THE BROMALITE COLLECTION AT THE NATIONAL MUSEUM OF NATURAL HISTORY (SMITHSONIAN INSTITUTION), WITH DESCRIPTIONS OF NEW ICHNOTAXA AND NOTES ON OTHER SIGNIFICANT COPROLITE COLLECTIONS

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Abstract—The National Museum of Natural History (Smithsonian Institution, Washington, D. C.) contains one of the largest collections of vertebrate coprolites (and other bromalites) in the world. Specimens come from the middle-upper Paleozoic (Devonian, Carboniferous, Permian), Mesozoic (Triassic, Jurassic, Cretaceous), Tertiary (Paleocene, Eocene, Miocene, Oligocene) and Quaternary (Pleistocene). We recognize two new ichnotaxa in the collection: *Iuloeidocoprus mantelli*, ichnogen et ichnosp. nov. – a widespread Late Cretaceous coprolite, and *Hirabromus seilacheri*, ichnogen et ichnosp. nov. – a cololite known from the Mesozoic and Cenozoic. Other important bromalites collections are at the: (1) New Mexico Museum of Natural and Science, whose extensive vertebrate trace fossil collection (including bromalites) is large, diverse and rapidly growing; (2) the Buckland Collection at the University of Oxford Museum of Natural History, the oldest collection of coprolites in the world; and (3) The Natural History Museum, a modest-sized but diverse collection.

INTRODUCTION

The National Museum of Natural History (Smithsonian Institution, Washington, D.C.) contains one of the largest collections of vertebrate coprolites in the world in terms of both quantity and diversity. This important collection, which also includes other bromalites, has received almost no study (an exception is Brown, 1962). The purpose of this paper is to discuss the importance of this collection and to describe new ichnotaxa represented within it. AMNH refers to American Museum of Natural History, New York, USA; GPIT refers to Geologisch-Paläontologisches Institut Tübingen, Germany; NHMUK refers to Natural History Museum, London, UK; NMMNH refers to New Mexico Museum of Natural History, Albuquerque, NM, USA; and USNM refers to the National Museum of Natural History (Smithsonian Institution), Washington DC, USA.

BROMALITE COLLECTION AT NATIONAL MUSEUM OF NATURAL HISTORY

Paleozoic

Devonian

The oldest specimens in the collection are three coprolites (USNM 4240) from the Lower Devonian along the Aa River, Livonia (Latvia/Estonia), which were received from the Museum of the Mining School of St Petersburg in 1899. Two of them are complete, rounded ovoids, and the third is a segment of a tapering cylinder. The best-preserved ovoid is 30 mm long and has a rounded cross section with a diameter of 9 mm, and rounded ends (Fig. 1A-C). Some portions of the exterior exhibit multiple fine, parallel striations, and the coprolite appears to have a spiral form. The single example of a tapered cylinder has a slightly knobby exterior surface, is 37.5 mm long and its cross section is ovoid with maximum dimensions of 14 mm and 9 mm (Fig. 1D-F). This specimen may have a crude spiral structure. Another uncatalogued specimen from the Devonian of Missouri is not a coprolite.

Carboniferous

The collection includes several specimens from the Carboniferous of the USA, UK and Belgium. Three small slabs of matrix from Little Mission Creek in Kansas are uncatalogued and contain individual coprolites (Fig. 1G-I). The largest piece of matrix contains one large coprolite and fragments of others. The principal specimen appears to be a flattened cylinder with rounded ends that is 21 mm long and 4.5 mm wide. This coprolite consists of two segments with a sulcus between them. The other two specimens are similar in morphology but consist of a single segment, one being 6 mm by 3 mm and the other 6 mm by 2 mm.

The uncatalogued specimens from the Carboniferous of Maffle, Hainaut in Belgium include four morphotypes. Three specimens are elongate, rounded cylinders. The most complete is 18 mm long and has a rounded cross section with a diameter of 3 mm (Fig. 1N), and the largest, incomplete specimen is 22 mm long with an ovoid cross section (5.5 by 3 mm). The second most common morphotype is a short, rounded ovoid with a rounded cross section (Fig. 1O), which has dimensions of 8.2 mm and 7 mm and widths of 2.5 mm and 3 mm. The third morphotype is a curved, tapering cone (Fig. 1P), and the fourth is a broken, straight, pointed tip of a larger coprolite (Fig. 1Q).

Three specimens derive from the "Soapstone bed" in the Lower Coal Measures (Upper Carboniferous) at Burnley, England. Two split concretions are elongate and ovoid and up to 55 mm long and 33 mm wide. One coprolite is 43 mm long and 13 mm wide (Fig. 1K), and the other is 42 mm long and 9 mm wide (Fig. 1J). USNM 4148 is larger (44 mm by 54 mm), more rounded and polished on one side. It contains fragments of a goniatite and the nautiloid *Orthoceras* (Fig. 1L-M).

Permian

The collection includes coprolites from the Permian of France and Oklahoma. USNM 16386 is two specimens from the "Magnesian Limestone" of Saône-et-Loire, France. One coprolite is microspiral and heteropolar with the maximum diameter posterior to the spiral demarcation (Fig. 1T-U) and thus is assignable to *Malericoprus* sp. (Hunt et al., 2007, fig. 5f). This coprolite is 44 mm long, ovoid in cross section (19 by 14.5 mm) and is the oldest occurrence of this ichnogenus. The other specimen is also microspiral and heteropolar (Fig. 1R-S), but the widest point is anterior of the posterior spire (*sensu* Hunt and Lucas, 2012b). It is 45 mm long and 45 mm in diameter. This specimen has about five coils at the posterior end and thus represents *Heteropolacoprus* rather than *Saurocoprus* (Hunt et al., 2007, fig. 6).

