VERTEBRATE COPROLITES FROM CRETACOUS CHALK IN EUROPE AND NORTH AMERICA AND THE SHARK SURPLUS PARADOX

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Abstract—Vertebrate coprolites from the Cretaceous Chalk of England were among the first to be described and identified. Coprolites occur commonly in the Cenomanian Grey Chalk Group and the Turonian-Maastrichtian White Chalk Group. A small number of coprolites have been described from the chalk of Denmark, Netherlands, Belgium, Germany and Poland. Coprolites are abundant in the Niobrara Formation of Kansas but poorly studied. A single specimen has been described from the Selma Chalk of Alabama. Coprolites are facies fossils, and their distribution reflects that of the producing organism. The majority of chalk coprolites are spiral, and their most distinctive characteristic seems to be that in lateral view there are many thin coils in which margins are thin and crenulated, which gives the general appearance of a fir cone. The majority of specimens are heteropolar, although a small number are amphipolar, including *Iuloeidocoprus mantelli.* The heteropolar coprolites are macrospiral. Vertebrate coprolites are clearly common, at least in the English and Kansas chalk, and there is a need for further collection and study. There is a disparity between the high taxonomic diversity of fish faunas in chalk (and other marine facies) and the low diversity of chondrichthyan-dominated coprolite ichnofaunas which we term the “shark surplus paradox.

INTRODUCTION

Vertebrate coprolites from the Chalk of England were among the first to be described and identified (Mantell, 1822; Buckland, 1835, 1836; Duffin, 2009). Subsequently, there have been scattered reports of coprolites from chalk lithologies in Europe and North America. The purpose of this paper is provide a brief review of the current record in part to stimulate further collection and study. Abbreviations are: **HM**, Hunterian Museum, Glasgow, Scotland; **USNM**, United States National Museum, Washington, DC., USA.

VERTEBRATE COPROLITES FROM CHALK FACIES

Europe

England

Mantell (1822, pl. 9, figs. 3-11: Fig.1) described and illustrated specimens that were later identified as coprolites from both the Cenomanian Lower Chalk (Grey Chalk Group) and the Turonian-Maastrichtian Upper Chalk (White Chalk Group)(Gale and Kennedy, 2002).

Mantell (1822, pl. 9, figs. 4, 5, 7, 8, 11: Fig. 1) described five specimens from the Grey Chalk Group. He referenced the fact that these specimens represent the same morphology as some described by Woodward (1729, part 2, p. 22) as, “Three cones seeming to be of the Larix. From *Cherry-Hinton* Chalk-pits near *Cambridge,”* and by Parkinson (1804, p.456) as “very near in resemblance to the juli of the larch tree” (Duffin, 2009: Fig. 2G-H). “These are the supposed “*fossil juli of the larch*,” for which the chalk pits of Cherry Hinton have been so long celebrated. Since the time of Woodward, these bodies have excited considerable attention, and yet their nature is still involved in obscurity (Mantell, 1822, p. 103). Mantell (1822, p.103-104) was obviously conflicted about the origin of these specimens as he quotes the differing opinions of five different individuals. He variously concludes that they are “aments or cones of unknown vegetables??” (Mantell, 1822, p. 103) or “supposed aments or cones of a species of Larch” (Mantell, 1822, p. 310, caption to pl. 9).

The White Chalk Group yielded two similar morphologies “the first differs but little from the bodies already described…………the other variety is more elongate, its surface nearly smooth, and it is solid throughout” (Mantell, 1822, p. 158, pl. 9, figs. 3, 6, 9, 10). Mantell (1822, p. 158) concluded that these specimens represented “supposed juli of the larch” despite the fact that “the constituent substance of these fossils, is precisely of the same nature as the vertebrae, and other bones of cartilaginous fishes………. This resemblance is so striking, that it is with considerable hesitation that I have noticed them in this place, being fully of opinion, that they may after prove to be parts of fishes.”

Buckland (1822, 1829) was the first to recognize fossil feces and to name them coprolites (Duffin, 2009; Hunt and Lucas, 2012a). Subsequently, after examining Early Jurassic coprolites he noted that “their structure so reminded me of the fossil Iuli of the chalk and chalk marl that have been described by Woodward, Parkinson, and others, as fir cones of the larch, it occurred to me that so-called Iuli must be also of faecal origin” (Buckland, 1835, p. 232). This hypothesis was supported by chemical analyses that indicated that the “Iuli” had a similar composition to fossil fish bones from the chalk as did Mantell’s second type of elongate smooth forms (Buckland, 1835).

