# NEW COPROLITE ICHNOTAXA FROM THE BUCKLAND COLLECTION AT THE OXFORD UNIVERSITY MUSEUM OF NATURAL HISTORY

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**Abstract—**The Buckland collection at the University of Oxford Museum of Natural History (UK) is the oldest collection of coprolites in the world. It comprises Mesozoic and Cenozoic coprolites and other bromalites, the majority of which are derived from the Lower Lias of southwestern England. The collection includes the most comprehensive samples of two important British coprofaunas – the Lower Liassic of Lyme Regis and the Rhaetic bone bed. We describe four new coprolite ichnotaxa from this collection: *Ichthyosaurolites duffini* ichnogen. et ichnosp. nov., *Strabelocoprus pollardi* ichnogen. et ichnosp. nov. and *Plektecoprus whitbyensis* ichnogen. et ichnosp. nov. from the Late Triassic and Early Liassic and *Hyaenacoprus bucklandi* ichnogen. et ichnosp. nov. from the Late Pleistocene.

## INTRODUCTION

William Buckland (1784-1856) was the first to study fossil feces and coined the term "coprolite" (Buckland, 1822, 1824, 1829a-d, 1830, 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 (the first ever) 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 and non-coprolite bromalites and infilled Recent shark intestines (Figs. 1-5).

Duffin (1979; Swift and Duffin, 1999) first restudied coprolites from the Rhaetic bone bed, from the Buckland and other collections, and recognized four broad morphological types of coprolites. Hunt et al. (2007) identified six morphotypes, including *Liassocopros hawkinsi* and *Saurocopros bucklandi*.

Duffin (2010) identified seven morphotypes of coprolites in the Buckland collection sample, and others, from the Lower Lias of the coastal area of Dorset, England, including *Falcatocoprus* isp., *Saurocoprus bucklandi*, *Saurocoprus* isp., *Liassocoprus hawkinsi* and three other morphotypes. Other bromalites from the Buckland collection, notably consumulites of ichthyosaurs, have been studied by several workers (e.g., Pollard, 1968; Taylor, 1993). The purpose of this paper is to describe four new ichnotaxa from the Buckland Collection of bromalites at the University of Oxford Museum of Natural History, three from the Triassic-Lias of Dorset and Somerset and one from the Pleistocene of Yorkshire, all from the United Kingdom.

## SYSTEMATIC PALEONTOLOGY

### *Ichthyosaurolites*, ichnogen. nov.

**Type ichnospecies:** *Ichthyosaurolites duffini* Hunt et al., 2012.

**Included ichnospecies:** Known only from the type ichnospecies.

**Etymology:** From ichthyosaur, for the contents of the ichnofossil, and the Greek *lithos* (rock).

**Distribution:** Lower Jurassic (Lower Liassic) of southwest England (Dorset).

**Diagnosis:** Bromalite that differs from other ichnogenera in consisting of a wide, flattened rectangle with a rounded tip with abundant phosphatic(?) groundmass and inclusions of multiple skeletal elements of juvenile ichthyosaurs (vertebral diameters typically about 12-15 mm).

**Discussion:** This distinct morphology of this bromalite was first recognized by Buckland (1836, pl. 15, fig. 18) and later by Duffin (2010, pl. 77, fig. 1). *Ichthyosaurolites* represents a concentration of juvenile bones, and thus it could potentially represent a gignolite (*sensu* Hunt and Lucas, 2012a) or a bromalite. Putative ichthyosaur embryos are well known (e. g., Böttcher, 1990, 1998; Deeming et al., 2001; Maxwell and Caldwell, 2003) and *Ichthyosaurolites* specimens differ from these in that: (1) the specimens are comprised principally of vertebrae in a disarticulated mass in contrast to an articulated series; (2) no small nonvertebral bones are preserved; and (3) the bones are contained in a distinct groundmass.

*Ichthyosaurolites* is not considered to represent a regurgitalite because of the the large volume of groundmass relative to bone. The discrete small volume of the specimens indicates that *Ichthyosaurolites* does not represent an infilling of a portion of the gastrointestinal tract and it is most parsimoniously considered a pelletized accumulation of fecal material (incorporeal pelletite or coprolite of Hunt and Lucas, 2012a). Thus, *Ichthyosaurolites* indicates active predation on juvenile ichthyosaurs. The size of the coprolites and the lack of spiral structure suggest that the originator is a large marine reptile.

Vertebrate consumulites are most commonly preserved in aquatic organisms, including ichthyosaurs (Fig. 2), because taphonomic factors (e.g., water chemistry, deposition rates) in aqueous environments increase the likelihood of the preservation of complete carcasses relative to subaerial conditions. In addition, ichthyosaurs have long been considered viviparous (Pearce, 1846). Thus, potentially a juvenile ichthyosaur skeleton within an adult one, as is known in about 50 instances (Wild, 1990), could represent an embryo (e.g., Pearce, 1846; Seeley, 1880) or an act of cannibalism (e. g., Quenstedt, 1858). There has been considerable discussion of these hypotheses (e.g., Branca, 1908; Drevermann, 1926; Liepmann, 1926) and it appears that both circumstances occur (McGowan, 1991). Cannibalism by ichthyosaurs is a possibility for the origin of *Ichthyosaurolites*, but the relative scarcity of these bromalites (five specimens known from Lyme Regis) relative to the large number of ichthyosaur specimens suggests that the predator was another taxon, possibly a plesiosaur. O'Keefe et al. (2009) demonstrated ingestion of a juvenile ichthyosaur (vertebral centra of 12-15 mm in diameter) by a plesiosaur. They considered the ichthyosaur to be a voided embryo, but the multiple specimens of *Ichthyosaurolites* suggest either that the size of newborn ichthyosaurs has been overestimated or that spontaneous abortions by ichthyosaurs were common.