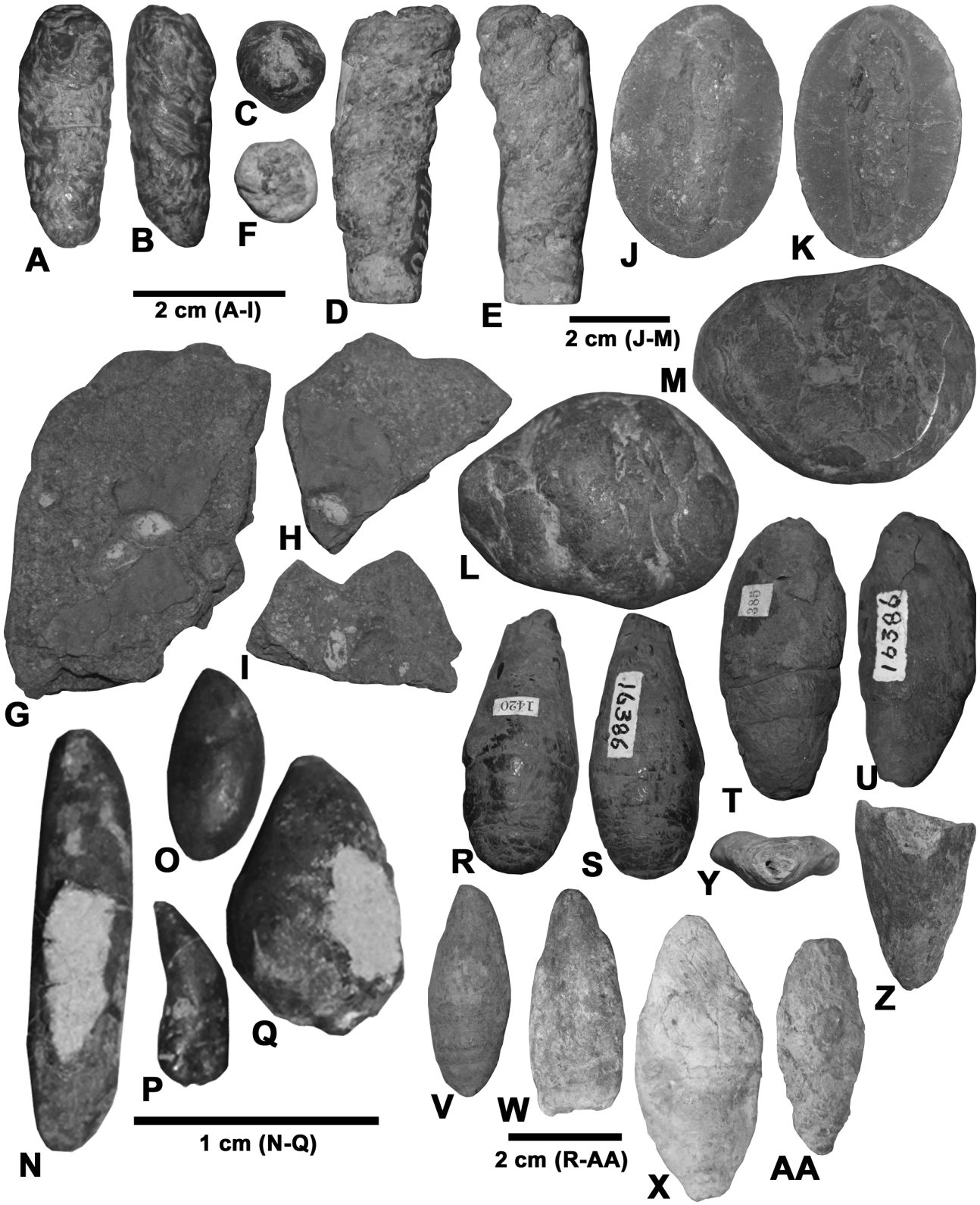

FIGURE 1. Paleozoic coprolites. **A-F**, USNM 4240, Coprolites from Lower Devonian of Livonia, **A-C**, striated ovoid coprolite in **A-B**, axial and **C**, polar views, **D-F**, tapering cylindrical coprolite in **D-E**, axial and **F**, polar views. **G-I**, Three USNM uncatalogued specimens from the Pennsylvanian of Kansas in axial view. **J-M**, Upper Carboniferous coprolites from the Lower Coal Measures, Burnley, England, **J-K**, split nodule in two views, **L-M**, polished coprolite in two views. **N-Q**, USNM uncatalogued, Carboniferous coprolites from Belgium, **N**, elongate rounded cylinders, **O**, short, rounded ovoid, **P**, curved, tapering cone and **Q**, straight pointed tip of a larger coprolite. **R-U**, USNM 16386, Coprolites from the Permian of France, **R-S**, *Heteropolacoprus* in axial views and **T-U**, *Malericoprus* in axial views. **V**, *Heteropolacoprus*, Coprolite from the Red River Oil Field, Permian of Oklahoma in axial view. **W-AA**, Coprolites from the Red River Oil Field, Taylor, Oklahoma, USA. **W**, *Heteropolacoprus* in axial view, **X-Y**, *Liassocoprus* in **X**, axial and **Y**, polar views, **Z**, cf. *Strophocoprus* in axial view, **AA**, cf. *Malericoprus* in axial view.

There are three uncatalogued samples of coprolites from the Lower Permian of Oklahoma. The first collection consists of eight, mainly incomplete coprolites from Baylor County. The smallest specimen is a rounded cylinder, and several other larger coprolites exhibit a spiral structure. The remaining two collections are from the Red River Oil Field and were collected by the U. S. Geological Survey in 1913. One sample consists of three coprolites from the SE1/4 sec. 3, T5S, R11W. One specimen is heteropolar and microspiral (*sensu* Hunt et al., 2007) and represents *Heteropolacoprus*; it is 38 mm long with the cross section of a flattened ovoid with dimensions of 14 mm and 8 mm (Fig. 1V). The other two specimens are incomplete but represent large coprolites. One specimen is the anterior segment of a heteropolar coprolite, and it is 45 mm long; the third is the anterior extremity of a similar morphology and it is 25 mm long.

The largest sample is from a locality a quarter of a mile SW of Taylor, Oklahoma, and was collected by a local rancher named Bailey. There are four principal morphotypes. The majority (10) of the coprolites are heteropolar and microspiral and can be assigned to *Heteropolacoprus*; they are up to 40 mm long (Fig. 1W). Four coprolites, two of them incomplete, are also spiral in form and are heteropolar and macrospiral in morphology. These flattened coprolites can be assigned to *Liassocoprus*. The largest specimen is 44 mm long, with a width of 19.5 mm and a depth of 9 mm (Fig. 1X-Z). Four specimens are broken ends of coprolites that are triangular in lateral view, with an ovoid cross section that has an external texture similar to *Strophocoprus* (Hunt et al., 2007, fig. 1K-M). The largest specimen is 39 mm long with a width of 20.5 mm and a depth of 14.5 mm (Fig. 1Z). One poorly-preserved spiral coprolite is reminiscent of *Malericoprus* (Fig. 1AA)

Mesozoic

Triassic

The USNM coprolite collection includes Late Triassic specimens from the American Southwest and England. The US coprolites are from the nonmarine Chinle Group. Several uncatalogued specimens are from the "vicinity of Petrified Forest" in northeastern Arizona and include a specimen of *Heteropolacoprus* and two indeterminate ones. Triassic outcrops near Petrified Forest National Park principally represent the lower Chinle Group, and this is consistent with the occurrence of *Heteropolacoprus*, which is much more common in the lower part of the unit than in upper formations (Hunt et al., 1998). A fourth specimen in the same box is very different in morphology and has a chalky texture and shell fragments and is probably from a different locality.