Mantell sent Buckland a new un-spiraled coprolite from the Lower Chalk (Grey Chalk Group) near Lewes that was described as nearly identical to a consumulite (*sensu* Hunt and Lucas, 2012a) of a specimen of the coelacanth *Amia lewesiensis* (now *Macropoma lewesiensis*). Buckland (1835, pl. 31, fig. 12) suggested the name *Amia-coprus* for this morphotype and hypothesized that such coprolites were more abundant in the lower chalk, whereas spiral forms were more prevalent in the upper chalk. Subsequently, Buckland (1836, p. 154) used the name *Macropoma mantelli* (=*Macropoma lewesiensis*) for the same consumulite-bearing fish (Mantell, 1822, pl. 38). Mantell (in Buckland, 1836) considered that heterospiral coprolites with wide coils (Buckland, 1836, pl. 15, figs. 8-9) were the coprolites that were most similar to the consumulites within *Macropoma,* whereas those that resembled fir cones (Buckland, 1836, pl. 15, figs. 5, 7) probably derived from *Ptychodus* because teeth of the chondrichthyan are commonly preserved with specimens of this morphology.

Duffin (pers. commun., 2015) indicated to us two other early illustrations of English chalk coprolites. Agassiz (1843, p. 336, pl. 65a, figs. 3-11) illustrated “divers coprolithes provenant de ce possion [*Macropona mantelli*]“ and Dixon (1850, pl. 30, fig. 33) illustrated a heteropolar and an apparent amphipolar coprolite, the latter assignable to *Iuloeidocoprus* isp. Dixon (1850, p.368) also mentioned two specimens of *Macropona mantelli* containing consumulites (“coprolites”).

Longbottom and Patterson (2002, pl. 63, fig. 4: Fig. 2I) illustrated a coprolite from the Middle Cenomanian (*H. subglobosus* Zone) at Dover. They noted that chalk coprolites were commonly attributed to *Macropoma* but that they likely pertained to sharks.

There is a large sample of coprolites from the chalk of England in the collections of the Hunterian Museum at the University of Glasgow (Figs. 2A-H, 3A-K), which are spiral heteropolar with two exceptions (Figs.2H, 3K). There are undoubtedly coprolites from the chalk in other museums in the United Kingdom that are in need of study.