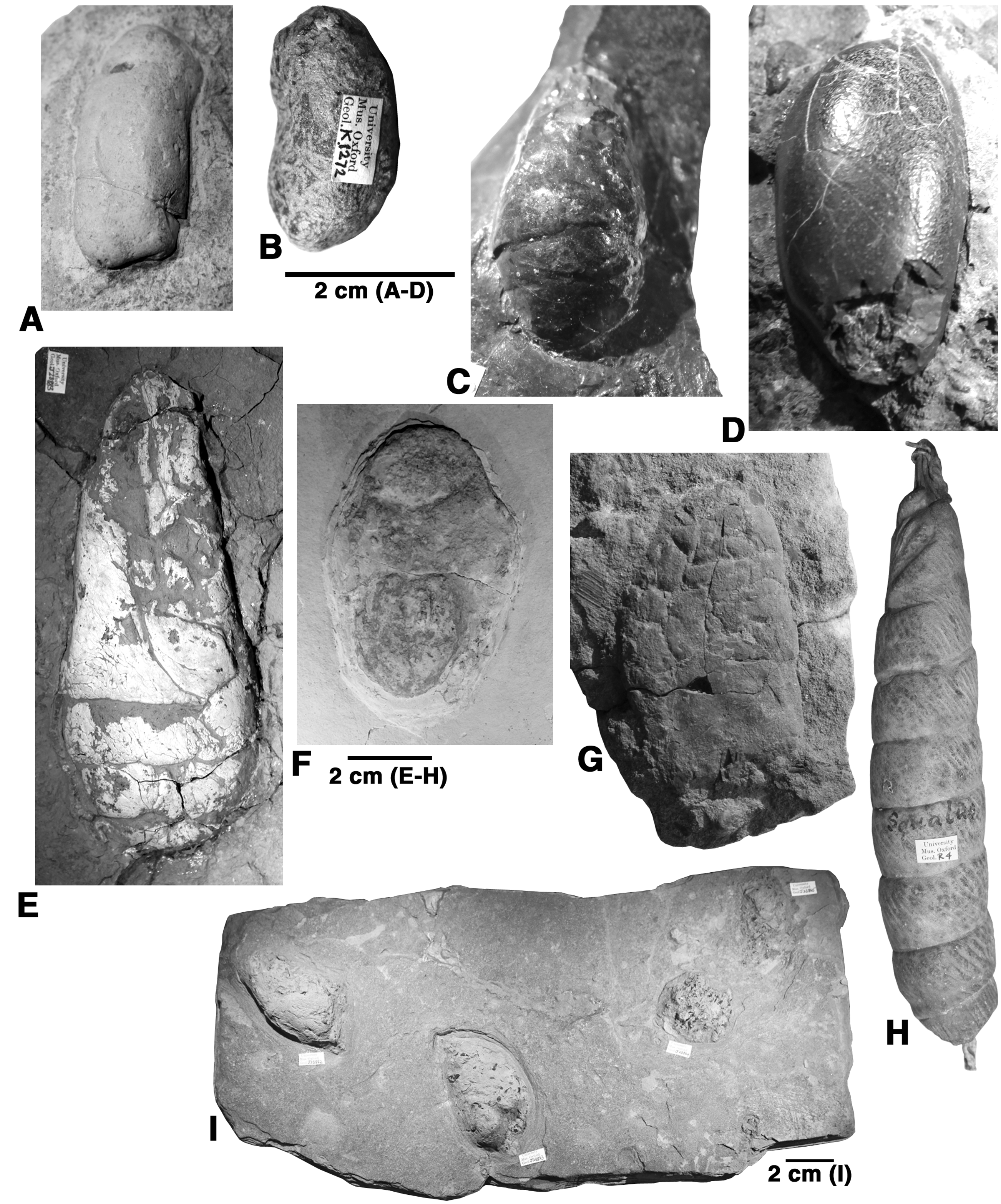


FIGURE 1. Coprolites and a related specimen from the Buckland Collection at the Oxford University Museum of Natural History. **A**, GZ 103, Coprolite from the Muschelkalk (Anisian-Ladinian), Lunéville, France. **B**, K 1272, Coprolite from Wiltshire, UK. The specimen label indicates that this coprolite derives from the Cambridge Greensand (Aptian), however this unit does not cropout in that county (C. Duffin, pers. commun., 2012). Thus, it is more likely that the specimen is from the Upper Greensand (Albian) or Lower Greensand (Aptian) if it is from Wiltshire (C. Duffin, pers. commun., 2012). **C**, GZ 105, *Liassocoprus* isp. coprolite from the Keuper (Alaunschiefer)(Ladinian), near Gaildorf, Germany. **D**, H 36, Coprolite from Rhaetic bonebed (Rhaetic), Aust Cliff, UK. **E**, J23883, *Saurocopros bucklandi* (Buckland, 1835, pl. 28, fig. 6) from the Lower Lias (Hettangian-Lower Pliensbachian) of Lyme Regis, UK. **F**, JZ 1701, Coprolite from Solnhofen Plattenhalk (Tithonian), Solnhofen, Germany. **G**, GZ 104, Coprolite from Gaildorfer Keuper (Alaunschiefer)(Ladinian), near Gaildorf, Germany. **H**, R 4, Roman cement infilled intestines of Recent dogfish (*Squalus*): Buckland, 1836, pl. 15, fig. 1. **I**, J23862-23865, Four coprolites on one block from the Lower Lias (Hettangian-Lower Pliensbachian), Lyme Regis, UK.

