchiate cephalopod hooklets	Early Jurassic	England	Pollard (1968)	
	Ichthyosaurus sp.	coleoid cephalopod hooklets	Early Jurassic	England	Lomax (2010)	
	Several	dibranchiate cephalopod hooklets	Early Jurassic	England	Pollard (1968)	

Mesozoic marine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Ichthyosauria	*Ophthalmosaurus natans*	gastric material consists of badly fragmented coleoid cephalopod hooklets, loosely cemented by calcite crystals	Late Jurassic	USA	Massare and Young (2005)	
	Pantosaurus striatus	gastric contents consisting of a mass of coleoid hooklets as well as disarticulated cardiocerid ammonite jaws	Late Jurassic	USA	Wahl (2012)	
	Thalassodraco etchesi	amorphous black material preserved in the body cavity with small, indeterminate clasts	Late Jurassic	England	Jacobs and Martill (2020)	
	Platypterygius longmani	hatchling-sized protostegid turtle, enantiornithine bird, actinopterygian fish and phosphatic nodules	Early Cretaceous	Australia	Kear et al. (2003)	gravid female ichthyosaur
Nothosauridae	*Silvestrosaurus buzzii*	*Cyamodus hildegardis* tooth bearing elements in the stomach region	Middle Triassic	Switzerland	Tschanz (1989)	
	Paranothosaurus sp.	stomach contents of pachypleurosaurs	Middle Triassic	Switzerland	Diedrich (2015)	
Mosasauridae	*Compressidens fraasi*	echinoid test found between teeth	Late Cretaceous	Belgium	Dollo (1913)	
	Plioplatecarpus sp.	two belemnites	Late Cretaceous	Belgium	Dollo (1913)	
	Tylosaurus (Hainosaurus) sp.	turtle bones	Late Cretaceous	Belgium	Dollo (1887a, b)	
	Mosasaurus missouriensis	fish	Late Cretaceous	Canada	Konishi et al. (2014)	
	Tylosaurus proriger	juvenile *Dolichorhynchops osborni* including two probable humeri	Late Cretaceous	USA	Sternberg (1922); Everhart (2004b)	the proximal and distal ends of both bones were partially digested by the mosasaur’s stomach acids

Mesozoic marine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Mosasauridae	*Tylosaurus nepaeolicus*	three small *Platecarpus* sp. individuals and a *Ptychodus* tooth	Late Cretaceous	USA	Bell and Barnes (2007)	
	Tylosaurus nepaeolicus	a scattering of smaller bone materials representing stomach contents	Late Cretaceous	USA	Bell et al. (2013)	
	Tylosaurus proriger	partially digested *Clidastes* vertebrae	Late Cretaceous	USA	Bell and Barnes (2007)	
	Tylosaurus proriger	a mosasaur (*Clidastes* sp.), a bird (*Hesperornis*), a shark (?*Cretolamna*), a teleost fish (*Bananogmius*)	Late Cretaceous	USA	Bjork (1981); Martin and Bjork (1987)	anterior to pelvis
	Tylosaurus proriger	mosasaur, *Cimolichthys*	Late Cretaceous	USA	Cicimurri and Everhart (2001)	
	Tylosaurus proriger	*Cimolichthys*	Late Cretaceous	USA	Everhart (2017)	
	Tylosaurus proriger	mosasaur as stomach contents	Late Cretaceous	USA	Everhart (2017)	
	Tylosaurus (Hainosaurus) sp.	mosasaur as stomach contents	Late Cretaceous	USA	Everhart (2017)	
	Prognathodon overtoni	fragments of a large and a small fish, a sea turtle (*Nichollsemys baieri*), and possibly a cephalopod	Late Cretaceous	Canada	Konishi et al. (2011)	anterior to pelvis
	Prognathodon kianda	partial skulls of *Platecarpus ptychodon*, *Mosasaurus* sp. and an indeterminate mosasaurine	Late Cretaceous	Angola	Strganac et al. (2015)	the skull roof, snout and other areas thinly fleshed in life are etched, and tooth crowns are dissolved above the gum line
	Plotosaurus tuckeri	teleost	Late Cretaceous	USA	Camp (1942)	

Mesozoic marine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Mosasauridae	*Platecarpus tympanticus*	gastrointestinal contents in the form of partially digested fish bones packed into a dense mass with an outline that appears to follow the course of the digestive tract.	Late Cretaceous	USA	Lindgren et al. (2010)	it is possible that the ingested bones derive from the anterior portion of the digestive system (displaced stomach contents), but the longitudinal axis of accumulation runs dorsally beneath and parallel to the vertebrae in the lumbar region; it is more likely that the residues represent processed food from within the colon
	Platecarpus sp.	*Cimolichthys*	Late Cretaceous	USA	Williston (1899)	
	Globidens sp.	bivalves	Late Cretaceous	USA	Martin (1994); Martin and Fox (2004, 2007)	
	mosasaurs	large teleosts	Late Cretaceous	USA	Williston (1914)	
	Simolestes vorax	cephalopods	Middle Jurassic	England	Martill (1992); Cicimurri and Everhart (2001)	gastroliths
	cf. *Pantosaurus striatus*	ichthyosaur embryo	Late Jurassic	USA	O'Keefe et al. (2009)	
	Peloneustes sp.	cephalopods	Middle Jurassic	England	Andrews (1910)	gastroliths
	pliosaur indet	*Pholidophorus bechei*	Early Jurassic	England	Patterson (1975)	
	Pliosaurus brachyspondylus	cephalopod hooklets	Late Jurassic	England	Tarlo (1959)	
	Pliosaurus brachyspondylus	ornithischian osteoderms	Late Jurassic	England	Taylor et al. (1993)	

Mesozoic marine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Plesiosauria	*Pliosaurus irgisensis*	fish, cephalopod hooklets	Late Jurassic	Russia	Zhuravlev, (1943); Gekker and Gekker (1955)	
	Kronosaurus sp.	turtle, limb, girdle, carapace	Early Cretaceous	Australia	McHenry (2009)	esophagus and stomach
	Kronosaurus sp.	1 bony fish vertebra, elasmosaur vertebra (prey within prey)	Early Cretaceous	Australia	McHenry (2009)	
	pliosaur	*Nautilus*, ammonites	Late Cretaceous	Japan	Sato and Tanabe (1998); Sato and Storrs (2000)	gastroliths
	?*Plesiosaurus* sp.	bony fish debris	Early Jurassic	England	Storrs (1995)	
	Tatenectes laramiensis	hybodont shark (teeth, dorsal spines and skin denticles) and coleoid cephalopod hooklets	Late Jurassic	USA	Wahl (1998); Cicimurri and Everhart (2001)	gastroliths
	Nichollsia borealis	fish vertebrae	Early Cretaceous	Canada	Druckenmiller and Russell (2008)	gastroliths
	Styxosaurus snowii	a fish bone hash was concentrated in a 1 by 2 meter area just behind the pectoral girdle on the right side – crop or gizzard; fragments of fish bone were the most abundant elements recovered from the stomach contents of and include cranial fragments of small clupeomorph fishes and several teeth, vertebrae, and scales of the teleost *Enchodus* sp.	Late Cretaceous	USA	Cicimurri and Everhart (2001)	many gastroliths
	Elasmosaurus platyurus	teleost fish *Enchodus* and 5 other species	Late Cretaceous	USA	Cope, (1868)	Everhart (2017) believes this to be just associated concretions
	Elasmosauridae indeterminate	*Clidastes*	Late Cretaceous	USA	Cope (1872); Storrs (1999)	

