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SELECTIVE FEEDING IN AN EARLY DEVONIAN TERRESTRIAL ECOSYSTEM

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ABSTRACT

Short chains of discoidal, rarely spheroidal, structures, recovered by acid maceration of Lower Devonian (Lochkovian) siltstones from the Welsh Borderland are interpreted as coprolites because they comprise comminuted or homogenized tissues. They are placed in a new species of the ichnogenus *Lancifaex*. Tissues include the smooth and banded tubes of *Nematasketum*, a close ally of *Prototaxites*, and rarer cuticles of *Nematothallus* and *Cosmochlaina*. All these taxa have been assigned to an extinct class, Nematophytales Lang 1937, which Lang thought was intermediate between higher plants and algae. More recently, there is more compelling evidence, particularly from *Prototaxites*, that the class had fungal affinities. We thus conclude that the producers of the coprolites were selective feeders on nematophytes, and hence on fungi. Prior evidence for the reconstruction of terrestrial ecosystems in the mid-Paleozoic has been dominated by mega- and mesofossils of primary producers because body fossil records of consumers, whether carnivores, herbivores, or detritivores, are rare. Coprolites previously described from the locality that contain spores and residues of higher plants provide indirect evidence, based on consideration of comparative body size of coeval animals recorded elsewhere, for detritivory, probably in millipedes. In a similar approach involving mites, collembolans and millipedes—animals known to be mycophagous today—it is concluded that millipedes were the most likely producers of the coprolites described here.

INTRODUCTION

The reconstruction of terrestrial ecosystems in the mid-Paleozoic is essential for any holistic approach to elucidating the history of the biosphere. Considerable progress has been made in the description of land plants based on the mega- and mesofossil record (e.g., Hao and Gensel, 2001; Edwards and Richardson, 2004) and the reconstruction of vegetation in the Early Devonian when vascular plants were diversifying on land (Hotton et al., 2001; Channing and Edwards, 2009). In contrast, the records of associated animals are far more rare (Selden, 2005). Paleozoological data have been supplemented by that from ichnofossils, e.g., arthropod tracks (Trewin and McNamara, 1995) and coprolites (Edwards et al., 1995; Habgood et al., 2004). The latter tell us little about the animals themselves, but have use in reconstructing trophic relationships. Broader considerations of the evolution of such relationships may be found in Gray and Boucot (1994) and Labandeira (2006a, 2006b, 2007).

Coprolites have been recovered from clastic rocks, where they tend to be dominated by spores (Edwards et al., 1995), and silicifications that possess far more diverse content, including macerated plant material, hyphae, plant and fungal spores, and mineral particles (Habgood et al., 2004). They are more frequently found in Carboniferous rocks, occurring both in coal balls (e.g., Scott, 1977; Baxendale, 1979; Scott and Taylor, 1983; Lesnikowska, 1990) and coal (Hower et al., 2011; Scott et al., 2011). The earliest possible terrestrial examples, which are ovoid to cylindrical pellets containing hyphae of a presumed ascomycete, provide evidence for mycophagy (Sherwood-Pike and Gray, 1985). In screening hundreds of mesofossils from a Lochkovian locality which has yielded large numbers of coprolites with abundant spores, we recovered a small number (~50) of highly distinctive coprolites, distinguished by their segmented shape and unusual content. They lack any evidence of derivation from higher plants; neither fragments of stems, sporangia, spores, nor tracheids; nor animals. Instead, they consist of comminuted and homogenized fragments of taxa placed by Lang (1937) in the Nematophytales. The affinities of these taxa, which include *Prototaxites sensu* Lang, are highly controversial and have covered algae, fungi, lichens, and liverworts, although Lang himself concluded that the Nematophytales was an extinct intermediate group. Hueber (2001) has argued persuasively that *Prototaxites* was a giant sporomorph of a basidiomycote, a relationship strongly supported by foraging and translocating linear structures which resemble cords or rhizomorphs in a close ally: *Nematasketum* (Edwards and Axe, 2012). These fossils show no characters suggestive of affinity with liverworts (Boyce and Hotton, 2010; Graham et al., 2010a, 2010b; Taylor et al., 2010).

Here, we describe coprolites showing not only remnants of the prototaxalean complex, but cuticles of *Nematothallus* and *Cosmochlaina*, which Lang (1937) and Edwards (1982, 1986), respectively, also assigned to the nematophytes. Not only do they provide evidence that the cuticles and hyphal fragments were related, but that the animal that produced the coprolites was a selective feeder and probably a mycetobiont.

GEOLOGY

The fossiliferous strata, exposed in a stream section to the north of Brown Clee Hill, Shropshire, UK (Fig. 1), are in the lower part of the Ditton Group (Fig. 2; Edwards and Richardson, 2004). A well-preserved dispersed spore assemblage belongs to the middle subzone of the *micrornatus-newportensis* Sporomorph Assemblage Biozone (Richardson and McGregor, 1986). This indicates an early Lochkovian (Early Devonian) age.