Denmark

Milàn et al. (2015) described the first vertebrate coprolite from

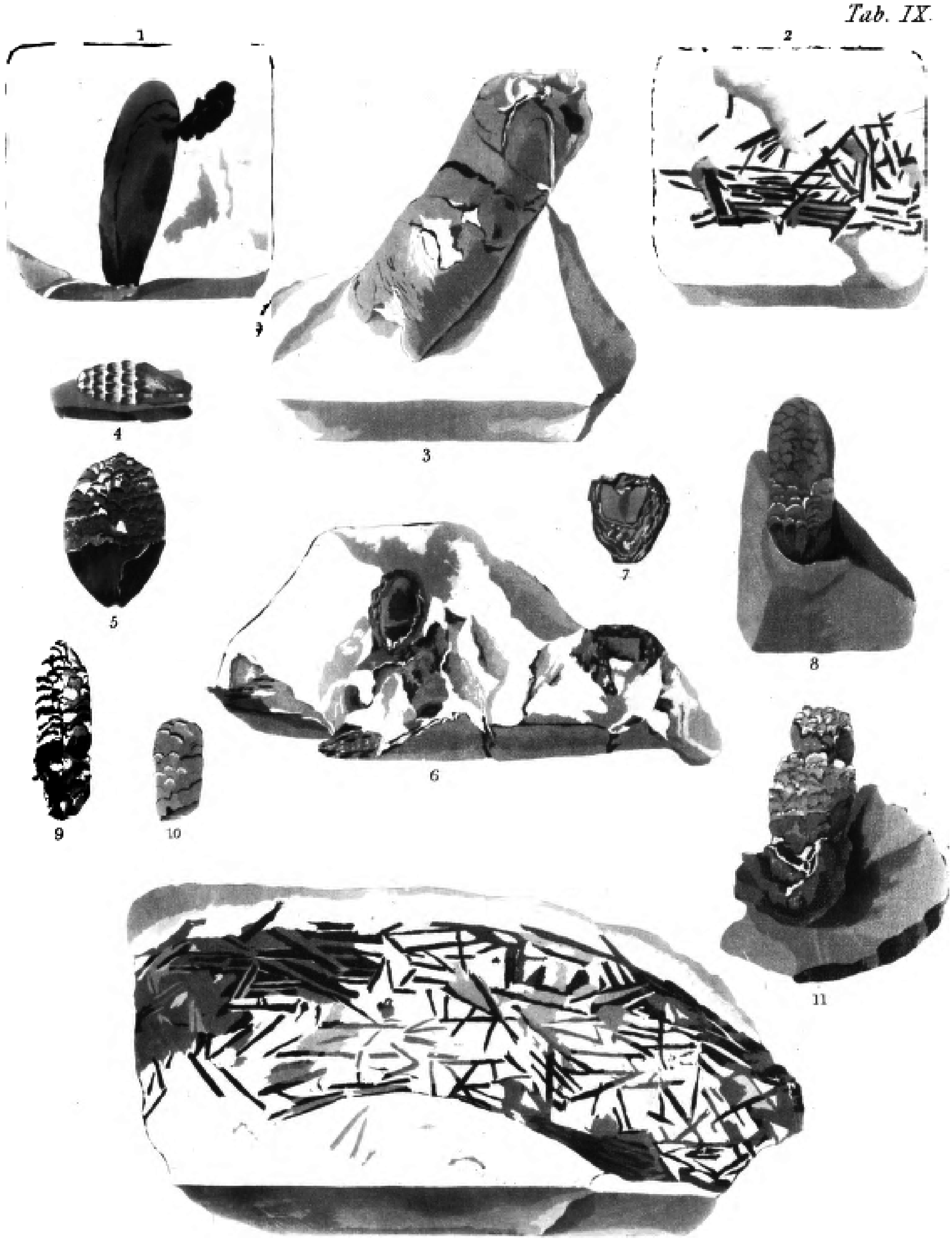

FIGURE 1. Tablet (=Plate) 9 from Mantell (1822). Original caption is: "TABLET IX Supposed vegetable bodies from the Chalk and Chalk Marl. Fig. 1. The remains of a winged seed? In chalk, p. 158.; Figs. 2, 12. Linear markings, resembling the foliage of a species of Pinus, p. 157.; Figs. 3, 6, 9, 10. Unknown fossil bodies from the chalk, generally supposed to be the remains of aments or cones, p. 158.; Figs. 4, 5, 7, 8, 11. Supposed aments or cones of a species of Larch, from Hamsey; p. 103."