Mesozoic marine consumulites

Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Plesiosauria	*Dolichorhynchops osborni*	teleost *Apateodus*	Late Cretaceous	Canada	Nicholls (1988)	
	Thalassomedon hanningtoni	ammonite	Late Cretaceous	USA	Cicimurri and Everhart (2001)	gastroliths
	elasmosaur	teleosts	Late Cretaceous	Canada	Nicholls (1998)	
	elasmosaur	many benthic invertebrates, predominantly bivalve shell fragments but also the remains of gastropods and pieces of crinoid; two bivalve shells are referable to *Macoyella*; free-swimming taxa are represented by belemnite endoskeletons and a single teleost plate	Early Cretaceous	Australia	McHenry et al. (2005)	92% gastropod and bivalve shell and 8% belemnite guards; there is no evidence of action by stomach acids on material in the bromalite or the stomach cavity; gastroliths
	elasmosaur	an intact decapod carapace, several crustacean fragments, and a fish scale.	Early Cretaceous	Australia	McHenry et al. (2005)	gastroliths
	plesiosaur	cephalopods	Late Cretaceous	Japan	Matsumoto et al. (1982)	gastroliths
	plesiosaur	teleosts	Late Cretaceous	USA	Martin and Kennedy (1988)	gastroliths
	plesiosaur	teleost, pterosaur, *Scaphites*	Late Cretaceous	USA	Brown, (1904)	gastroliths
Pterosauria	*Pteranodon* sp.	fragments of undetermined fishes preserved in the throat area	Late Cretaceous	USA	Brown, (1943); Bennett, (2001)	or regurgitalite (Bennett, 2001); partly digested fish remains represent gut contents regurgitated during death throes
	Pteranodon sp.	*Enchodon* sp.	Late Cretaceous	USA	Hargrave (2007)	in association with possible consumulites

TABLE A.9. Mesozoic nonmarine consumulites.

Mesozoic nonmarine consumulites						
Higher level Taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Coelacanthiformes	*Undina penicillata*	*Undina penicillata*	Late Jurassic	Germany	Schultze (1972)	Watson (1927) suggests represents ovoviparous behavior as in Recent *Latimeria* (Smith, 1975; prey ingested head first
Palaeonisciformes	*Hulettia americana*	consumulites that consist of small fish(?) bones, and, possibly scales of *Todiltia schoewei*(?)	Middle Jurassic	USA	Schaeffer and Patterson (1984); Lucas et al. (1985b); Hunt and Lucas (2014)	a few specimens
Actinopterygii	*Todiltia schoewei*	consumulites are preserved as a white or yellowish, featureless phosphatic mass, which suggests a microphagous diet	Middle Jurassic	USA	Schaeffer and Patterson (1984); Lucas et al. (1985b); Hunt and Lucas (2014)	70% of the specimens preserve consumulites, a large stomach anteriorly, separated by a sphincter from an intestine that looped ventrally, rose dorsally again above the pelvic fins, then passed obliquely down to the anus, in front of the anal fin
	Heterolepidotus radiato-punctatus	pycnodonts	Late Jurassic	Germany	Viohl (1990)	
	Oenoscupus sp.	rhynchocephalian	Late Jurassic	France	Eastman (1911)	prey ingested head first
Aspidorhynchiformes	*Belonostomus* sp.	*Homeosaurus*	Late Jurassic	France	Eastman (1911)	prey ingested head first
	Belonostomus sp.	*Notagogus*	Late Jurassic	France	De Saint Seine (1949)	prey directed posteriorly
	Belonostomus cf. *B. kochi*	*Orthogonikleithrus hoelli*	Late Jurassic	Germany	Ebert et al. (2015)	three specimens, one in pharynx, two in stomach
	Belonostomus tenuirostris	two specimens of cf. *Leptolepides* and possibly a juvenile *Caturus* sp.	Late Jurassic	Germany	Kogan and Licht (2013)	
	Aspidorhynchus sp.	*Rhamphorhynchus* in which a small leptolepidid fish is in the esophagus and its stomach is full of fish debris	Late Jurassic	Germany	Frey and Tischlinger (2012)	pterosaur is aspirationalite, consumulite within a consumulite

Mesozoic nonmarine consumulites

Higher level Taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Salmoniformes	*Orthogonikleithrus hoelli*	conspecific	Late Jurassic	Germany	Ebert et al. (2015)	21 specimens, 5 in pharynx, 16 in stomach
	Orthogonikleithrus n.sp.1	*Orthogonikleithrus hoelli*	Late Jurassic	Germany	Ebert et al. (2015)	12 specimens, 1 in pharynx, 11 in stomach
Amiiformes	*Caturus furcatus*	*Leptolepides sprattiformis, ?Aaethalion angustissimus, ?Ascalabos voithi, , ?Eichstaettia mayri, Tharsis dubious,* pycnodont and unidentified	Late Jurassic	Germany	Viohl (1983, 1990)	28 specimens; 11 prey ingested tail first 10 prey ingested head first – in 5 cases prey is only half-swallowed and body juts out of mouth - aspirationalites
	Caturus pachyurus	fish	Late Jurassic	Germany	Viohl (1990)	
	Caturus giganteus	piece of pycnodont (too large to be swallowed whole)	Late Jurassic	Germany	Viohl (1990)	
	Caturus sp.	*Tharsis dubius*	Late Jurassic	Germany	Viohl (1990)	prey ingested head first, half swallowed and extending out of mouth - aspirationalite
	Ionoscopus cyprinoides	fish	Late Jurassic	Germany	Stuetzer (1972); Viohl, (1990)	
	Urocles lepidotus	teleost	Late Jurassic	Germany	Viohl (1990)	prey ingested head first
	Urocles polyspondylus	*Urocles(?)*	Late Jurassic	Germany	Lange (1968); Viohl (1990)	
Pholidophoriformes	*Eurycormus speciosus*	fish	Late Jurassic	Germany	Viohl (1990)	
Pachycormiformes	*Asthenocormus titaius*	*Tharsis dubius*	Late Jurassic	Germany	Viohl (1990)	no preferential orientation, but fish small compared to consumer
	Hypsocormus insignis	*Tharsis dubius*	Late Jurassic	Germany	Wagner (1860); Viohl (1990)	5 specimens
	Pholidophorus microcephalus	*Tharsius dubius*	Late Jurassic	Germany	Viohl (1990)	2 specimens; 1 prey ingested tail first
	Ascalabos voithi	fish	Late Jurassic	Germany	Nybelin (1974); Viohl (1990)	

Mesozoic nonmarine consumulites						
Higher level Taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Aspidorhynchiformes	*Aspidorhynchus acutirostris*	*?Aaetbalion sp., ?Eichstaettia mayri, Pholidophorus microcephalus,* indeterminate fish	Late Jurassic	Germany	Viohl (1990)	3 prey ingested tail first, 2 ingested head first
	Belonostomus tenuirostris	*Notagogus*	Late Jurassic	France	Saint-Seine (1949)	prey ingested head first
Clupeiformes	*Daitingichthys tischlingeri*	*?Anaethbalion* sp., teleost	Late Jurassic	Germany	Arratia (1987); Viohl (1990)	2 specimens, 1 prey ingested tail first
Elopiformes	*Anaethbalion angustissimus*	teleosts including *?Anaethbalion*	Late Jurassic	Germany	Von Münster (1842); Nybelin (1967); Viohl (1990)	2 specimens, both prey ingested tail first
Ichthodectiformes	*Thrissops formosus*	*Leptolepides sprattiformis*	Late Jurassic	Germany	Neumayer (1929); Nybelin (1958); Viohl (1990)	8-10 specimens, 4 with heads of prey ingested head first
	Thrissops subovatus	*Leptolepides sprattiformis*	Late Jurassic	Germany	Viohl (1990)	2 specimens, 1 prey ingested head first
	Allothrissops mesogaster	*Leptolepides sprattiformis*	Late Jurassic	Germany	Viohl (1990)	prey ingested head first
	Pachythrissops sp.	fish	Late Jurassic	Germany	Viohl (1990)	prey ingested tail first
	Thrissops cf. *formosus*	*Orthogonikleithrus hoelli* in stomach	Late Jurassic	Germany	Ebert et al. (2015)	3 specimens
Crossognathiformes	*Bavarichthys incognitus*	*Orthogonikleithrus hoelli* in stomach	Late Jurassic	Germany	Ebert et al. (2015)	
Teleostei	Teleostei n.sp.1	*Orthogonikleithrus hoelli*	Late Jurassic	Germany	Ebert et al. (2015)	20 specimens, 13 in pharynx, 7 in stomach (including 1 specimen with multiple specimens)