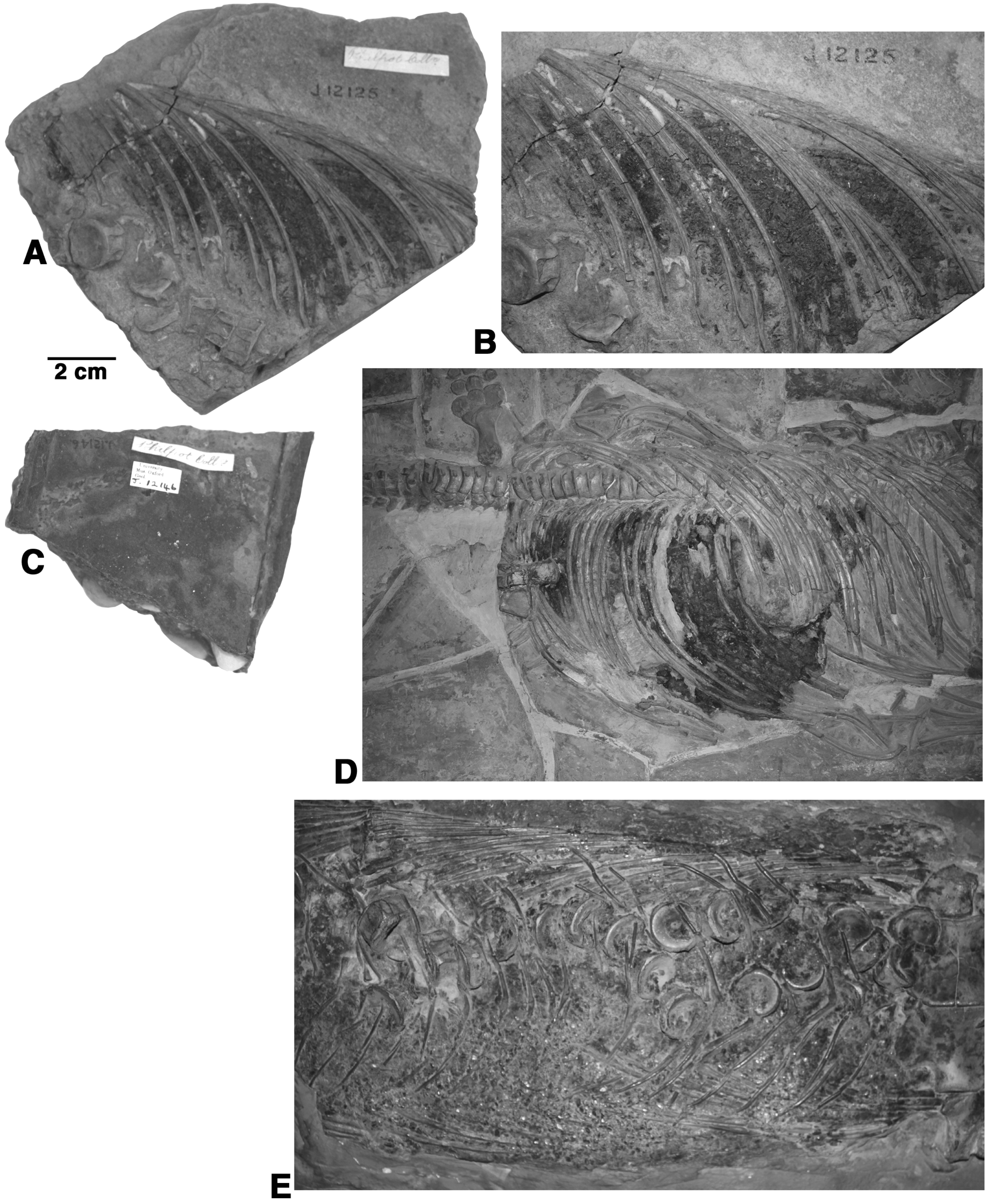


FIGURE 2. Consumulites in ichthyosaur skeletons from the Buckland Collection at the Oxford University Museum of Natural History from the Lower Lias (Hettangian-Lower Pliensbachian) of Lyme Regis, UK. **A-B**, OUM J12125, Consumulite in **A**, overview and **B**, close up (also see Pollard, 1968, pls. 72-73). **C**, J OUM 12146, Consumulite in lateral view. **D**, OUM J10320, Consumulite in lateral view. **E**, OUM J13593, Consumulite in lateral view (also see Buckland, 1836, pl. 14).

There are indications of Liassic ichthyosaur diet from the Posidonienschiefer of Germany, for example, suggesting that prey selection changed through ontogeny (from fish to cephalopods) (Böttjer, 1989, 1998). There is also specific evidence that the Liassic *Temnodontosaurus trigodon* preyed on *Stenopterygius* spp. (Böttjer, 1989, 1998), so it is also possible that *Ichthyosaurolites* represents the coprolite of a large ichthyosaur such as *Temnodontosaurus*.

### *Ichthyosaurolites duffini*, ichnosp. nov.

**Holotype:** OUM J 23905 (Fig. 3A-E; Buckland, 1836, pl. 15, fig. 18; Keller, 1977, fig. 6B; Duffin, 2010, pl. 77, fig. 1)

**Etymology:** For Christopher Duffin, to honor his contributions to the study of coprolites and of the life and work of William Buckland.

**Type locality:** Lyme Regis, England.

**Type horizon:** Lower Liassic (Hettangian-Lower Pliensbachian).

**Distribution:** As for genus.

**Referred specimens:** OUM J 23922 (Figs. 3F-G), OUM J 23911 (Fig. 3M), OUM J23888a-b (Figs. 3J-L) and OUM J23771 (Figs. 3H-I), all from the Lower Lias of Lyme Regis, England.