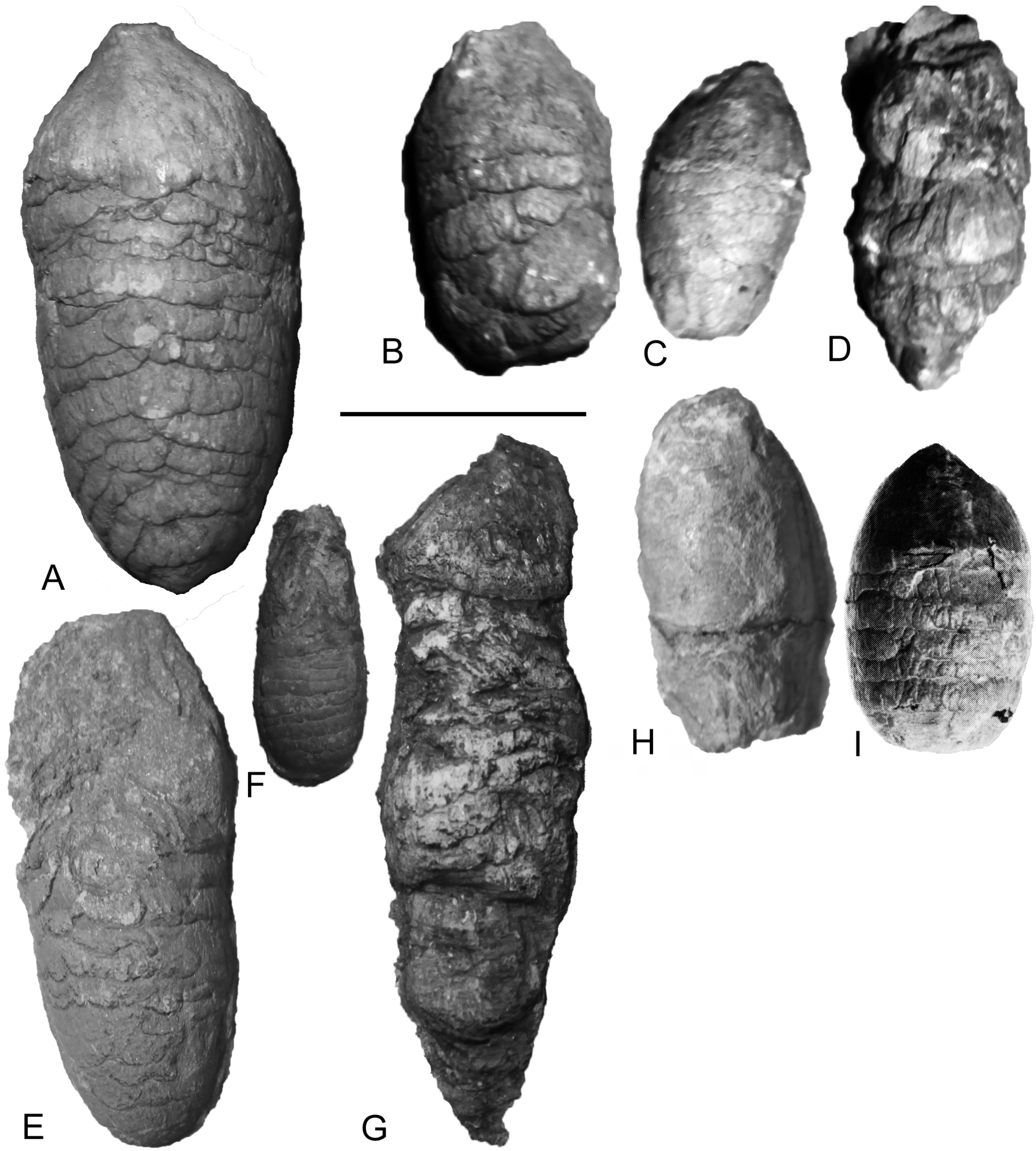

FIGURE 2. **A-D**, HM V3810, coprolites from the Cenomanian Grey Chalk Group of Folkestone, Kent in lateral view. **E**, unnumbered HM, coprolite from the Cretaceous of England in lateral view. **F,** coprolite from the chalk of Dorking, Surrey. **G,** HM V. 1581, coprolite from the lower chalk of Cherry Hinton, Cambridgeshire in lateral view. **H**, HM L 411, coprolite from the lower chalk of Cherry Hinton, Cambridgeshire in lateral view. **I**, unnumbered specimen from the Cenomanian Grey Chalk Group (from Longbottom and Patterson, 2002, pl. 63, fig. 4). Scale bar is 2 cm.

the Upper Maastrichtian chalk of Denmark. Computed Tomography scanning of the specimen demonstrated a tightly coiled structure. The coprolite was attributed to a small shark. They noted that the lack of recorded coprolites from the Danish chalk probably reflects a collecting bias rather than a scarcity.

Netherlands/Belgium

Buckland (1835, p. 234, pl. 39, figs. 9-11) described three coprolites from the Sint-Pietersberg ("mountain of St. Peter") south of Maastricht, which he considered to be identical to Iulo-eido-