Mesozoic nonmarine consumulites						
Higher level Taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Urodela	*Jeholotriton paradoxus*	50-100 conchostracan (*Euestheria luanpingensis*) carapaces in the abdominal region, valves are clustered, overlapping heavily, relatively circular; in contrast, oval valves outside of the body, suggesting softening of the chitinous valves during digestion, most preserved dorsally with the two valves open, suggesting the adductor muscle had been digested before burial; no tooth marks, implying swallowed whole, occupy nearly the entire body cavity, probably because the carapaces broke the gut and entered the coelom as they were pressed during burial	Middle Jurassic	China	Dong et al. (2012)	carapace valves stomach contents based on: (1) clustered, overlapping heavily, and the margin cluster is below the vertebral column and between the forelimbs and hind limbs in abdominal region; (2) small, whereas others from locality are normally dispersed, which suggests selection of prey size by the predator; (3) relatively circular, in contrast to the more or less oval carapace valves outside the salamander's body; the rounded shape could be a result of softening of the chitinous valves during digestion; and (4) a proportionally large number are preserved dorsally with the two valves open, suggesting the adductor muscle had been digested before burial
	Chunperpeton tianyiensis	abundant intact conchostracans in the gut cavity	Middle Jurassic	China	Gao and Shubin (2003)	small larval
	Chunperpeton tianyiensis	stomach contents contain insect *Yanliaocorixa chinensis* – one individual contains 5; the corixids are exclusively adults or last larval instars, suggesting size-based selective feeding of the live predator; in addition, there are no tooth marks on the eaten corixids, indicating that they were probably swallowed whole	Middle Jurassic	China	Dong et al. (2012)	9 juvenile specimens; the head or fore wings of these corixids are sometimes disarticulated, indicating that the joints were digested in the stomach
	salamander	indeterminate gut contents	Early Cretaceous	Spain	Evans (2016)	

Mesozoic nonmarine consumulites

Higher level Taxon	Taxon	Contents	Age	Location	References	Notes
Anura	*Genibatrachus baoshanensis*	skeleton of salamander, cf. *Nuominerpeton*	Early Cretaceous	China	Xing et al. (2019)	
	unidentified frog	stomach contents	Late Cretaceous	Brazil	Leal and Martill (2007)	
Thalassochelydia	*Thalassemys bruntrutana*	elongate body can be seen through the central plastral fontanelle, irregular, wavy and phosphatic	Late Jurassic	Germany	Joyce et al. (2021)	location midbody combined with its relatively narrow diameter is broadly consistent with the small intestine of extant marine turtles
Choristodera	*Monjurosuchus splendens*	7 juvenile skulls of *Monjurosuchus splendens*	Early Cretaceous	China	Wang et al. (2005)	
Phytosauria	*Parasuchus hislopi*	a few skull bones of a rhynchosaur in “stomach;” *Malerisaurus robinsoni,* which may be a synonym of *Trilophosaurus buettneri* (Spielmann et al., 2006)	Late Triassic	India	Chatterjee (1978, 1980)	
	Pseudopalatus pristinus	series of dorsal centra of the metoposaurid amphibian *Apachesaurus gregorii*	Late Triassic	USA	Hunt (1991, 2001); Hunt and Lucas (2014b)	male, altirostral skull
	Pseudopalatus pristinus	proximal pubis of a smaller phytosaur and a series of centra of *Vancleavea campi*	Late Triassic	USA	Hunt (1991, 1994, 2001); Hunt and Lucas (2014b)	female, dolichorostral
Paracrocodylomorpha	*Postosuchus alisonae*	gastrolite a partial skeleton of a small stagonolepidid (cf. *Aetosaurus*), a snout, left coracoid, and left humerus of the traversodont cynodont *Plinthogomophodon herpetairus*, two articulated phalanges of a large dicynodont, and a fragment of an unidentified ?temnospondyl bone	Late Triassic	USA	Sues et al. (2003); Peyer et al. (2008)	some of the bones bear tooth marks and show periosteal erosion, possibly caused by digestion
Crocodylifomes	*Aplestosuchus sordidus*	sphagesaurid	Late Cretaceous	Brazil	Godoy et al. (2014)	

Mesozoic nonmarine consumulites

Higher level Taxon	Taxon	Contents	Age	Location	References	Notes
Theropoda	*Notatesseraeraptor frickensis*	bones in preserved contents of the stomach include a well preserved maxilla of the rhynchocephalian *Clevosaurus*	Late Triassic	Switzerland	Unterrassner (2009); Zahner and Brinkmann, (2019)	
Coelophysidae	*Coelophysis bauri*	possible oralite containing small premaxillary and other teeth of *Coelophysis*	Late Triassic	USA	Rinehart et al. (2009)	
	Coelophysis bauri	three specimens have bromalitic material with indistinct structure and a granular matrix; some specimens located between the ischia and the proximal caudal vertebrae and apparently represent incorporeal pelletites	Late Triassic	USA	Rinehart et al. (2009)	
	Coelophysis bauri	gastrolite consisting of specimens of *Hesperosuchus*	Late Triassic	USA	Nesbitt et al. (2006)	
Dromaeosauridae	*Velociraptor mongoliensis*	azhdarchid pterosaur	Late Cretaceous	Mongolia	Hone et al. (2012)	
Tyrannosauridae	*Raptorex kreigsteini*	*Lycoptera* or Ellimmichthyiformes	Early or Late Cretaceous	Mongolia or China	Sereno et al. (2009); Fowler et al. (2011)	
	Daspletosaurus sp.	acid etched vertebrae and a fragmentary dentary from juvenile hadrosaur dinosaur	Late Cretaceous	USA	Varricchio (2001)	two part stomach
Megalosauridae	*Poekilopleuron bucklandii*	a tooth of the hybodont shark *Polyacrodus* sp., and fragments that resemble skeletal fragments of cartilaginous fishes	Middle Jurassic	France	Eudes-Deslongchamps (1838)	
Spinosauridae	*Baryonyx walkeri*	both fish and terrestrial vertebrates - *Iguanodon*	Early Cretaceous	England	Charig and Milner (1986, 1997)	
Deinocheiridae	*Deinocheirus mirificus*	fish	Late Cretaceous	Mongolia	Lee et al. (2014)	fish remains (vertebrae, scales)
Oviraptosauria	*Ningyuansaurus wangi*	seeds	Early Cretaceous	China	Ji et al. (2012)	
	Jinfengopteryx elegans	seeds?	Early Cretaceous	China	Ji et al. (2005)	