The other Chinle Group coprolites are from the South Bent Canyon Post Office in the Purgatoire River Valley in Las Animas County, Colorado and probably derive from the Cobert Canyon Sandstone Bed of the Baldy Hill Formation (cf. Heckert et al., 2012). The largest coprolite is a rounded cylinder that is 89 mm long and broken at one end (Fig. 2A). This is the largest known nonmarine Triassic coprolite. A small, partial coprolite is heteropolar in morphology and similar to *Hetropolacoprus*. Two partial coprolite segments represent a curved cylindrical form with a rounded end and longitudinal striations and can be assigned to *Alococoprus triassicus* (Fig. 2B-E; Hunt et al., 2007).

USNM 16388 is a sample from the Rhaetic bonebed from England that includes two cylindrical coprolites as well as a smaller rounded one and several vertebrate body fossils, including rib fragments (Fig. 2F).

Jurassic

All the Jurassic specimens of coprolites at USNM are from the Lias of Lyme Regis in southwestern England. USNM 8334 is four casts of spiral coprolites (Fig. 2G). Two are microspiral and tapering and represent *Saurocoprus bucklandi*, and the others are macrospiral and pertain to *Liassocoprus hawkinsi* (Hunt et al., 2007). USNM 7053 is a cast of a poorly-preserved coprolite but it is also macrospiral and can be assigned to *Liassocorprus* sp. (Fig. 2H). The remaining specimen, USNM 15145, is a polished section of a coprolite.

Cretaceous

The USNM collection includes Late Cretaceous coprolites from the Southeast and West of the USA and from Germany. Uncatalogued specimens from the Black Creek Formation of North Carolina (5 specimens) and the Coachman Formation of South Carolina (2 coprolites) are principally cylindrical in morphology (Fig. 2K). The Black Creek specimens include a partial spiral coprolite (Fig. 2L).

USNM 5853 is a large cylindrical coprolite from the Eutaw Formation of Georgia (Fig. 2M). The coprolite is 135 mm long, with a subrounded cross section with diameters of 24.5 and 25.5 mm and contains numerous fish scales. There is poorly-developed spiraling at one end.

The two coprolites from the Blufftown Formation (USNM 15610) include an unusual bilobed specimen (Fig. 2N-P). The longitudinal striations indicate that the specimen represents *Alococoprus*, but this coprolite is distinct from other specimens assigned to that ichnogenus in being straight, rather than curved, in lateral view and by being composed of two connected subspherical segments. The other specimen from Alabama is from the Selma Chalk (Fig. 2Q-T) and represents a morphology reminiscent of a fir cone, that was first recognized more than 175 years ago from the Upper Cretaceous of England and The Netherlands (Buckland, 1835, pl. 31, figs. 1-11; 1836, pl. 15, figs. 5-7). This morphotype is spiral in form with evenly spaced coils and longitudinal striations. This coprolite is named in the Appendix as *Iuloeidocoprus mantelli*, ichnogen. et ichnosp. nov.

The coprolites from Western North America are from the North Horn Formation of Utah and the Fruitland(?) Formation of New Mexico. The nine North Horn specimens are rounded and either cylindrical or ovoid, with one being preserved on a piece of matrix (Fig. 2U). They were collected on National Forest lands around North Horn Mountain. One of the smaller specimens has fine striations on its surface (Fig. 2V). The uncatalogued specimen from New Mexico was collected from one mile NE of the "Bisti Trading Company Store" (Bisti Trading Post of most usage), and this is almost certainly from the Fossil Forest Member of the Fruitland Formation (e. g., Hunt and Lucas, 1992). The coprolite is 100 mm long with one end broken. It is flattened on one side, presumably the lower (Fig. 2X), with an irregular upper surface (Fig. 2W).

The German specimens are all from the Upper Cretaceous. There are three specimens from the Turonian near Dresden in Saxony. One Turonian coprolite is a nearly complete rounded cylinder that is 64 mm long and 19 mm in diameter (Fig. 2Y). The other two specimens represent a distinct spiral morphology. The best preserved one is the posterior end of a spiral coprolite preserved on matrix (Fig. 2Z-BB). This coprolite is 19 mm in diameter and has a preserved length of 23 mm. It is similar to *Iuloeidocoprus* in having evenly spaced spirals and distinct longitudinal striations. A second specimen preserved in lateral view is badly broken, but one end preserves a small section with closely spaced spirals with longitudinal striations (Fig. 2CC).

The other German specimen is from the Chalk of Saxony. USNM 16409 is a macrospiral heteropolar coprolite that is flattened and is referable to *Liassocoprus* (Fig. 2DD-EE). This specimen is 76 mm long with a width of 45 mm and a thickness of 22.5 mm.

Cenozoic

Early Tertiary

The collection includes four coprolite samples from the Eocene of western (New Mexico, Colorado and Wyoming) and eastern (Maryland) North America. USNM 19957 is a slightly pointed, rounded ovoid from the Bridgerian (middle Eocene) of Uinta County, CO, which exhibits some longitudinal striations (Fig. 3A-C). The specimen label indicates that this specimen was found with a "crocodile." The New Mexico coprolite, USNM 7077, is from the Lower Eocene San Jose Formation and is a rounded, elongate cylinder with a length of 71 mm and diameters of 22.5 and 23.5 mm (Fig. 3D). The collection includes two uncatalogued