**Diagnosis:** As for genus.

**Description:** OUM J 23905 is 64 mm long and 39 mm wide with a thickness of 24.4 mm. The only visible bones are many small ichthyosaur centra (six are visible on one surface), and they have widths ranging from 14.1 to 15.4 mm (Figs. 3J-L). The matrix, which contains many small bones, is eroded around the ichthyosaur elements, and they protrude from the surface.

**Discussion:** There are four referred specimens (OUM J23888a-b, OUM J 23922, OUM J 23911 and OUM J23771). OUM J23888a-b consists of two parts that fit together, and they provide the best information about the overall morphology of a complete coprolite (Figs. 3J-L). OUM J23888a is a rectangular (99.3 mm by 84.2 mm) piece, and OUM J23888b is narrower, subtriangular and has a rounded end. When fitted together the coprolite is 143.2 mm long, with one side relatively smooth and presumably approximating the original outer surface of the coprolite, and the other very irregular (eroded?). The coprolite contains several ichthyosaur vertebrae (10.6 to 14.6 mm in diameter) and other angular bone fragments.

OUM J 23922 is a flattened ovoid, 73.3 mm long, 50.6 mm wide and 29.4 mm thick (Figs. 3F-G). It contains several bone fragments and vertebrae (diameters of 7.01, 10.8, 11.8 and 14.5 mm). This specimen was mentioned by Keller (1977, p. 131, fig. 6b), who noted that it "contains a sphenoid and a basioccipital bone of one individual. From the size of these bones the body length of the swallowed and digested prey can be estimated at 60-70 cm" (translation courtesy of L. H. Vallon). OUM J 23911 (57.1 mm by 71.2 mm) is preserved on a sheet of matrix (57.1 mm by 71.2 mm) and seems flattened and lacks the distinct margin seen in the other specimens. This specimen contains angular bone fragments and several vertebrae (diameters of 15.2, 15.6 and 13.6 mm). OUM J23771 is a coprolite with one surface (51.6 by 50.7 mm ) ground and polished and exhibiting bone fragments that are larger than in the other specimens (Fig. 3H-I). The obverse side is irregular, with many bone fragments. There are no obvious vertebrae in this specimen.

### *Strabelocoprus*, ichnogen. nov.

**Type ichnospecies:** *Strabelocoprus pollardi* Hunt et al., 2012.

**Included ichnospecies:** Known only from the type ichnospecies.

**Etymology:** From the Greek *strabelos* (snail) in allusion to the similarity in shape to a gastropod, and the Greek *kopros* (feces).

**Distribution:** Rhaetian Penarth Group (see discussion below) and Lower Jurassic (Lower Liassic) of southwest England (Dorset and Somerset).

**Diagnosis:** Heteropolar, microspiral coprolite that differs from other ichnogenera in having a small number of coils (<3) in lateral view, exhibiting very wide spirals in posterior view and in having a width that exceeds half of its length.

**Discussion:** This ichnogenus is named for its gastropod-like morphology. It is currently only known from the Upper Triassic and Lower Lias of southwestern England. The spiral morphology suggests that the coprolite was produced by a less derived fish such as a chondricthyan that must have been of very large size. What clearly distinguishes *Strabelocoprus* from other large microspiral copolites (e.g., *Megaheteropolacoprus*) is the large width to length ratio.

### *Strabelocoprus pollardi*, ichnosp. nov.

**Holotype:** OUM J23743, coprolite (Fig. 4A-D).

**Etymology:** For John Pollard, to honor his contributions to ichnology, including coprolite studies, in the UK.

**Type locality:** Watchet, Somerset, England.

**Type horizon:** Rhaetian Penarth Group (see discussion below).

**Distribution:** As for ichnogenus.

**Referred specimens:** OUM J23741, Lower Liassic (Hettangian-Lower Pliensbachian) of Lyme Regis, England (Fig. 4E).

**Diagnosis:** As for ichnogenus.

**Description:** OUM J23743 is a complete phosphatic coprolite with a length of 102.2 mm and a subcircular cross section with a maximum width of 62 mm and a lesser width of 58.3 mm (Figs. 4A-D). The coprolite is heteropolar and microspiral with three coils and a relatively elongate posterior spire (*sensu* Hunt et al., 2007; Hunt and Lucas, 2012b). Fish scales are visible in several areas and are prominent on the lip of the posterior spire. Adherent bilalves occur on one side of the coprolite,

**Discussion:** The holotype was collected in 1840, and its provenance is listed as Lias. However, Duffin (pers. commun., 2012) has raised legitimate issues with this putative stratigraphic derivation of the holotype of *Strabelocoprus pollardi*. The stratigraphic sequence at Watchet includes both the Lower Lias and the Rhetian Penarth Group. The adherent bivalves on the holotype are *Atreta intusstriata* (Duffin, pers. commun., 2012), which is most common in the Rhaetian Lilstock Formation (upper Penarth Group: Swift, 1999), although it rarely occurs in the Westbury Formation (lower Penarth Group) and also in the Lias (Ivimey-Cook et al., 1999, p. 98, pl. 13, figs. 3-4). *Atreta intusstriata* in the Lilstock Formation is "often attached to hard substrates" (Ivimey-Cook et al., 1999, p. 98).

The referred specimen of *Strabelocoprus pollardi* (OUM J23741), from the Lias of Lyme Regis, is flattened, but preserves the same overall morphology and is of similar dimensions as the holotype, with a length of 107.6 mm and a width of 73.4 mm (Fig. 4E). This specimen exhibits some decay around the margins.