Mesozoic nonmarine consumulites						
Higher level Taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Compsognathidae	*Compsognathus longipes*	lepidosaur *Bavarisaurus* cf. *macrodactylus*	Late Jurassic	Germany	Ostrom (1978)	
	Scipionyx samniticus	fish and lepidosaurian reptiles	Early Cretaceous	Italy	Dal Sasso and Signore (1998); Dal Sasso and Maganuco (2011)	
	Sinosauropteryx prima	two specimens, one has pair of eggs (probably gignolites) and semi-articulated skeleton of lizard, including skull	Early Cretaceous	China	Chen et al. (1998); Dong and Chen (2000)	
	Sinosauropteryx prima	bones of an unidentified small mammal; the jaws of triconodont (*Sinobaatar*) and symmetrodont (*Zhangheotherium*) mammals	Early Cretaceous	China	Currie and Chen (2001); Hurum et al. (2006)	2 specimens
	Huaxiagnathus orientalis	chunks of a partially digested meal (bones)	Early Cretaceous	China	Hwang et al. (2004)	
	Sinocalliopteryx gigas	*Sinornithosaurus, Confuciusornis,* unidentified ornithiscian	Early Cretaceous	China	Ji et al. (2007); Xing et al. (2012)	
	Sinocalliopteryx gigas	incomplete dromaeosaurid leg preserved in abdominal cavity	Early Cretaceous	China	Ji et al. (2007); Xing et al. (2012)	
Dromaeosauridae	*Microraptor zhaoianus*	partially articulated skeleton of *Indrasaurus wangi* in stomach	Early Cretaceous	China	O'Connor et al. (2019)	ingested whole and head first
	Microraptor gui	small mammal bone	Early Cretaceous	China	Larsson et al. (2010)	
	Microraptor gui	enantiornithine bird partial skeleton	Early Cretaceous	China	O'Connor et al. (2011)	
	Microraptor gui	gut contents composed of teleost fish remains	Early Cretaceous	China	Xing et al. (2013)	
Anchiornithidae	*Anchiornis* sp.	gastric pellet comprising lizard bones preserved in the oesophageal area	Early Cretaceous	China	Zheng et al. (2018b)	

Mesozoic nonmarine consumulites

Higher level Taxon	Taxon	Contents	Age	Location	References	Notes
Ankylosauria	*Kunbarrasaurus ieversi*	short fragments of plant debris in matrix of micrite, mainly vascular bundles including seeds, complete fruiting bodies of angiosperms or their endocarps	Early Cretaceous	Australia	Molnar and Clifford (2000, 2001); Leahey et al. (2015)	previously referred to *Minmi* sp.
	Liaoningosaurus paradoxus	fish bones	Early Cretaceous	China	Ji et al. (2016)	gastrolite/intestinilite
	Borealopelta markmitchelli	leaf tissue dominated (85%) by leptosporangiate ferns with low cycad–cycadophytes (3%) and trace of conifer foliage	Late Cretaceous	Canada	Brown (2017); Brown et al. (2020)	
Hadrosauridae	*Brachylophosaurus canadensis*	abundant plant fragments (mainly mm size leaf fragments) occupy a volume of at least 5750 cm^3 including about 63% clay from flowing water that entered through openings in the carcass	Late Cretaceous	USA	Tweet et al. (2008, 2016)	
	Edmontosaurus sp.	needles and twig fragments of conifer	Late Cretaceous	Canada	Kräusel (1922)	disputed by Abel (1922b)
	Corythosaurus sp.	conifers	Late Cretaceous	Canada	Taggert and Cross (1997)	
	hadrosaurs	conifer	Late Cretaceous	Canada	Ostrom (1964); Currie et al. (1995)	
Confuciusornithiformes	*Eoconfuciusornis zhengi*	?plant propagules	Early Cretaceous	China	Mayr et al. (2021)	previously identified as ovarian follicles (Zheng et al., 2017)
	Confuciusornis sanctus	fish bones in crop, not in articulation but in cluster, tentatively indentified as primitive teleost fish, *Jinanichthys*	Early Cretaceous	China	Dalsätt et al. (2006)	partly underlying the ventral region of the seventh and eighth cervical vertebrae; position on the ventral side of the distal one-third of the neck of the bird suggests that the bones were processed in the alimentary system at the time of death

Mesozoic nonmarine consumulites						
Higher level Taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Jeholornithiformes	*Jeholornis prima*	many seeds, including *Carpolithus* in ventriculus	Early Cretaceous	China	Zhou and Zhang (2002); O'Connor et al. (2018)	4 specimens
	Jeholornis prima	plant propagules	Early Cretaceous	China	Mayr et al. (2021)	previously identified as ovarian follicles
Sapeornithiformes	*Sapeornis chaoyangensis*	6 with seeds in cropalite, one also has incorporeal pelletite intestinilite	Early Cretaceous	China	Zheng et al. (2011, 2014); Chiappe and Meng (2016)	3 specimens also have gastroliths
	Sapeornis chaoyangensis	4 with seeds in ventriculus, one has two size classes	Early Cretaceous	China	Zheng et al. (2014)	2 specimens also have gastroliths
Ornithuromorpha	*Hongshanornis longicresta*	mass of small seeds in crop	Early Cretaceous	China	Zheng et al. (2011)	gastroliths in gizzard
	Yanornis martini	One or more whole fish (7) or fish bones (4) in crop and two pellets and also material in ventriculus (12), which is dominantly macerated fish (9)	Early Cretaceous	China	Zhou et al. (2004); Wang et al. (2016); Zheng et al. (2014); Chiappe and Meng (2016)	13 specimens
	Yanornis sp.	more than one whole fish in crop, possible material in ventriculus	Early Cretaceous	China	Wang et al. (2013)	one specimen has gastroliths
Enantiornithes	*Eoalulavis hoyasi*	crustacean exoskeletal elements in ventriculus	Early Cretaceous	Spain	Sanz et al. (1996);O'Connor (2019)	
	Enantiophoenix electrophyla	small pieces of amber	Late Cretaceous	Lebanon	Dalla Vecchia and Chiappe (2002); Cau and Arduini (2008)	sap feeding
	Linyiornis amoena	plant propagules	Early Cretaceous	China	Mayr et. al. (2021)	previously identified as ovarian follicles (Wang et al., 2016)
	indeterminant	pellet with fish bones	Early Cretaceous	China	Wang et al. (2016)	
	indeterminant	enigmatic diminutive "corpuscles" in the pelvic area inferred to have derived from intestines	Early Cretaceous	Spain	Knoll et al. (2018)	perinate bird
	indeterminant	plant propagules	Early Cretaceous	China	Mayr et al. (2021)	7 specimens, previously identified as ovarian follicles

Mesozoic nonmarine consumulites

Higher level Taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Ornithuromorpha	*Piscivoravis lii*	macerated fish bones in ventriculus and fish bones in a pelletin ventriculus	Early Cretaceous	China	Zhou et al. (2014); O'Connor (2019)	
	Eogranivora edentulata	seeds in cropalite	Early Cretaceous	China	Zheng et al. (2011, 2018a)	gastroliths
Eudimorphodontidae	*Eudimorphodon ranzii*	fish remains referred to *Parapholidophorus*	Late Triassic	Italy	Wild (1978); Dalla Vecchia (2003)	
Rhamphorhynchidae	*Rhamphorhynchus muensteri*	indeterminate vertebrate elements	Late Jurassic	Germany	Hone et al. (2015)	
	Rhamphorhynchus muensteri	small leptolepidid fishes	Late Jurassic	Germany	Wellnhofer, (1975a-b, 1991); Witton (2013, 2018)	2 specimens; shows size of gut and that must have possessed highly mobile and distensible throat tissues, much like those of modern fish-eating birds
	Rhamphorhynchus muensteri	a pair of dark brown elements close to the gastralia appear to be osteichthyan scales or teeth; a mass of additional fish parts lies between the gastralia and dorsal ribs; these include a putative series of vertebrae, a fin ray, and a series of small discs that may be scales	Late Jurassic	Germany	Hone et al. (2013)	
	Rhamphorhynchus sp.	swallowing head first, a leptolepidid fish, tail stuck in the pharyngeal region	Late Jurassic	Germany	Frey and Tischlinger (2012)	pterosaur killed by *Aspidorhynchus* and swallowing not completed of prey
Euctenochasmatia	*Pterodactylus* sp.	fish debris in the gular area tentatively interpreted as the contents of a throat pouch	Late Jurassic	Germany	Kellner (2006)	
	"*Pterodactylus propinquus*"	disarticulated fish debris in and around the region of the gular pouch, including a 10 mm-long series of articulated vertebrae and fin debris	Late Jurassic	Germany	Broili (1938); Wellnhofer (1970)	specimen lost

Mesozoic nonmarine consumulites						
Higher level Taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Tapejaromorpha	*Nemicolopterus crypticus*	yellow-colored matrix occasionally forming rounded structures represents decayed soft tissues or amorphous gut content	Early Cretaceous	China	Wang et al. (2008)	
Anhangueridae	*Ludodactylus sibbicki*	large leaf between the mandibular rami	Early Cretaceous	Brazil	Frey et al. (2003); Witton (2018)	frayed leaf margin is interpreted as evidence of attempts to dislodge the leaf from the gular pouch, and the pterosaur’s inability to do this led to its death
Mammalia	*Repenomamus robustus*	juvenile *Psittacosaurus* as stomach contents	Early Cretaceous	China	Hu et al. (2005)	

TABLE A.10. Cenozoic marine consumulites.