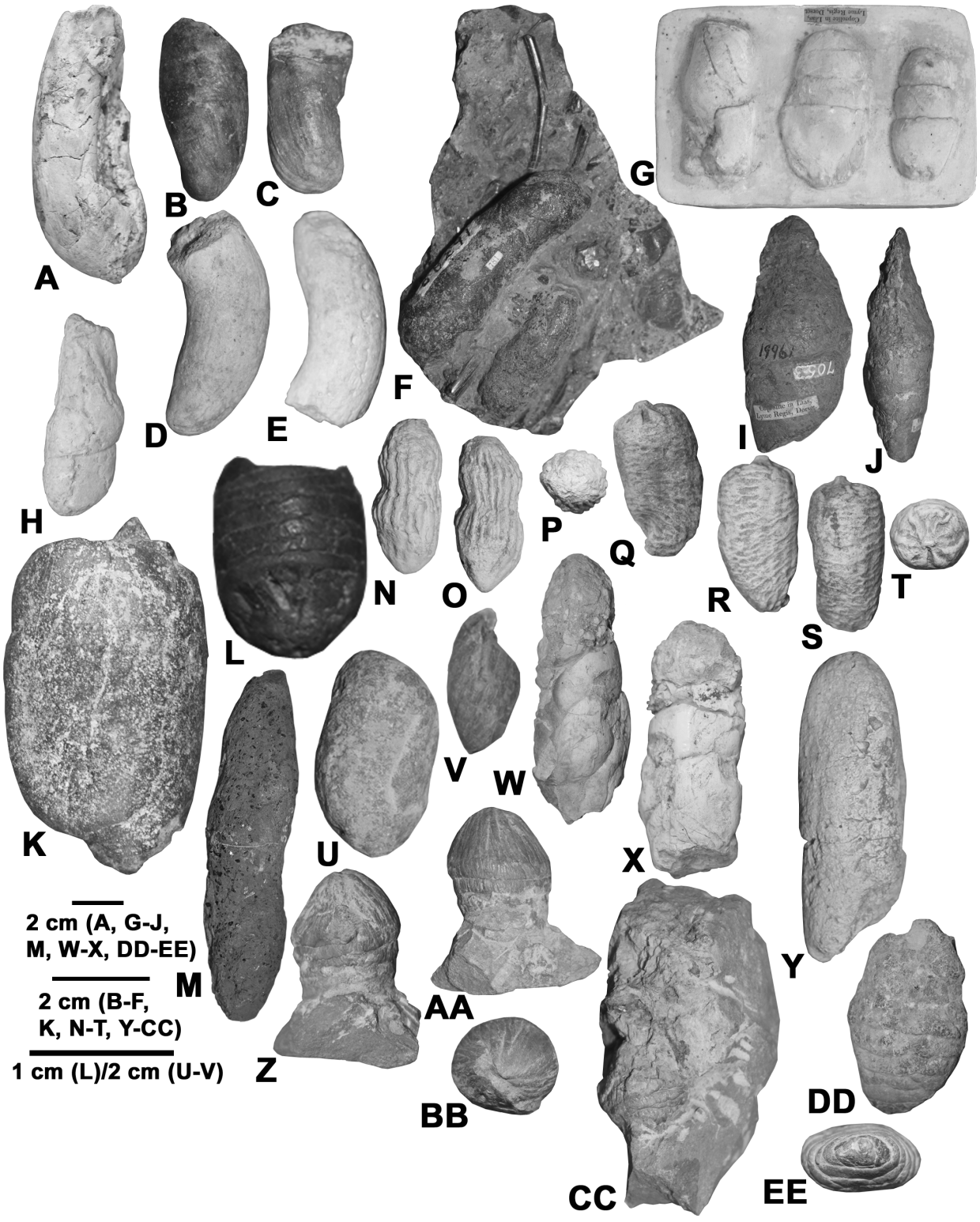

FIGURE 2. Mesozoic coprolites. **A-E**, Three USNM uncatalogued coprolites from the Triassic of the Purgatoire Valley, Colorado. **A**, Large coprolite in axial view and **B-E**, two curved striated coprolites in axial views. **F**, USNM 16388, Coprolite from the Rhaetic bone bed, England. **G-H**, USNM 8434, Casts of coprolites in axial view from the Lower Lias of Lyme Regis, England. **I-J**, USNM 7053, Spiral coprolite from Lower Lias of Lyme Regis, England in axial view. **K**, USNM uncatalogued, Coprolite from the Cretaceous of South Carolina in axial view. **L**, USNM uncatalogued, Coprolite from the Cretaceous of North Carolina in axial view. **M**, USNM 5853, Coprolite from the Upper Cretaceous Eutaw Formation of Georgia, in axial view. **N-P**, USNM 15610, striated coprolite, from the Blufftown, Upper Cretaceous of Alabama, in **N-O**, axial and **P**, polar views. **Q-T**, USNM uncatalogued, *Iuloeidocoprus mantelli* holotype, from the Selma Group of Alabama, in **Q-S**, axial and **T**, polar views. **U-V**, USNM uncatalogued, Coprolites from North Horn in axial views. **W-X**, USNM uncatalogued, Coprolite in axial view from the Fruitland Formation, Bisti, NM. **Y-CC**, USNM uncatalogued, Coprolites from the Turonian of Germany, **Y**, oblong coprolite in axial view, **Z-BB**, wrinkled button coprolite in **Z-AA**, axial and **BB**, polar views, **CC**, wrinkled coprolite in axial view in matrix. **DD-EE**, USNM 16409, Coprolite in DD, axial and EE, polar views from the Chalk of Saxony.