Hunt and Lucas (2010) noted that coprolites are commonly preserved in hydrodynamically-accumulated intraformational conglomerates and bone beds in marine and nonmarine environments (e. g., Martill, 1999, fig. 6; Hunt and Lucas, 2010, fig. 2; Hunt et al., 2012, fig. 2F). There is little actualistic information about the decay of feces, but the excrement of the Recent lungfish *Neoceratodus forsteri* and *Protopterus annectans* remains intact for several hours in an aqueous environment (Jain, 1983). Thus, it is possible that the coprolites preserved in bone beds could represent recently excreted feces. However, it seems more parsimonious that coprolites preserved in bone beds represent previously-lithified feces (cf. Reif, 1971). The *Atreta intusstriata* attached to one side of the holotype of *Strabelocoprus pollardi* indicate that this specimen represents a lithified coprolite that lay on a sediment surface before being incorporated in a sediment layer. Thus, OUM J23743 is a taphonomically important specimen because it demonstrates that the hypothetical circumstance of feces becoming lithified and subsequently incorporated into a younger stratigraphic unit can in fact occur.

### *Plektecoprus*, ichnogen. nov.

**Type ichnospecies:** *Plektecoprus whitbyensis* Hunt et al., 2012.

**Included ichnospecies:** Known only from the type ichnospecies.

**Etymology:** From the Greek *plekte* (rope) in reference to the shape, and the Greek *kopros* (feces).

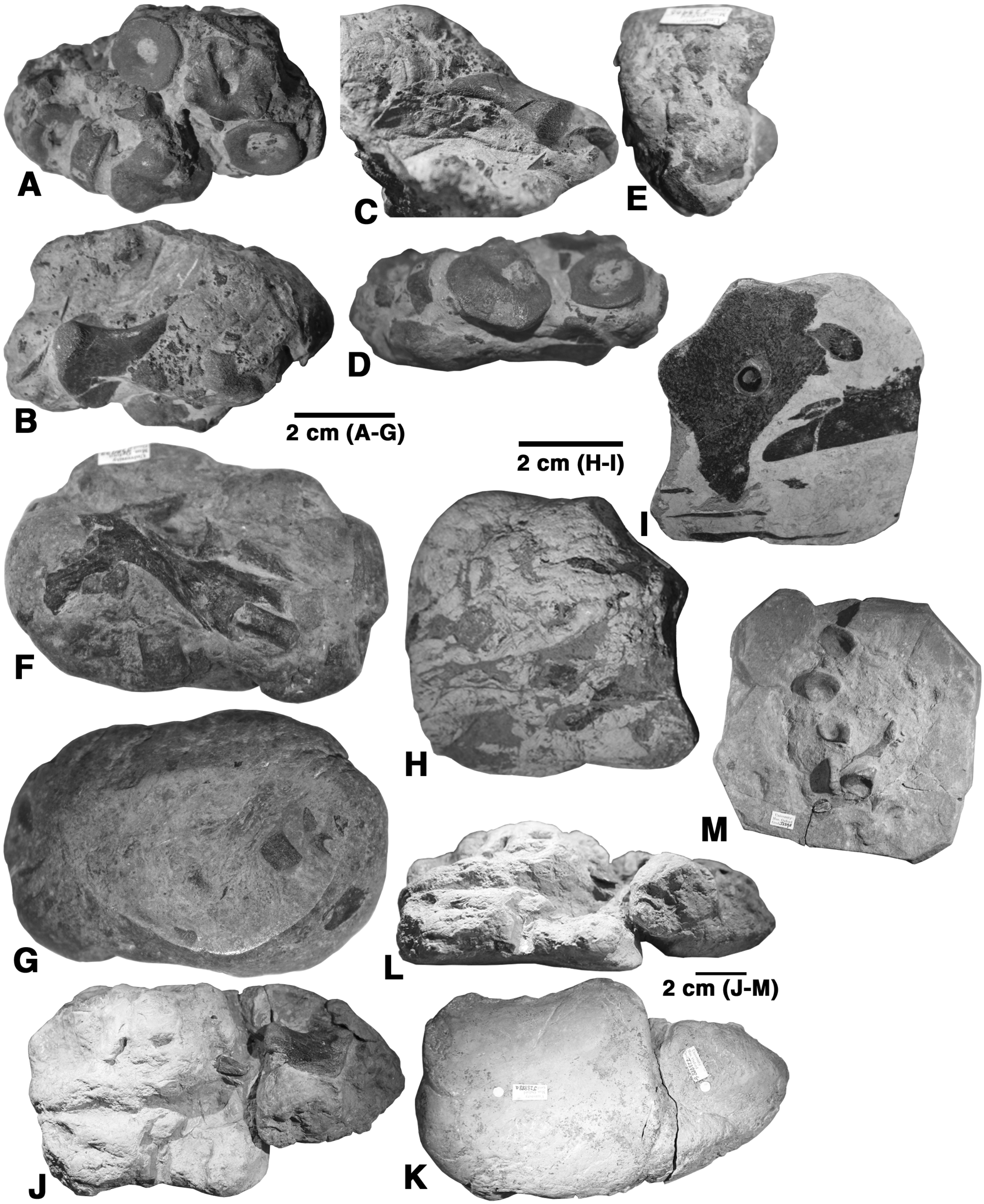


FIGURE 3. *Ichthyosaurolites duffini* ichnogen. et ichnosp. nov. from the Lower Lias (Hettangian-Lower Pliensbachian) of Lyme Regis, UK. **A-E**, OUM J 23905, Holotype coprolite in lateral (**A-D**) and terminal (**E**) views. **F-G**, OUM J 23922, Coprolite in lateral views. **H-I**, OUM J23771, Coprolite in lateral views. **J-L**, OUM J23888a-b, Coprolite in lateral views. **M**, OUM J 23911, Coprolite in lateral view.