Cenozoic marine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Lamniformes	*Cosmopolitodus hastalis*	*Sardinops* sp. cf. *S. sagax*	Miocene	Peru	Collareta et al. (2017c)	between the 25th and the 33rd vertebra
	Cosmopolitodus hastalis	fish remains as fossilized stomach contents including several scales and an opercle of *Sardinops* cf. *S. sagax*	Late Miocene	Peru	Collareta et al. (2017c); Bosio et al. (2021)	
Carcharhiniformes	*Galeorhinus cuvieri*	skeleton of barracuda, *Sphyraena bolcensis*	Early Eocene	Italy	Friedman and Carnevale (2018)	
	Galeorhinus cuvieri	stomach contents of 6 articulated distal caudal vertebrae and dismembered caudal fin rays of *Sphyraena bolcensis*	Early Eocene	Italy	Fanti et al. (2016)	evidence that a predator–prey relationship between *Galeorhinus* and *Sphyraena* in the modern coral reefs has roots in the Eocene
Anguilliformes	*Paranguilla tigra*	*Cyclopoma gigas*	Early Eocene	Italy	Viohl (1990)	prey ingested head first
	indeterminate	fragments of 4 fish	Early Eocene	Italy	Viohl (1990)	1 ingested head first, 3 ingested tail first
	Paranguilla tigrina	indeterminate	Early Eocene	Italy	Sorbini (1972)	prey ingested head first
Perciformes	*Carangodes cephalus*	fish	Early Eocene	Italy	Viohl (1990)	prey ingested head first
	Ductor vestenae	fish	Early Eocene	Italy	Viohl, (1990)	prey ingested head first
	Callipteryx speciosus	indeterminate	Early Eocene	Italy	Agassiz (1833-1845b)	1 prey ingested head first and 1 ingested tail first
	Serranus budensis	*Serranus budensis*	Oligocene	Romania	Paucă (1933)	prey ingested head first
Acanthomorpha	*Blochius longirostris*	indeterminate	Early Eocene	Italy	Agassiz (1833-1845a)	prey ingested head first
Osmeriformes	smelt	argentinoid	Early Eocene	Denmark	Bonde (1987)	prey ingested head first
Scombriformes	*Scomberomorus (Cybium)* sp.	12 clupeids	Early Oligocene	Germany	Weiler (1931)	prey ingested head first

Cenozoic marine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Stomiiformes	*Scopeloides glarisianus*	crustaceans such as ostracods and copepods, and small fish, principally *Scopeloides glarisianus*	Oligocene	Poland, Ukraine, Czech Republic, northern Caucasus in Russia and Abkhazia	Přikryl et al. (2012)	crustaceans in smaller specimens and fish in larger specimens
Lophiiformes	*Antennarius monodi*	a nearly complete percomorph fish, possibly belonging to the family Sparidae	Miocene	Algeria	Carnevale and Pietsch (2006)	the prey is longer than the predator; frogfishes of Antennariidae are able to swallow very large prey because of rapid expansion of the oral and opercular cavities that produces suction pressure for prey capture
Aulopiformes	*Lestidiops (Lestioliops)*	*Bregmoceras* and unidentified fish	Pliocene	Italy	Viohl (1990)	prey ingested head first
Stomiiformes	*Chauliodus eximius*	?bathypelagid	Middle Miocene	USA	Crane (1996)	prey ingested head first
Pycnodontiformes	pycnodonts	small pieces of coral	unspecified	unspecified	Maisey (1996)	
Basilosauridae	*Basilosaurus isis*	smaller whales (juvenile *Dorudon atrox)* and large fishes *(Pycnodus mokattamensis)*	Late Eocene	Egypt	Voss et al. (2019)	
	Basilosaurus cetoides	fishes and sharks ranging up to approximately 50 cm in length	Late Eocene	Egypt	Swift and Barnes (1996)	
	Durudon atrox	fish	Late Eocene	Egypt	Uhen (2004)	
	Cynthiacetus peruvianus	head of a large scombrid teleost fish aff. *Scombramphodon* (c. 1.5 m long) in anterior of thoracic region	Late Eocene	Peru	Martínez-Cáceres et al. (2017)	hypothesized that head remained caught in the throat of the predator in the process of swallowing, which may have caused its death by suffocation

Cenozoic marine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Odontoceti	*Messapicetus gregarius*	clupeiform *Sardinops* sp. cf. *S. sagax*	Late Miocene	Peru	Lambert et al. (2015); Bosio et al. (2021)	aggregate between the posterior left ribs suggests it derives from cetacean forestomach
Mysticeti	undescribed	clupeiform *Sardinops* bones and scales, discrete small mass between ribs	Late Miocene	Peru	Collareta et al. (2015)	first direct evidence of piscivory in an ancient edentulous mysticete
Gaviiformes	?*Colymboides metzleri*	dense package of remains of small fishes (diameter of vertebrae from 0.4–1.0 mm) represents the stomach contents	Early Oligocene	Germany	Mayr (2004)	

TABLE A.11. Cenozoic nonmarine consumulites.

Cenozoic nonmarine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Perciformes	*Mioplosus labracoides*	*Knightia humilis*	Early Eocene	USA	Jepsen (1967); Grande (1980, 2013)	prey ingested head first, aspirationalite
	Rhenanoperca minuta	aquatic larvae of nematocerous Diptera and parts of fish skeletons	Middle Eocene	Germany	Richter and Baszio (2006)	less than 30 mm long contain arthropods and longer contain fish
	Mioplosus labracoides	*Knightia eocaena* oralite	Early Eocene	USA	Grande (2013)	half body out of mouth, aspirationalite
	Mioplosus labracoides	*Diplomystus dentatus* and other taxa	Early Eocene	USA	Grande (2013)	*Mioplosus labracoides* has most consumulites in Green River Formation
	Priscacara serrata	*Knightia eocaena*	Early Eocene	USA	Grande (2013)	aspirationalite, prey ingested head first
	Priscacara serrata	*Priscacara serrata*	Early Eocene	USA	Grande (2013)	aspirationalite, prey ingested head first, juvenile predator
	Lepidocottus sp.	planorbid snails	Miocene	Germany	Cockerill (1915)	
Clupeiformes	*Diplomystus dentatus*	*Knightia humilis*	Early Eocene	USA	Grande (1980, 1984)	prey ingested head first
	Diplomystus dentatus	*Knightia eocaena* oralite	Early Eocene	USA	Ulrich (1978), Grande (1984)	prey ingested head first, only head in mouth, aspirationalite
	Diplomystus dentatus	*Cockerellites liops*	Early Eocene	USA	Grande (2013)	two apirationalites, prey ingested head first
	Diplomystus dentatus	*Knightia eocaena*	Early Eocene	USA	Grande (2013)	gastrolite, dozens of *Diplomystus* specimens have consumulites of which at least 10 contain *Cockerellites* or *Priscacara*
	Diplomystus dentatus	*Diplomystus dentatus*	Early Eocene	USA	Grande (2013)	aspirationalite
Lepisosteiformes	*Lepisosteus simplex*	*Diplomystus* sp. oralite	Early Eocene	USA	Ulrich (1978); Grande (1980, 1984)	prey ingested head first, tail extends out of oral cavity, aspirationalite
	Atractosteus simplex	*Diplomystus dentatus*	Early Eocene	USA	Grande (2013)	two specimens, both aspirationalites, prey ingested head first
Osteoglossiformes	*Phareodus encaustus*	*Mioplosus labracoides*, *Knightia eocaena* oralites	Early Eocene	USA	Grande (2013)	3 examples of tail extending out of mouth, aspirationalites