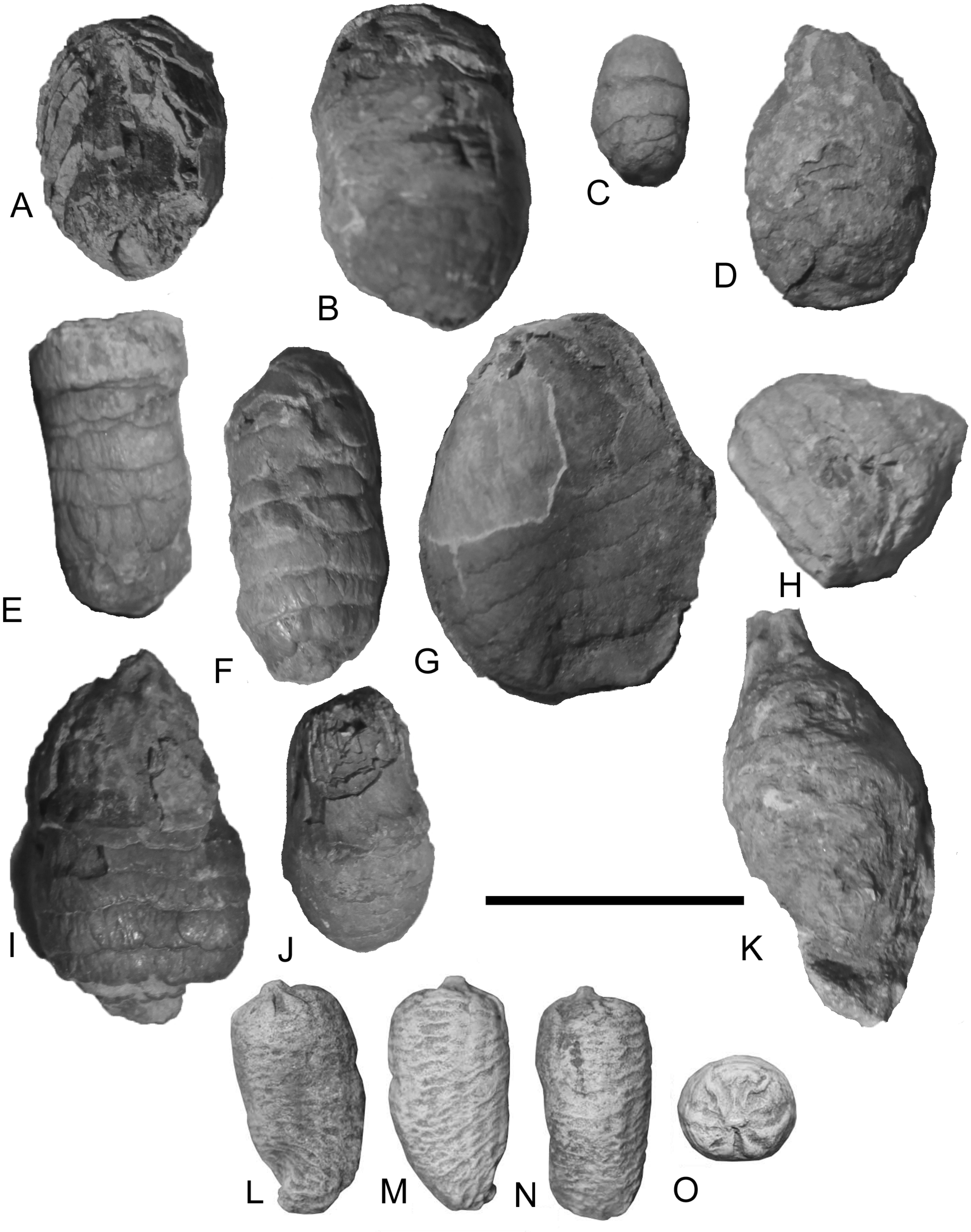

FIGURE 3. Vertebrate coprolites from Upper Cretaceous chalk in Europe and North America. **A-K**, Vertebrate coprolites from the Cenomanian Grey Chalk Group of England (HM V3810) in lateral view. **L-O**, USNM uncatalogued, *Iuloeidocoprus mantelli* holotype, from the Selma Group of Alabama in lateral (L-N) and terminal (O) views (after Hunt et al., 2012, fig 2Q-T). Scale bars are 2 cm.

coprus from English Chalk. The stratigraphic level of these finds is unknown. Recent field work in the type area of the Maastrichtian Stage (southeastern Netherlands, northeastern Belgium), in particular in the upper part of the Gulpen Formation and lower portion of the overlying Maastricht Formation (both of late Maastrichtian age) has yielded several vertebrate coprolites. These coprolites are usually phosphatic and brittle and some contain inclusions of ?teleost bone.. There has been a definite collecting bias in this area. There are many specimens of sharks, rays, bony fish and reptiles (mosasaurs, turtles) but few of coprolites. There is a strong potential for finding more coprolites in these strata.

Germany

USNM 16409 is a macrospiral heteropolar coprolite from the chalk of Saxony. Hunt et al. (2012a, fig. 2DD-EE) referred this specimen to *Liassocoprus* isp.