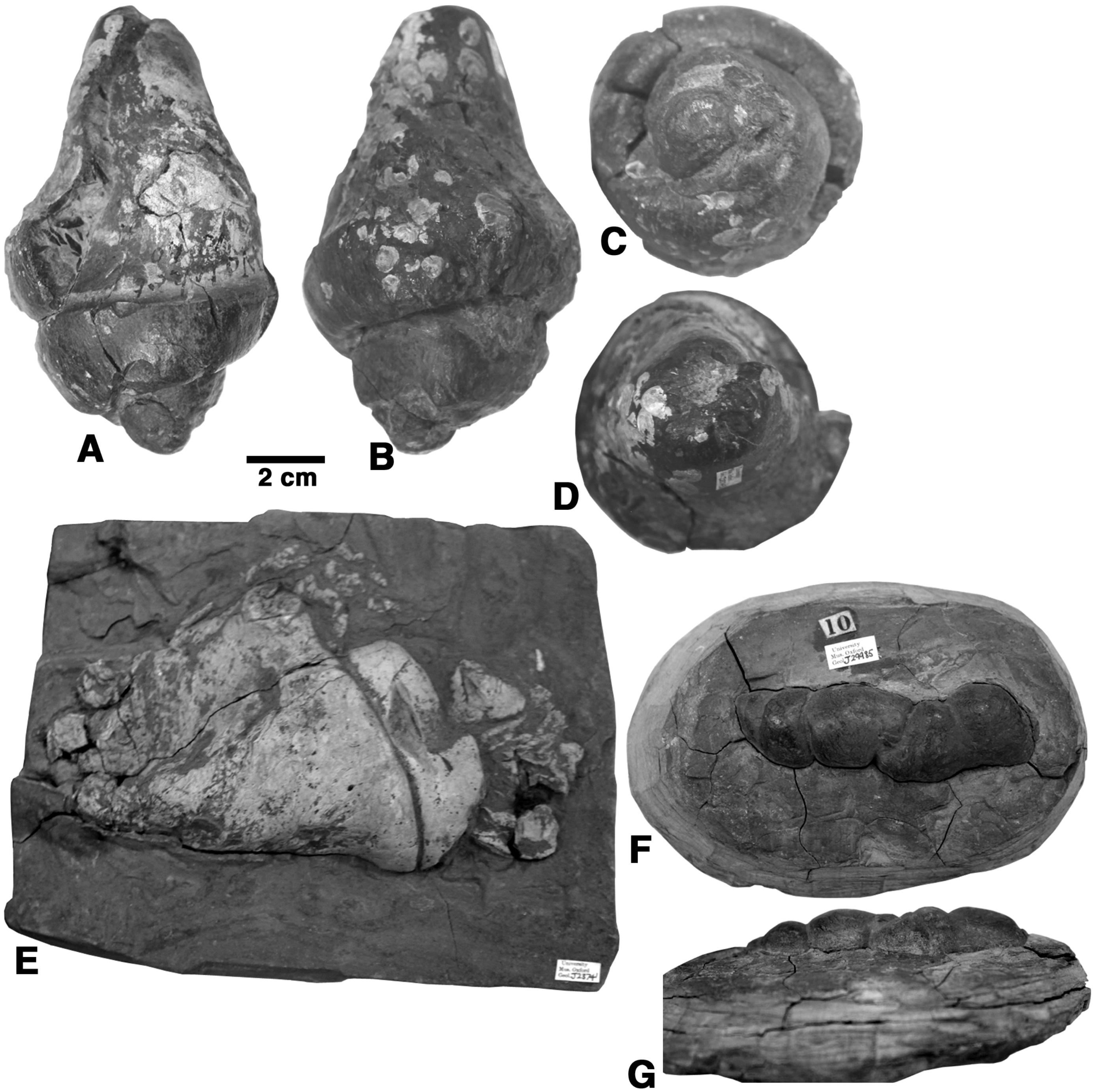


FIGURE 4. *Strabelocopros pollardi* ichnogen. et ichnosp. nov. and *Plektecoprus whitbyensis* ichnogen. et ichnosp. nov. (Hettangian-Lower Pliensbachian). **A-D**, *Strabelocoprus pollardi* ichnogen. et ichnosp. nov., OUM J23743, Holotype in **A-B**, lateral, **C**, posterior and **D**, anterior views. **E**, OUM J23741, Referred specimen, coprolite in matrix block. **E-F**, *Plektecoprus whitbyensis* ichnogen. et ichnosp. nov., OUM J29985, Holotype in two axial views.

**Distribution:** Lower Jurassic (Lower Liassic) of Yorkshire, England.

**Diagnosis:** Coprolite that differs from other ichnogenera in being elongate, rounded in cross section with a loose spiral coil and having a conical posterior end and a broad, rounded anterior end.

**Discussion:** This ichnogenus is currently only known from the Lower Lias of Yorkshire. The producer of this coprolite could be a marine reptile, given its size and lack of a tight spiral morphology.

### *Plektecoprus whitbyensis*, ichnosp. nov.

**Holotype:** OUM J29985, coprolite (Fig. 4F-G).

**Etymology:** For the town of Whitby, the type locality.

**Type locality:** Whitby, Yorkshire, England.

**Type horizon:** Lower Liassic (Hettangian-Lower Pliensbachian).

**Distribution:** As for ichnogenus.

**Referred specimens:** None.

**Diagnosis:** As for ichnogenus.

**Description:** OUM J29985 is preserved in semi-relief on an ovoid sheet of shale (Figs. 4F-G). The coprolite is complete, with a maximum length of 69.3 mm with a loose spiral coil. The anterior end is conical, and the posterior end is rounded.