Cenozoic nonmarine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Amiiformes	*Amia unintaensis*	*Diplomystus,* which, in turn, contains *Knightia*	Early Eocene	USA	Boreske (1974); Grande (1980)	stomach ruptured during burial and prey is extruded; prey ingested head first
	Amia pattersoni	*Mioplosus*	Early Eocene	USA	Grande (2013)	gastrolite, stomach distended
Acipenseriformes	*Crossophilis magnicaudatus*	*Mioplosus labracoides*	Early Eocene	USA	Grande (2013)	gastrolite
Salmoniformes	*Thaumaturus intermedius*	abundant arthropod cuticular fragments, intestinal contents originate from small Crustacea (Cladocera) and larvae of Diptera (Culicidae and Chaoboridae)	Middle Eocene	Germany	Richter and Baszio (2001a)	21 specimens
Anura	*Palaeobatrachus* sp.	disarticulated and poorly preserved fish bones, correspond in size to a small specimen of *Palaeorutilus enspelensis*, mainly isolated vertebrae and fin ray elements embedded and covered in a brown mass	Late Oligocene	Germany	Wuttke and Poschmann (2010)	
	Pelobates sp.	group of black roundish spots in the abdominal region	Early Miocene	Turkey	Dubois et al. (2009)	3 specimens, spots could represent seeds, bacterial or fungal aggregations or eggs
	Rana pueyoi	stomach contents composed of overlapping gastropod shell fragments (32 specimens) of aquatic genera of planorbiid and bithyniid families, single specimens also include the water plant *Ruppia*, seeds, sponge spicules, vertebral column of a larval anuran, fragments of arthropod cuticle, and rare patches of layered, densely packed fibers may represent fragments of ingested tissues	Miocene	Spain	McNamara et al. (2009); Wuttke and Poschmann (2010)	61% of specimens (n=71) have stomach contents

Cenozoic nonmarine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Anura	*Rana pueyoi* tadpoles	fine-grained granular sedimentary detritus consisting of silt-sized grains of calcium carbonate and fragmented diatom frustules; siliceous sponge spicules also present	Miocene	Spain	McNamara et al. (2010)	
	Pelobates decheni and *Eopelobates anthracinus* tadpoles	granular gut contents	Oligocene	Germany	Maus and Wuttke (2002)	
	tadpoles	granular gut contents	Tertiary	Europe	Špinar (1972)	
Testudinidae	*Stylemys* sp. and *Stylemys nebrascensis*	hackberry (*Celtis*) seeds	Oligocene	USA	Marron and Moore (2013)	2 specimens
Iguania	*Geiseltaliellus maarius*	globular plant remains	Middle Eocene	Germany	Smith and Scanferla (2016)	
Scincoidea	*Ornatocephalus metzler*i	gastrolite contains plant matter and insect cuticle	Middle Eocene	Germany	Weber (2004)	3 specimens
Alethinophidia	*Eoconstrictor fischeri*	gastrolite of crocodilian probably *Diplocynodon* sp.	Middle Eocene	Germany	Greene (1983); Scanferla and Smith (2020)	
lethinophidia	*Eoconstrictor fischeri*	lizard *Geiseltaliellus maarius* in stomach which in turn has insect in its gut	Middle Eocene	Germany	Schall (2004); Smith and Scanferla (2016)	lizard swallowed head first; consumulite within a consumalite
Crocodilia	*Menatalligator bergouniouxi*	*Amia*	Paleocene	France	Wedmann et al. (2018)	
	Pristochampsus vorax	nearly complete hindlimb of perissodactyl, *Helaletes* sp.	Eocene	USA	Alexander and Burger (2001)	
“Insectivore”	indeterminate	stomach contents	Paleocene	France	Guth (1962); Wedmann et al. (2018)	
Mustelidae	*Mustela nigripes*	undetermined	Pleistocene	Canada	Youngman (1994); Hunt and Lucas (2007)	

Cenozoic nonmarine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Canidae	borophagine *Carpocyon* (*Tomarctus robustus*)	rabbit (*Hypolagus*), pocket mouse and other small mammals in limey mass in the abdominal cavity behind the pelvis	Late Miocene	USA	Green (1948); Stirton (1959); Tedford in Boucot (1990)	
Proviverridae	*Lesmesodon edingeri*	teeth, bone fragments including one amphibian or reptile jaw, an insectivore jaw and tooth	Middle Eocene	Germany	Morlo et al. (2012); Schaal (2016); Gunnell et al. (2018)	juvenile specimen that is regurgitalite/digestilite produced by a boid snake, probably *Palaeopython*
Pantolestidae	*Palaeosinopa didelphoides*	fish bones	Early Eocene	USA	Grande (2013)	
	Buxolestes piscator	fish debris in one specimen, plant debris in second	Middle Eocene	Germany	Richter (1987); Von Koenigswald et al. (1992, 2018)	2 specimens
Eomanidae	*Eomanis waldi*	coarse sand and plant debris in stomach, insect chitin in only one specimen	Middle Eocene	Germany	Von Koenigswald et al. (1981); Richter (1988); Storch and Richter, (1992); Gunnell et al. (2018)	5 specimens
Ischyromyidae	*Ailuravus macrurus*	leaf fragments of laurel in one specimen and of *Polyspora* in another	Middle Eocene	Germany	Ruf and Lehmann (2018)	2 specimens
Gliridae	*Eogliravus wildi*	fruits, seeds, buds	Middle Eocene	Germany	Ruf and Lehmann (2018)	
Dichobunidae	*Messelobunodon schaeferi*	fungi in one specimen, seeds and leaves in another, only one contains small pieces of insect cuticle	Middle Eocene	Germany	Richter (1981); Richter in Boucot (1990)	
Equidae	*Propalaeotherium*	mainly leaves but also some fruit (grape pits)	Middle Eocene	Germany	Franzen (1976, 1977, 1984, 1985); Collinson (1990, 1999)	several specimens from Messel
	Propalaeotherium isselanum	densely packed plant material, especially leaf fragments but also fruits/seeds and pollen, in a dense matrix of organic material with interspersed quartz grains	Middle Eocene	Germany	Wilde and Hellmund (2010)	specimen from Geiseltal

Cenozoic nonmarine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Equidae	*Equus lambei*	intestinal contents included not only remains of what the horse had been feeding on, but also elements of the surrounding environment; grasses, sedges, poppies, mustards, pink family, buttercups and members of the rose family	Pleistocene	Canada	Harington (2002)	
Pseudorhyncocyonidae	*Leptichtidium nasutum*	insect fragments	Middle Eocene	Germany	Maier et al. (1986); Richter (1988)	
Amphilemuridae	*Pholidocercus hassiacus*	insect cuticle, fruit tissue and leaves	Middle Eocene	Germany	Storch and Richter (1994); Storch (2001); von Koenigswald et al. (2018)	3 specimens, 2 predominantly insects including beetles, 1 mainly plant material including fruit and leaves
	Macrocranion tupaiodon	fish, seeds, fruit, insect cuticle, leaves, fungus, fish	Middle Eocene	Germany	Storch and Richter (1994); Storch (2001); von Koenigswald et al. (2018)	10 specimens, 3 almost exclusively fish, one partially fish
Dichobunidae	*Aumelasia* cf. *gabineaudi*	fruit pulp, seeds, fungi	Middle Eocene	Germany	Franzen and Richter (1992); Lehmann and Ruf (2018)	
	Eurodexis sp.	fruit pulp, seeds, fungi	Middle Eocene	Germany	Lehmann and Ruf (2018)	
Choeropotamidae	*Masillabune martini*	leaves of Laurel	Middle Eocene	Germany	Tobian (1980); Lehmann and Ruf (2018)	
Bovidae	*Bison priscus*	Poaceae, Apiaceae, mosses and horsetails	Holocene	Russia	Van Geel et al. (2014); Boeskorov et al. (2016)	
Rhinocerotidae	*Coelodonta antiquitatis*	spore and pollen analyses of the stomach contents indicate that grasses and sagebrushes formed the main part of the diet	Pleistocene	Russia	Boeskorov et al. (2011)	