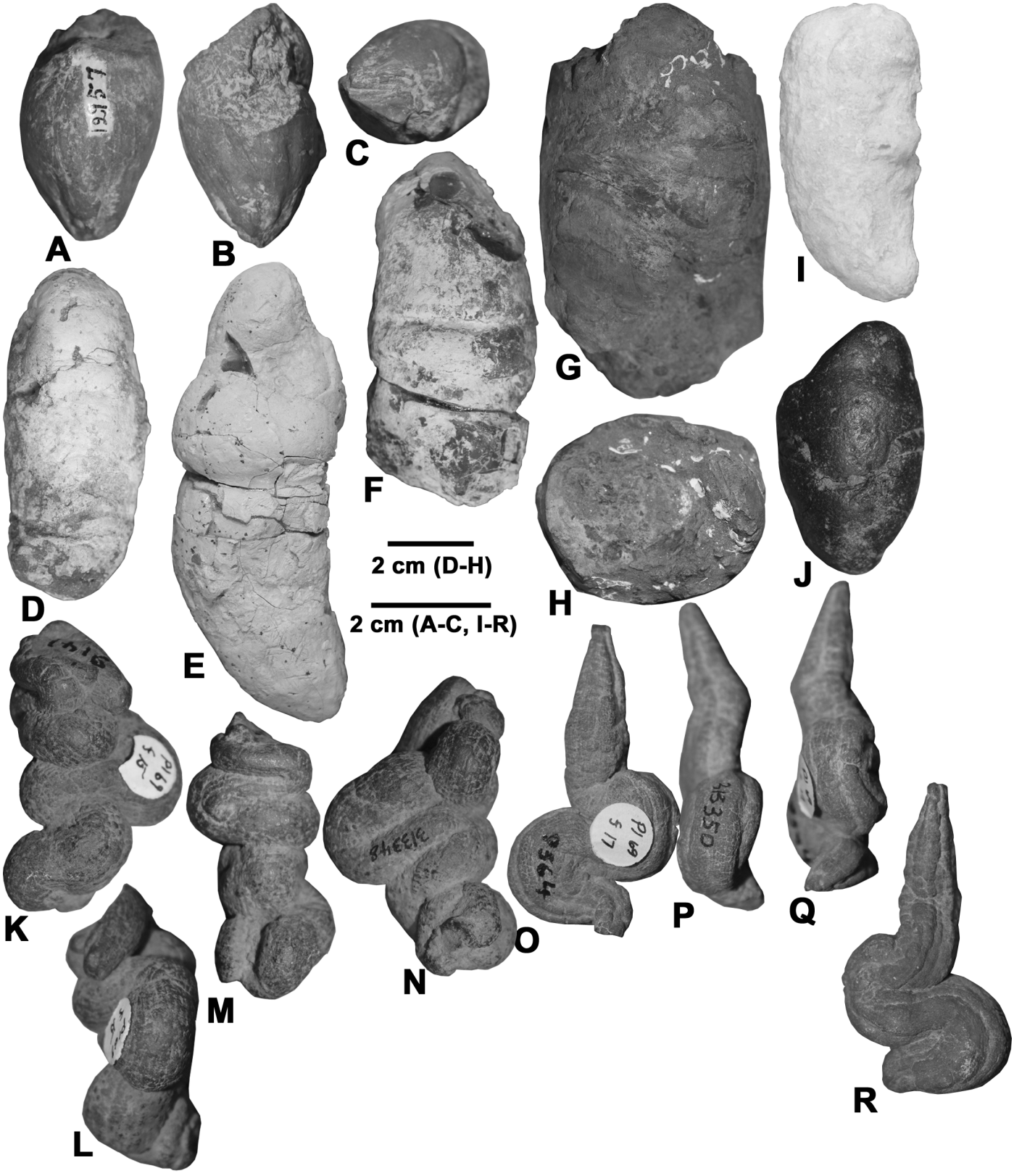

FIGURE 3. Cenozoic bromalites. **A-H**, Eocene coprolites. **A-C**, USNM 19957, Coprolite in **A-B**, axial and **C**, polar views from the Bridgerian of Colorado. **D**, USNM 7077, Coprolite in axial view from San Jose Formation, NM. **E-F**, Uncatalogued USNM, Coprolite coprolites in axial view from Bridger Formation, Wyoming. **G-H**, USNM 2307, Coprolite in **G**, axial and **H**, polar views from the Eocene of Maryland. **I**, USNM uncatalogued, Coprolite in axial view from the Oligocene of Wyoming. **J**, USNM uncatalogued, Coprolite in axial view from the Miocene of North Carolina. **K-R**, *Hirabromus seilacheri*. **K-N**, USNM 313348, Holotype cololite in axial views from the Miocene of Salmon Creek, Washington. **O-R**, USNM 313350, Cololite in axial views from the Paleocene Fort Union Formation.

coprolites from the Bridgerian of Wyoming. One coprolite is 123 mm long with a diameter of 33 mm. It is slightly curved in lateral view and has some evidence of coiling at one end (Fig. 3E). The second specimen is a segment of a cylinder that is flattened on one side (Fig. 3F). It is 88 mm long, 46 mm wide and 33 mm in thickness. USNM is a sample that includes a large cylindrical coprolite from Liverpool Point, Maryland (Fig. 3G-H) as well as 25 fragments. The large coprolite fragment is 85 mm in length with widths of 50 and 57 mm.

The USNM collection includes five uncatalogued cylindrical coprolites from the Oligocene Brule Formation of Niobrara County, Wyoming (Fig. 3I). Another uncatalogued coprolite from the Miocene of North Carolina is a broken, rounded ovoid (Fig. 3J).

The only published specimens in the bromalite collection at the USNM are from the Paleocene Fort Union Formation of North Dakota and the Miocene Wilkes Formation of Washington (Brown, 1962). Brown (1962, p. 91) succinctly characterized these specimens as "ropy striated concretions blunt pointed at both ends when perfect." "They are found with others that are more irregular, warty, and without striations…….specimens from a clayey, silty stratum in the Fort Union formation, 8 miles south of Rhame, N. Dak……are composed of limonite and are rusty brown on the surface. That they were chiefly siderite before they were oxidized to limonite is inferred from the fact that the comparable specimen ……from Miocene strata (Roberts, 1958, p. 35) on Cedar Creek, a tributary of Salmon Creek, Wash., is still largely siderite, without discernible organic matter, like most of its kind at that locality. These come from a bluish clay containing some woody material and, locally, well-preserved leaves and seeds." USNM 313348 is a 48-mm long specimen with a complex three-dimensional morphology that consists of an elongate, longitudinally-striated cylinder that is folded in a convoluted pattern (Fig. 3K-N: Brown, 1962, pl. 69, fig. 15). USNM 313350 is a specimen from North Dakota with a less complex morphology that is designated in the Appendix as the holotype of *Hiabromus seilacheri*, ichnogen. et ichnosp. nov. (Fig. 3O-R: Brown, 1962, pl. 69, fig.17).

Similar ichnofossils occur in the Permian of China, and in the Cretaceous of Canada and Madagascar, and there has been a long debate as to their origin (coprolites, pseudofossils or casts of internal organs), particularly with regard to those from the late Miocene of Washington (e.g., Amstutz, 1958; Brown, 1962; Broughton et al., 1977; Broughton, 1981; Schmitz and Benda, 1991; Spencer, 1993; Mustoe, 2000; Seilacher et al., 2001). Seilacher et al. (2001) convincingly argued that these specimens are both ichnofossils and cololites (*sensu* Agassiz, 1833; Hunt and Lucas, 2012a) that represent fossilized sections of the gastro-intestinal tract of vertebrates. Specifically they represent evisceralites (sensu Hunt and Lucas, 2012b) which are cololites that are preserved independent of a skeleton.