**Discussion:** The elongate shape of this ichnospecies and its loose coil may have made it susceptible to mechanic destruction, so *Plektecoprus* may be rarely preserved.

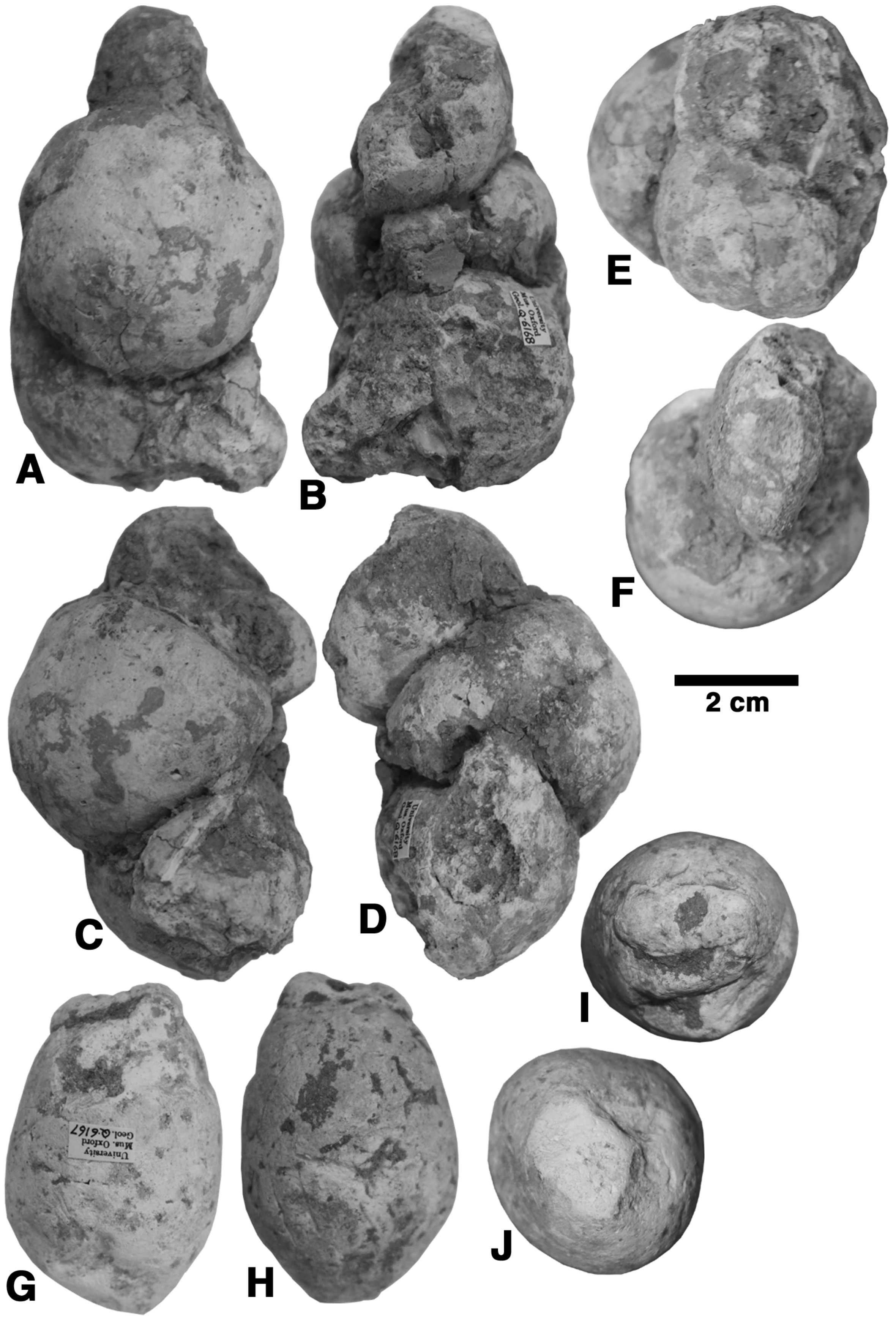


FIGURE 5. *Hyaenacoprus bucklandi* ichnogen. et ichnosp. nov. from the Late Pleistocene of Kirkdale Cave, Yorkshire, UK. **A-F**, OUM Q6168, Holotype partial coprolite in **A-D**, axial and **E-F**, polar views. **G-J**, Q6167, Partial coprolite in **G-H**, axial and **I-J**, polar views.

### *Hyaenacoprus*, ichnogen. nov.

Album graecum: Buckland, 1822, p. 186, pl. 24, fig. 6
Album graecum: Buckland, 1824, p. 20, pl. 10, fig. 6
Hyaino-coprus: Buckland, 1829a, p. 143
Hyaena-coprus: Buckland, 1830, p. 24

**Type ichnospecies:** *Hyaenacoprus bucklandi* ichnosp. nov.

**Included ichnospecies:** Known only from the type ichnospecies.

**Etymology:** Based on the term employed by Buckland (1830, p. 24), suggesting that these are hyaena coprolites.

**Distribution:** Upper Pliocene-Pleistocene of Europe, Asia and Africa.

**Diagnosis:** Phosphatic coprolite that differs from other ichnogenera in being composed of a series of rounded segments (pellets of Diedrich, 2012), some of which are sub-spherical and are white in color with many small angular bone fragments.