Cenozoic nonmarine consumulites

Higher level taxon	Taxon	Contents	Age	Location	References	Notes
Elephantidae	*Mammuthus primigenius*	pollen and plant macro-remains show that grasses and sedges were the main food, with considerable amounts of dwarf willow twigs and a variety of herbs and mosses	Pleistocene	Russia	van Geel et al. (2008)	fruit bodies of dung-inhabiting ascomycete fungi indicate coprophagy
	Mammuthus primigenius	intestinilite with plant detritus, some animal remains and mineral matter; plant remains are dominated by branches of mosses with rare herbaceous plants; animals are ephippia of *Daphnia* sp., worm remains, a few fragments of insects and arachnids, and a single bone of a micromammal	Pleistocene	Russia	Kosintsev et al. (2012)	very young specimen; most plant remains are crushed and fractured into separate fibers by chewing by an adult, suggesting coprophagy; also suggested by the abundance of ascospores of coprophilous fungi in the pollen spectrum
Adapidae	*Darwinius masillae*	seed of fruit, leaves	Middle Eocene	Germany	Franzen and Wilde (2003); Franzen et al. (2009)	first fossil primate consumulite
Chiroptera	*Palaeochiropteryx tupaiodon,*	insects, principally lepidopteran wings, bat hair	Middle Eocene	Germany	Richter and Storch (1980); Richter (1988); Habersetzer et al. (1994, 2018)	16 specimens; hair is presumably from grooming
	Palaeochiropteryx spp.	small moths, and caddis flies	Middle Eocene	Germany	Habersetzer et al. (1994)	hunting slow and low flying insects
	Hassianycteris spp.	beetles and other insects with thick cuticules	Middle Eocene	Germany	Habersetzer et al. (1994, 2018)	
	Tachypteron franzeni	black area below ribs	Middle Eocene	Germany	Habersetzer et al. (2018)	
	Archaeonycteris spp.	beetle cuticle	Middle Eocene	Germany	Habersetzer et al. (2018)	
Mammalia	mummified mammals	various	Pleistocene	various	Harington (2007)	
Eurypygiformes	*Messelornis cristata*	*Rhenanoperca minutus* in esophagus, seeds in gut	Middle Eocene	Germany	Morlo (2004)	
Cariamiformes	*Strigogyps sapea*	preserves plant material in its crop and stomach or gut regions	Middle Eocene	Germany	Mayr and Richter (2011)	

Cenozoic nonmarine consumulites						
Higher level taxon	**Taxon**	**Contents**	**Age**	**Location**	**References**	**Notes**
Gruiformes	*Salmila robusta*	unidentified material	Middle Eocene	Germany	Mayr (2002)	
Coraciiformes	*Primobucco frugilegus*	fruits are preserved as stomach contents	Middle Eocene	Germany	Mayr et al. (2004)	
Coraciiformes	*Eocoracias brachyptera*	large bean-shaped seed, surrounded by grit	Middle Eocene	Germany	Mayr and Mourer-Chauviré (2000)	
Zygodactylidae	*Primozygodactylus major*	seeds, including Vitaceae	Middle Eocene	Germany	Mayr (2009)	
Coliiformes	*Eoglaucidium pallas*	Annonaceae seeds	Middle Eocene	Germany	Mayr and Peters (1998)	
	Masillacolius brevidactylus	large seed	Late Eocene	Germany	Mayr (2015)	
Galliformes	*Palaeortyx* cf. *gallica*	fibrous plant material in stomach and seeds in crop	Oligocene	Germany	Mayr et al. (2006)	
Colliiformes	*Oligocolius psittacocephalon*	fruitstones, six in crop, two in stomach	Late Oligocene	Germany	Mayr (2013)	
Aves incertae sedis	*Pumiliornis tessellatus*	gastrolite containing numerous pollen grains of an eudicotyledonous angiosperm also contains a few unidentifiable insect remains	Middle Eocene	Germany	Mayr and Wilde (2014)	earliest and first direct fossil evidence of bird feeding on flowers
Vertebrata	multiple taxa	various	Middle Eocene	Germany	Richter (1987, 1988, 1992)	

APPENDIX B

GLOSSARY OF TERMS

Accretionary latrinite: Latrinite that results from accumulation due to physical, rather than biological, processes (Hunt and Lucas, 2012a).

Accretionary purgolite: Purgolite that results from accumulation due to physical, rather than biological, processes (Hunt and Lucas, 2012a).

Amphipolar: Spiral coprolite that preserves coils that extend for the majority of the length of the coprolite (>75%) in lateral view (Neumayer, 1904; Hunt and Lucas, 2012b; Figs. B.1-2).

Anisopolar: Non-spiral coprolite with terminations of different shapes (Thulborn, 1991) (Fig. B.3).

Aspirationalite: Consumulites that preserve prey in the oral cavity, with a significant portion extending exteriorly (this paper).

Anterior coil: The anterior end of a spiral coprolite consisting of a single, antero-posteriorly elongate coil (Hunt and Lucas, 2012b; Fig. B.1).

Bromalite: All trace fossils that represent food items that have entered the oral cavity and/or gastrointestinal tract of an animal and have been expelled (either anteriorly or posteriorly and either pre- or post-mortem) from, or retained within, them (Hunt, 1992).

Chiropteraguanolite: Guanolite produced by bats (Hunt and Lucas, 2012a).

Coil: The external expression of the spiral, conular elements of a spiral coprolite (Hunt and Lucas, 2012b; Fig. B.1).

Cololite: Consumulite preserved in the gastrointestinal tract posterior to the stomach (sensu Hunt and Lucas, 2012a).

Consumulite: All fossilized digested food material preserved within the body cavity (Hunt and Lucas, 2012a).

Coprolite: Fossil fecal material that has been ejected from the posterior end of the gastrointestinal tract (Buckland, 1829; Hunt and Lucas, 2012a).

Cropalite: Consumulite preserved contents in the crop (this paper).

Cumulite: Accumulation of organic or inorganic material concentrated by an organism (Hunt and Lucas, 2012a).

Demalite: Skeletal material preserved within the body cavity of a vertebrate or invertebrate animal that does not pertain to it (could be consumulite, gignolite, artifact or not discernable) (Hunt and Lucas, 2012a).

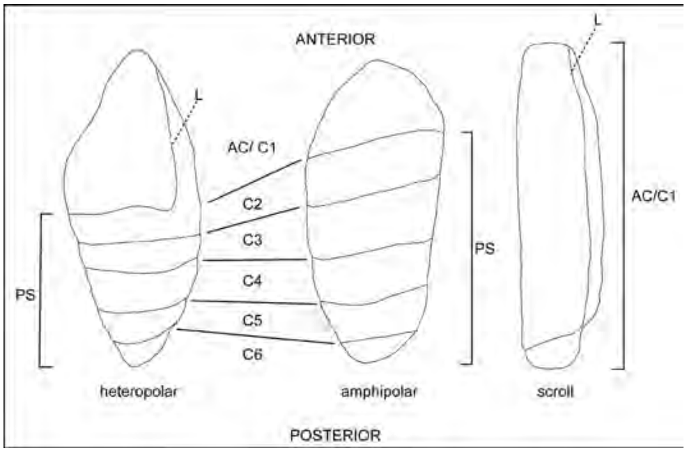


FIGURE B.1. Descriptive terminology of spiral coprolites. **AC** is anterior coil, **C** is coil, **L** is lip, **PS** is posterior spire (from Hunt and Lucas, 2012b, fig. 3).