Quaternary

Pleistocene

The largest collections of coprolites in the USNM collection are from Late Pleistocene cave deposits of the southwestern United States. The majority of specimens are from Rampart Cave in Grand Canyon National Park, Arizona. Rampart Cave was one of the first caves to be studied in Grand Canyon National Park, and it contained the most significant coprolite resources, notably extensive Shasta ground sloth (*Nothrotheriops shastensis*) coprolites (e. g., Martin et al., 1961; Santucci et al., 2001, figs. 9-12; McDonald, 2003, fig. 1.6; Hunt et al., 2005, fig. 5; Hunt and Lucas, 2007, fig. 6A; Hunt et al., 2012b, fig. 2H Mead and Swift, 2012). The USNM collection includes numerous uncatalogued coprolites of Shasta ground sloth (*Nothrotheriops shastensis*) (Fig. 4A-H), Harrington's Mountain Goat (*Oreamnos harringtoni*) (Fig. 4I-J), felids (Fig. 4K-L) and mustelids (Fig. 4O). Other *Nothrotheriops* coprolites in the collection are from Dry Cave near Las Vegas, Nevada (Fig. 4P-Q).

SCOPE AND DEVELOPMENT OF SIGNIFICANT COPROLITE COLLECTIONS

The USNM bromalite collection is one of the largest in the world. The pre-Quaternary bromalite collection is housed in contiguous drawers within the main vertebrate fossil collection, but the level of institutional value placed on the collection is perhaps evidenced by the large percentage of the specimens that are uncatalogued. The Smithsonian is a national institution, so several specimens were received as gifts (or trades) from other museums such as an accession in 1899 from the Museum of the Mining School, St. Petersburg (Devonian coprolites) and one in 1898 from The Manchester Museum, Owens College (now the University of Manchester). In addition, several specimens were deposited from the U. S. Geological Survey (USGS). USGS specimens often have more specific locality information than others and include USNM 1887, collected from the Eocene of New Mexico by John Wesley Powell in 1887, and uncatalogued specimens from the Permian of Oklahoma, and the Upper Cretaceous of Alabama and Georgia. Some specimens were collected directly by USNM staff (e.g., uncatalogued specimen from the Miocene of NC, Rampart Cave collection from the Quaternary of Arizona). One name that appears on more than one specimen as a collector is George Pearce (e. g., uncatalogued specimen collected in 1930 from the Eocene of Wyoming; uncatalogued specimens collected in 1942 from the Oligocene of WY), who was a distinguished field collector of fossil vertebrates who worked extensively for the American Museum of Natural History in New York. Pearce was a school teacher who mostly worked in Albuquerque, New Mexico, but, during the summers, collected for both the AMNH and the USNM, mostly at upper Cenozoic mammal localities in the western USA. Other specimens derive from the War Department (e.g., USNM 16388 from the Rhaetic bonebed in the England; uncatalogued specimen of *Liassocoprus* ["Coprolites mantelli"] from the Chalk of Saxony). Although there are no details as to how these specimens were acquired, it seems reasonable to assume that military personnel collected fossils, much as they did archeological artifacts (e. g., Saunders, 2007), while on active service abroad.

Arguably three of the other most important collections of vertebrate coprolites are at the New Mexico Museum of Natural History (Albuquerque), the Oxford University Museum of Natural History (Oxford) and the Natural History Museum (London). The New Mexico Museum of Natural History and Science (NMMNH) is unique among similar institutions in that for over a quarter of a century it has considered vertebrate coprolites (and other trace fossils) to be worthy of collection during all field collecting programs. Initially, SGL (e.g., Lucas et al., 1985) and then APH (e.g., Hunt, 1992; Hunt et al., 2005) collected coprolites and studied specimens in the collection. Coprolites ranging in age from Pennsylvanian to Pleistocene were collected in association with osteological paleofaunas and also from discrete localities rich in this type of trace fossil (Hunt et al., 2011). Thus, NMMNH has more than 600 catalogued specimens/lots of coprolites, including coprolites from outside the state and the country, but the majority are from New Mexico. As a result, NMMNH has the best sample of coprolites from any discrete area (state of New Mexico) (Hunt et al., 2011). The overall size of the collection is on a par with the Smithsonian or larger. This collection has received more extensive study than any other (e.g., Lucas et al., 1985; Hunt, 1992; Hunt et al., 2005, 2007, 2012c-e; Lucas et al., 2012a-b; Suazo et al., 2012). The NMMNH and USNM collections are the largest in the world.

The coprolite collection at the Oxford University Museum of Natural History is principally due to the work of one individual and was the first such in the world. William Buckland (1784-1856) was the first to study coprolites and coin the term (Buckland, 1822, 1824, 1829a-c, 1835, 1836; Duffin, 2006, 2009, 2012a-b; Hunt and Lucas, 2012a; Pemberton, 2012). Buckland held academic positions at the University of Oxford, first as Reader in Mineralogy and subsequently as Reader in Geology (Duffin, 2006). He built up a collection of coprolites at the