**Discussion:** Buckland (1822, 1824) described the geology and paleontology of Kirkdale Cave in Yorkshire, which he interpreted to be a Late Pleistocene hyena den. He discovered "many small balls of the solid calcareous excrement of an animal that had fed on bones, resembling the substance known in the old Materia Medica by the name of album graecum …. its external form is that of a sphere, irregularly compressed, as in the feces of sheep, and varying from half an inch to an inch in diameter; its colour is yellowish white, its fracture is usually earthy and compact, resembling steatite, and some-times granular; when compact, it is interspersed with minute cellular cavities: it was at first sight recognised by the keeper of the Menagerie at Exeter Change, as resembling, both in form and appearance, the faeces of the spotted or Cape Hyaena, which he stated to be greedy of bones, beyond all other beasts under his care. This information I owe to Dr. WOLLASTON, who has also made an analysis of the substance under discussion, and finds it to be composed of the ingredients that might be expected in faecal matter derived from bones, viz. phosphate of lime, carbonate of lime, and a very small proportion of the triple phosphate of ammonia and magnesia; it retains no animal matter, and its originally earthy nature and affinity to bone, will account for its perfect state of preservation" (Buckland, 1822, p. 186-187). Subsequently, Buckland was able to conduct actualistic studies to confirm his hypothesis: "I have had an opportunity of seeing a Cape Hyaena at Oxford, in the travelling collection of Mr. Wombwell, the keeper of which confirmed in every particular the evidence given to Dr. Wollaston by the keeper at Exeter 'Change……The keeper pursuing this experiment to its final result [the feeding of bones to the hyena], presented me the next morning with a large quantity of album graecum, disposed in balls, that agree entirely in size, shape, and substance with those found in the den at Kirkdale" (Buckland, 1824, p. 38). Buckland illustrated one specimen of album graecum (Buckland, 1822, pl. 24, fig. 6; 1824, pl. 10, fig. 6). This is a term that was used by apothecaries to refer to dog feces that were especially rich in phosphate as a result of feeding a bone-rich diet to dogs (Duffin, 2009). (Buckland (1829a, p. 143) later applied the term "Hyaino-coprus" to "the Album Graecum of the fossil hyena" (Hyaena-coprus in Buckland, 1830, p. 24). We use the latter name for the new ichnogenus to honor Buckland.

Hyena excrement is robust due to early diagenesis and cementation of the bone phosphate that commences in the intestines, and they can survive hydrodynamic transport (Diedrich, 2012). Trampled latrinites (*sensu* Hunt and Lucas, 2012a) occur in some European caves such as in the Lindenthaler Hyänenhöhle in Germany (Liebe, 1876; Diedrich, 2012).

*Hyaenacoprus bucklandi* is widespread in Late Pleistocene caves in the Old World. There is clearly an ichnofacies in North American caves distinct from those in Europe, Asia and Africa. Old World caves are dominated by hyena coprolites (e.g., Scott, 1987; Pesquero et al., 2011; Diedrich, 2012), whereas those in North America are dominated by diverse herbivore coprolites (e. g., Mead and Agenbroad, 1989; Hunt and Lucas, 2007; Mead and Swift, 2012).

### *Hyaenacoprus bucklandi*, ichnosp. nov.

**Holotype:** OUM Q6168, partial coprolite (Figs. 5A-F).

**Etymology:** For the collector of the holotype, William Buckland, to honor his contributions to the study of coprolites.

**Type locality:** Kirkdale Cave, Yorkshire, England.

**Type horizon:** Late Pleistocene cave fill.

**Distribution:** As for ichnogenus.

**Referred specimens:** OUM Q6167, partial coprolite (Figs. 5G-J).

**Diagnosis:** As for ichnogenus.

**Description:** OUM Q6168 is a white coprolite fragment composed of three principal, generally-rounded segments or pellets (*sensu* Diedrich, 2012), the middle of which is sub-spherical on one side (Figs. 5A-F). These pellets are within the types e-f (irregular to round) of Diedrich (2012). One side of the coprolite is generally flat and irregularly pitted. The total length of the fragment is 55.4 mm, with a width of 57.4 mm. There are several small angular shards of bone visible in the coprolite.

**Discussion:** Referred specimen OUM Q6167 is a white ovoid pellet with a nearly round cross section (Figs. 5G-J). It is 51.4 mm long with widths of 31.4 and 32.6 mm. Each rounded end has a small broken attachment for an adjoining pellet. This specimen corresponds to a type d (long oval) pellet of Diedrich (2012).

We believe that Buckland was correct in hypothesizing that *Hyaenacoprus* is the product of a hyena. However, in Africa today both the lion and hyena produce feces of broadly similar morphology that are tapering, segmented cylinders (Stuart and Stuart, 2000). Fresh hyena feces are greenish in color, but they whiten when dry because of the high bone content. Lion feces are usually dark in color, but they can also be white if the diet is high in bone (Stuart and Stuart, 2000, p. 161 unnumbered fig. on lower left). Lion feces are usually of a larger size than those of hyenas, typically over 4 cm in diameter, although this is not always the case (Stuart and Stuart, 2000). Recent and fossil hyena feces/coprolites are usually concentrated at latrine/latrinite sites (Stuart and Stuart, 2000; Diedrich, 2012). Both hyenas (*Crocuta crocuta spelaea*) and lions (*Panthera leo spelaea*, *Panthera leo fossilis*) occupied caves and other sites in Pleistocene Europe and there is potential for confusion in identifying their coprolites. Cave lions were larger than Recent subspecies and so we hypothesize that their coprolites could be distinguished from those of hyenas by larger size (greater than 4 cm in diameter) and isolated occurrence. There is need for more study of Pleistocene coprolites in Europe to test this hypothesis.

## CONCLUSIONS

The Buckland Collection at the University of Oxford Museum of Natural History is not only the oldest collection of coprolites but also one of the most important. There is need for more description of this collection, which includes the most comprehensive samples of two important British coprofaunas – the Lower Liassic of Lyme Regis and the Rhaetic bone bed.

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