Dentalite: Traces produced on a substrate by the teeth or oral cavity of a vertebrate or invertebrate (Hunt et al., 2018).

Digestichnia: Ethological class that comprises all trace fossils (and their recent counterparts) originating from the digestive process of animals, including coprolites, regurgitalites and gastroliths (Vallon, 2012).

Digestilite: Fossil specimens that preserve evidence of digestion (this paper).

Dislocational evisceralite: Evisceralite in which a portion of the gastrointestinal tract is physically removed from a carcass (this paper).

Esophogalite: Consumulite preserved in the gastrointestinal tract anterior to the stomach (Hunt and Lucas, 2012a).

Emetolite: Regurgitalite from animal that habitually egests pellets (Myrhvold, 2011).

Enterospira: Cololite preserved in a spiral valve (sensu Hunt and Lucas, 2012a).

Ethological latrinite: Latrinite that results from behavior of an organism (Hunt and Lucas, 2012a).

Ethological purgolite: Purgolite that results from behavior of an organism (Hunt and Lucas, 2012a).

Evisceralite: Cololite that is a preserved segment of infilled fossilized intestines preserved independent of, or exterior to, a carcass (Hunt and Lucas, 2012a).

Excorporeal pelletite: Pelletite preserved outside body cavity, coprolite (Hunt and Lucas, 2012a).

Gastrolith: Sand and/or gravel swallowed by an animal and retained in the digestive tract (this paper).

Gastrolite: Fossilized wholly or partially digested food material preserved in the stomach (Northwood, 2005).

Gignolite: Trace and body fossils related to reproduction (Hunt and Lucas, 2012a).

Guanolite: Fossil guano deposit (Hunt and Lucas, 2012a).

Heteropolar: Spiral coprolite with the coils concentrated at one end in lateral view (Neumayer (1904; Figs. B.1-2).

Incorporeal pelletite: Pelletite preserved within the body cavity (Hunt and Lucas, 2012a).

Intestinelite: Cololite preserved within the body cavity (Hunt and Lucas, 2012a).

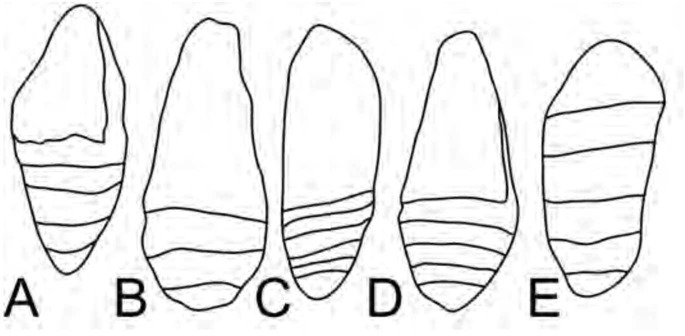


FIGURE B.2. Principal morphotypes of spiral coprolites: Macrospiral heteropolar (**A**), microspiral heteropolar (**B-D**) and amphipolar coprolites (**E**). **A,** *Liassocopros*. **B,** *Saurocopros*. **C,** *Malericopros*. **D,** *Heteropolacopros*. **E**, *Hyronocopros*. Not to scale (adapted from Hunt et al., 2007, fig. 6).

Isopolar: Non-spiral coprolite with terminations of the same shape (Thulborn, 1991).

Latrinite: An accumulation of coprolites (Hunt and Lucas, 2012a).

Lip: An exposed edge of a flap on the anterior coil of a heteropolar coprolite (Jain, 1983; Fig. B.1).

Macrospiral: Heteropolar coprolite in which the posterior spire constitutes 50%-75% the length of the coprolite in lateral view (Hunt and Lucas, 2012b; Fig. B.2).

Microspiral: Heteropolar coprolite in which the posterior spire constitutes less than 50% of the length of the coprolite in lateral view (Hunt and Lucas, 2012b; Fig. B.2).

Micturalite: Trace fossil produced by interaction between liquid urine and substrate (Hunt and Lucas, 2012a).

Mololite: From the Latin *molo* (to grind), for wear features on fossil teeth (this paper).

Mucro: Anterior end of an anisopolar coprolite that is tapered to a point (Thulborn, 1991; Fig. B.3).

Neotomalite: Fossil packrat midden (Hunt and Lucas, 2012a).

Nest: Structure made by, or the place chosen by, an animal for spawning, breeding and/or laying eggs and sheltering young (Lucas and Hunt, 2006).

Oralite: Consumulite preserved wholly or partially within the oral cavity (Hunt and Lucas, 2012a).

Ornithoguanolite: Guanolite produced by birds (Hunt and Lucas, 2012a).

Pabulite: Fossilized food that never entered the digestive tract (Klug et al., 2021a).

Paleomidden: Fossilized mammalian midden (Hunt and Lucas, 2012a).

Pelletite: Fossil fecal pellets preserved inside (incorporeal pelletite) or outside (excorporeal pelletite) the body cavity (Hunt and Lucas, 2012a).

Pinnipedaguanolite: Guanolite produced by pinnipeds (Hunt and Lucas, 2012a).

Posterior spire: The posterior segment of heteropolar coprolites that consists of a number of closely spaced coils (Hunt and Lucas, 2012b: Fig. B.1).

Postilite: Fossil site used repeatedly by an organism for defecation or urination to mark territory (Hunt and Lucas, 2012a).

Preservational evisceralite: Evisceralite resulting from preferential fossilization of the gastrointestinal tract (this paper).

Proventrilite: Consumulite preserved in proventriculus (this paper).

Regurgitalite: Trace fossil that includes all manipulated or digested/partially digested food material egested via the oral cavity (Hunt, 1992).

Saccatalite: Fossil accumulation of dried liquid urine (Hunt and Lucas, 2012a).

Scroll: Spiral coprolite with the structure of a rolled sheet of paper that consists essentially of a single coil (Hunt and Lucas, 2012b; Fig. B.1).

Segments: Discrete, longitudinal elements of a non-spiral coprolite (Hunt et al., 2012b; Fig. B.3).

Urolite: Fossil nonliquid urinary secretions (sensu Hunt and Lucas, 2012a).

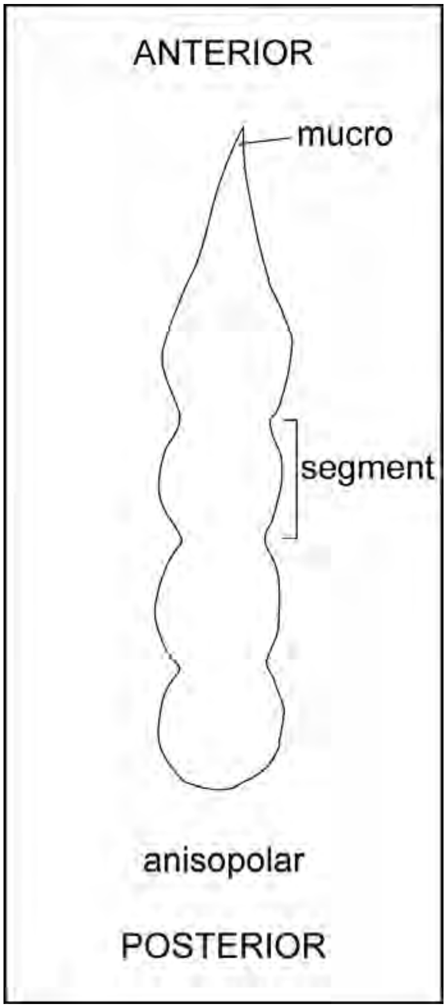


FIGURE B.3. Descriptive terminology of non-spiral coprolites (from Hunt and Lucas, 2012b, fig. 5).