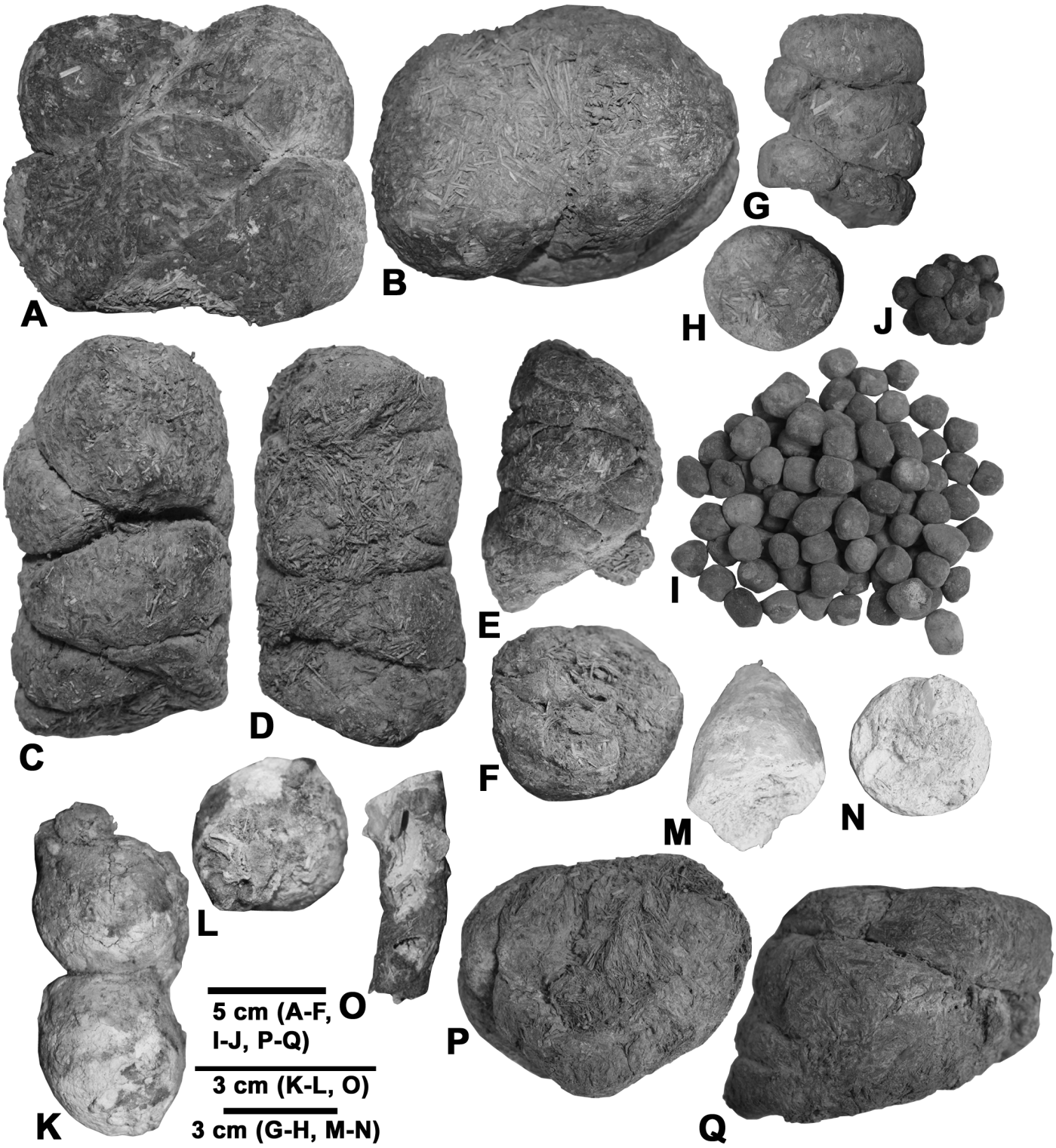

FIGURE 4. Pleistocene coprolites. **A-O**, Coprolites from Rampart Cave, Grand Canyon National Park, Arizona. **A-H**, USNM ucatalogued, Four Shasta ground sloth (*Nothrotheriops shastensis*) coprolites in **A**, **C-E**, **G**, axial and **B**, **F**, **H**, polar views. **I-J**, USNM uncatalogued, Two groups of Harrington's Mountain Goat (*Oreamnos harringtoni*) coprolites. **K-L**, USNM 509327, Felid coprolite in **K**, axial and **L**, polar views. **M-N**, USNM 50923, Felid coprolite in **M**, axial and **N**, cross-sectional view. **O**, USNM uncatalogued, Mustelid coprolite in axial view. **P-Q**, USNM 12677, Shasta ground sloth (*Nothrotheriops shastensis*) coprolite in axial views from Dry Cave, Nevada.

Oxford University Museum of Natural History through personal field work, purchases from the famous fossil collector Mary Anning and fossil dealers and specimens donated from a wide network of colleagues (Duffin, 2012a, b). His collection at the University of Oxford Museum of Natural History is dominated by coprolite specimens from the Early Jurassic, but it also includes specimens from the Late Triassic, Late Jurassic, Early Cretaceous and Late Pleistocene, as well as non-coprolite bromalites (Hunt et al., 2012a). Subsequent to Buckland, Duffin (1979; 2010; Swift and Duffin, 1999) has restudied both coprolites from the Rhaetic bone bed and from the Lower Lias of the coastal area of Dorset, England. Other bromalites from the Buckland collection, notably consumolites of ichthyosaurs, have been studied by several workers (e.g., Pollard, 1968; Taylor, 1993). Hunt et al. (2012a) described four new ichnotaxa from the Buckland collection at the University of Oxford Museum of Natural History.

The Natural History Museum in London, like the USNM, is a national collection (Hunt et al., 2012b). It is probably the second oldest collection of coprolites, after Oxford, and includes several Liassic specimens collected by Mary Anning and others and described by Hawkins (1834, 1840). Perhaps institutional ambivalence is demonstrated by the fact that the collection is housed in the basement away from the main vertebrate fossil collections, but the majority of specimens are catalogued. The collection includes both Paleozoic and Mesozoic coprolites and one from the Tertiary (Hunt et al., 2012b). Paleozoic coprolites include specimens from the Carboniferous of Scotland (NHMUK 15332 from Granton, NHMUK 14054 from Glasgow) and Germany (NHMUK 28490 from Saarbrücken) and the Lower Permian of Texas (NHMUK 3464). The collection includes Rhaetic coprolites from Aust Cliff near Bristol (NHMUK 3117) and Frome in Somerset (NHMUK 47041). The Jurassic sample includes eight catalogued specimens from the Lias of the southwest coast of England as well as a single specimen from the Solnhofen Limestone of Germany (NHMUK 47453), 35 specimens from the Middle Purbeck of England (NHMUK 48259) and a large coprolite and multiple small specimens from the Oxford Clay of England (NHMUK R2094). Cretaceous specimens include a partial coprolite from the Cambridge Greensand in England (NHMUK 4914) and a number of specimens from the upper Cretaceous of India. The single Tertiary specimen in the Natural History Museum collection is from the Eocene of Nigeria (NHMUK 11869). Other specimens include a shark intestine infilled by Roman cement and a pseudocoprolite (Hunt et al., 2012b).

The collection at the Natural History Museum includes specimens from other museums (e.g., Permian coprolites from the Munich Museum) and several collections (Hawkins collection – Liassic of England, Haberlein collection – Upper Jurassic of Germany, Beckles collection – Lower Jurassic of England, Matley collection – Upper Cretaceous of India). Most of the coprolite collection is from the England, but a few coprolites are from the former British Empire (Nigeria, India). Duffin (1979; Swift and Duffin, 1999) described Rhaetian coprolites from England from the collection and. Hunt et al. (2007, 2012b) described and named new ichnotaxa based on specimens in the collection from the Lower and Upper Jurassic and Lower Cretaceous of England and the Upper Cretaceous of India.

CONCLUSIONS

The coprolite collection at USNM is one of the largest in the world and it represents a wide geographic and stratigraphic range. The most numerous specimens are from the upper Pleistocene of Rampart Cave in Grand Canyon National Park.