Poland

Occasional spiral coprolites occur in the Opole area of southwestern Poland in Lower-Middle Turonian strata, notably from the so-called Lower Clayey Marls (*Inoceramus apicalis* Zone; see Kędzierski, 2008). These specimens are similar to the specimen illustrated by Longbottom and Patterson (2002, pl. 63, fig. 4) from the Middle Cenomanian of England. Isolated teeth of the genus *Ptychodus* are also fairly common (Mazurek, 2008; J.W.M. Jagt, pers. obs.).

North America

Alabama

Hunt et al. (2012, fig. 2Q-T) described an amphipolar coprolite from the Upper Cretaceous Selma Chalk as a new ichnotaxon, *Iuloeidocoprus mantelli.* This morphotype is spiral in form with evenly spaced coils and longitudinal striations. They named it after Buckland's (1835) term Iulo-eido-coprus because of its apparent similarity to specimens from the English chalk.

Kansas

The Upper Cretaceous Niobrara Formation has yielded vertebrate coprolites, but few have been described. Stewart (1978, figs 4, nos. 1-4, 7, figs. 5-6) noted several morphotypes of coprolites (including his "enterospirae") that can be categorized as: (1) heteropolar with well- or poorly-preserved internal structure and occasional inclusions; (2) large oblong specimens loosely coiled around the short axis that rarely contain inclusions; (4) large oblong specimens coiled around the long axis; and (5) oblong specimens of all sizes, having no external or internal structure, which frequently contain bones of teleosts.

DISCUSSION

Coprolites are facies fossils and their distribution reflects that of the producing organism. Certain morphotypes appear to be characteristic of chalk facies but there is not a large data set of other Late Cretaceous coprolite faunas for comparison. The majority of chalk coprolites are spiral and their most distinctive characteristic seems to be that in lateral view there are many narrow coils in which the margins are thin and crenulated (e.g, Fig. 2A), which gives the general appearance of a fir cone. The majority of specimens are heteropolar, although a small number are amphipolar (Fig. 3C, F?), including *Iuloeidocoprus mantelli.* The heteropolar coprolites are macrospiral, as the posterior spire represents 50% or more of the length (Hunt et al., 2007; Hunt and Lucas, 2012b). Buckland (1835) hypothesized that different coprolites were present in the Lower and Upper Chalk but more ichnotaxonomc analysis is required to evaluate this idea. Vertebrate coprolites are clearly common, at least in the English and Kansas chalk, and there is a need for further collection and study.

SHARK SURPLUS PARADOX

The English Chalk has the best sample of vertebrate coprolites of this facies. The vast majority of specimens are heteropolar in morphology which strongly suggests that that they were produced by chondrichthyans as other fish which may have yielded spiral coprolites (e.g., sarcopterygians) are not abundant. However, the English Chalk has a rich fauna of other taxa of fish (e.g., Woodward, 1902-1912; Patterson, 1964). Similarly, large coprolite samples from shallow marine strata of the Early Mesozoic and Tertiary are also dominated by chondrichthyan specimens (e.g., Buckland, 1835, 1836; Diedrich and Felker, 2012; Stringer and King, 2012). There is clearly a disparity between the high taxonomic diversity of fish faunas of these ages and the low diversity of chondrichthyan-dominated coprolite ichnofaunas. We term this the "shark surplus paradox." Late Paleozoic coprolite ichnofaunas are commonly dominated by spiral forms (e.g., Hunt et a l., 2012b) but many less-derived fish are presumed to have spiral valves and so it is not so obvious that sharks are disproportionately represented (Hunt and Lucas, 2012b), although this may be the case. The most probable explanations of the shark surplus paradox are taphonomic including, in probable decreasing order of likelihood: (1) chondrichthyan feces have physical or/and chemical properties which result in them being preferentially lithified or preserved in a recognizable form; (2) chondrichthyan coprolites have physical properties which allow them better to survive transport than those of other fish; and (3) marine environments that favor the preservation of coprolites have fish faunas dominated by chondrichthyans.

ACKNOWLEDGMENTS

We thank Neil Clark for access to collections under his care at the Hunterian Museum, University of Glasgow. Chris Duffin provided important historical information and together with Allan Lerner produced helpful reviews of an earlier draft of this manuscript.

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