ACKNOWLEDGMENTS

We thank Michael Brett-Surman, USNM Collections Manager for access to collections and Chris Duffin and Jesper Milàn for thorough reviews.

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APPENDIX

SYSTEMATIC PALEONTOLOGY

Iuloeidocoprus, ichnogen. nov.

Type ichnospecies: *Iuloeidocoprus mantelli* Hunt et al., 2012.

Included ichnospecies: Known only from the type ichnospecies.

Etymology: From William Buckland's term Iulo-eido-coprolites and the Greek *koprus* (dung).

Distribution: Upper Cretaceous of North America and Europe.

Diagnosis: Coprolite that differs from other ichnogenera in being characterized by a cylindrical shape with multiple, closely-spaced spirals.

Discussion: Mantell (1822, p. 103, pl. 9, figs.4-11) described "aments or cones of unknown vegetables" from the Grey Chalk Marl of Sussex, England. These specimens encompassed both heteropolar (*Liassocoprus*: Mantell, 1822, pl. 9, figs 4-5) and amphipolar (Mantell, 1822, pl. 9, figs. 6-11) coprolites. Buckland (1829a, p. 143) noted that "the supposed fir-cones or Iuli in the chalk and chalk marl ….. are also of faecal origin…….for these the provisional name of Coprus iuloides is proposed." Subsequently, Buckland (1835, p. 234) utilized the term Iulo-eido-coprolites. Later, Mantell acknowledged that these fossils represented coprolites, possibly of sharks (Buckland, 1836, p. 155).

Iuloeidocoprus mantelli, ichnosp. nov.

Holotype: USNM unnumbered (Fig. 2Q-T).

Etymology: For Gideon Mantell, who first described this form of coprolites (as plant specimens) from the Upper Cretaceous Chalk of southwestern England (Mantell, 1822, pl. 94-11).

Type locality: Roadcut in Alabama State Highway 26, 3.4 miles east of Huntsboro, Russell County, Alabama.

Type horizon: Selma Group (Santonian-Maastrichtian).

Distribution: As for genus.

Referred specimens: None.

Diagnosis: As for genus.

Description: The holotype specimen is 32 mm long with a subrounded cross section (15 by 15.5 mm). It is amphipolar with multiple narrow spirals. The posterior(?) end is rounded and terminates in a narrow, twisted tip. The anterior(?) end is flattened with a central tip and radial patterning (Fig. 2T).

Discussion: This ichnospecies is common in the Upper Cretaceous chalk in North America and Europe.

Hirabromus, ichnogen. nov.

Type ichnospecies: *Hirabromus seilacheri* Hunt et al., 2012.

Included ichnospecies: Known only from the type ichnospecies.

Etymology: From the Greek *hira* (gut or intestine), and the Greek *bromus* (food).

Distribution: Permian of China, Cretaceous of Canada and Madagascar, Paleocene and Miocene of United States.

Diagnosis: Bromalite that that differs from other ichnogenera in consisting of a elongate, convoluted, longitudinally-striated cylinder with tapering terminations composed of siderite.

Discussion: These ichnofossils have been identified from the Permian of China, the Cretaceous of Canada and Madagascar, and the Paleocene and Miocene of the United States and have variously been interpreted as coprolites, pseudofossils or casts of internal organs (Amstutz, 1958; Broughton et al., 1977; Broughton, 1981; Schmitz and Benda, 1991; Spencer, 1993; Mustoe, 2000; Seilacher et al., 2001). Seilacher et al. (2001) argued that they are both ichnofossils and cololites and we concur with this conclusion. Hunt and Lucas (2012b) recognize two types of cololites, intestinelites that are preserved within a body cavity and evisceralites for those, such as *Hirabromus*, that occur in the absence of a carcass. Distinctive features of these bromalites that indicate that they are cololites include: (1) longitudinal striations that represent taenial muscle bands; (2) sinuous shape; (3) prominent tapering at both ends; and (4) more complex specimens (e.g., Fig. 3K-N) consist of segments whose opposing ends taper in opposite directions (Seilacher et al., 2001).

Hirabromus seilacheri, ichnosp. nov.

Holotype: USNM 313350 (Fig. 3O-R; Brown, 1962, pl. 69, fig. 17).

Etymology: For Adolph Seilacher, to honor his important study of the origin of this ichnotaxon.

Type locality: 8 miles south of Rhame, ND.

Type horizon: Fort Union Formation, Paleocene (Torrejonian).

Distribution: As for ichnogenus.

Referred specimens: Upper Permian, China (Seilacher et al., 2001, fig. 1A): Upper Miocene Wilkes Formation, WA: USNM 313348 (Fig. K-N; Brown, 1962, pl. 69, fig. 15); GPIT 1860/1 (Seilacher et al, 2001, fig 1B); GPIT 1860/2 (Seilacher et al, 2001, fig 1C); GPIT 1860/3 (Seilacher et al. 2001, fig. 3A): GPIT 1860/4 (Seilacher et al. 2001, fig. 3B): GPIT 1860/5 (Seilacher et al. 2001, fig. 3C); YPM56257 (Seilacher et al. 2001, fig. 4): Paleocene Fort Union Formation , ND: USNM 313349 (Brown, 1962, pl. 69, fig. 16); USNM 313723 (Brown, 1962, pl. 69, fig. 18); USNM 313724 (Brown, 1962, pl. 69, fig. 19): Paleocene Golden Valley Formation, ND, YPM 56410 (Seilacher et al. 2001, fig. 5 center); YPM 56411 (Seilacher et al. 2001, fig. 5 right).

Diagnosis: As for ichnogenus.

Description: USNM 313350 is an elongate (54 mm-long), longitudinally-striated cylinder with acute tips at either end (Fig. 3O-R: Brown, 1962, pl. 69, fig.17). The specimen is only flexed in one dimension, with two tight curves in lateral view.

Discussion: Given its size and preservation in a Paleocene fluvial environment, the holotype probably represents a crocodylian. In contrast, large specimens from the upper Miocene of Washington presumably pertain to a mammal and therefore different higher level taxa are represented within this ichnotaxon. We concur with Seilacher et al. (2001, p. 11) in believing that "devoted scatologists may also describe, compare and classify cololites in terms of parataxonomy – in the hope that the parataxa can eventually be tied to particular kinds of vertebrates." In addition, it may be useful to discriminate different portions of the gastrointestinal tract (e.g., caecum cast identified by Seilacher et al., 2001, fig. 4).