METHODS

The coalified mesofossils occur in a gray, loosely consolidated, fluvial siltstone. The fossils are three-dimensionally preserved and assumed to be charcoalifications (Glasspool et al., 2006). They were isolated using dilute hydrochloric acid followed by 40% hydrofluoric acid (HF) and repeated washing in water, but omitting centrifugation because this fragments the small fossils. They were then prepared for scanning and light microscopy as described in detail in Morris et al. (2011). For the former, following mounting on carbon discs on stubs, the specimens were sputter-coated with gold-palladium, before viewing in a FEI (Philips) XL30 ESEM FEG at 20 kV. For light microscopy, specimens, already scanned, were put into Schulze's solution (saturated solution of potassium chlorate in nitric acid) overnight, then embedded in TAAB

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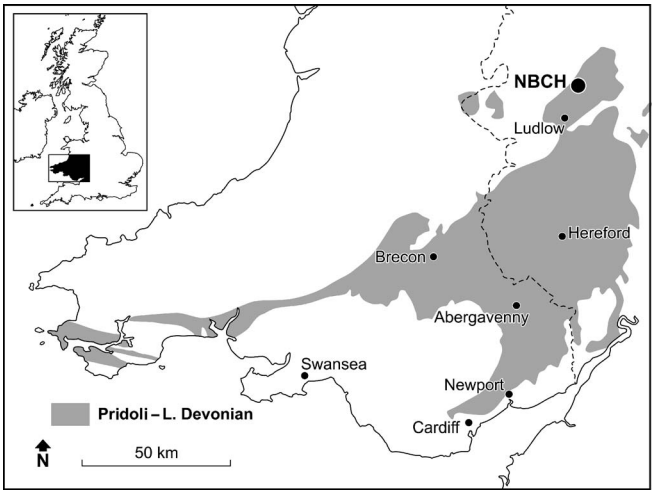

FIGURE 1—Locality map: NBCH = North Brown Clee Hill, Shropshire, UK.

low-viscosity resin and finally sectioned on a Reichert-Jung Ultracut E ultramicrotome, using a DiATOME diamond knife, into 0.9–1.0 µm thick sections. These were air-dried onto slides, mounted under a cover slip in DePe X mounting medium and examined using a Leica DMR-X microscope. Images were captured using a Leica DFC480 digital camera. Outline drawings (Fig. 3) were made from some of the specimens illustrated in the photographs (Figs. 4–11).

RESULTS

General Morphology of Segmented Forms

The specimens are made up of a number (2–6) of discrete units (Figs. 3A–AC, 4A–M), which are usually laterally compressed, forming discoidal structures. More spherical units characterize rare longer (4+) forms (Figs. 4A, B), but not invariably so (Fig. 4D). The coprolites vary in length (<3800 µm), mainly dependent on the number of units and their thickness (Fig. 4D, E) and in width (235–2280 µm), although width is usually approximately constant along a single coprolite (Table 1). Exceptions occur where there is a marked change in shape of individual units (e.g., Figs. 4F, G). Specimens with two units slightly outnumber those with three (13 = 43%, 12 = 40%, n = 30) although there is some evidence from remains of contact areas that both, particularly the 2-unit forms, may originally have been longer (e.g., Figs. 4H, M). Such evidence comes from specimens with incomplete ends (Fig. 4C). Figure 4I shows a relatively small contact area; the majority are more extensive (Figs. 4J, K). Contacts may be very small where units are somewhat adpressed (Fig. 4H) or extended, producing dumbbell shapes in the case of two units (Figs. 4L, M).

Surface Features.—At low magnification, surfaces in the majority of specimens are smooth with occasional small depressions (Figs. 4C, E, G, H). Others have less regular deeper depressions and occasional smooth areas (Figs. 4A, F, L). Figure 5A shows the surface expression of tissues that are almost completely homogenized within the coprolite. A few specimens possess an extremely irregular topography often comprising sheets of cells (Figs. 5B, C) and patches of cuticles (Figs. 5D, G). The cuticles include *Nematothallus* (Figs. 5E, F), ?*Cosmochlaina* (Fig. 5G), an unidentified form (Fig. 5D), and a nematophyte currently under investigation in Cardiff (Fig. 5H). Figure 6A shows an example where the only recognizable cells are banded tube fragments or, in one specimen, collapsed spores which lack haptotypic features and are smaller than embryophyte examples (Fig. 6B). Some smooth surfaces at high magnifications reveal granular (Fig. 6C) or tubular comminuted material or minutely punctate ?cuticle (Fig. 6D). In some smooth examples, fractured sections show a

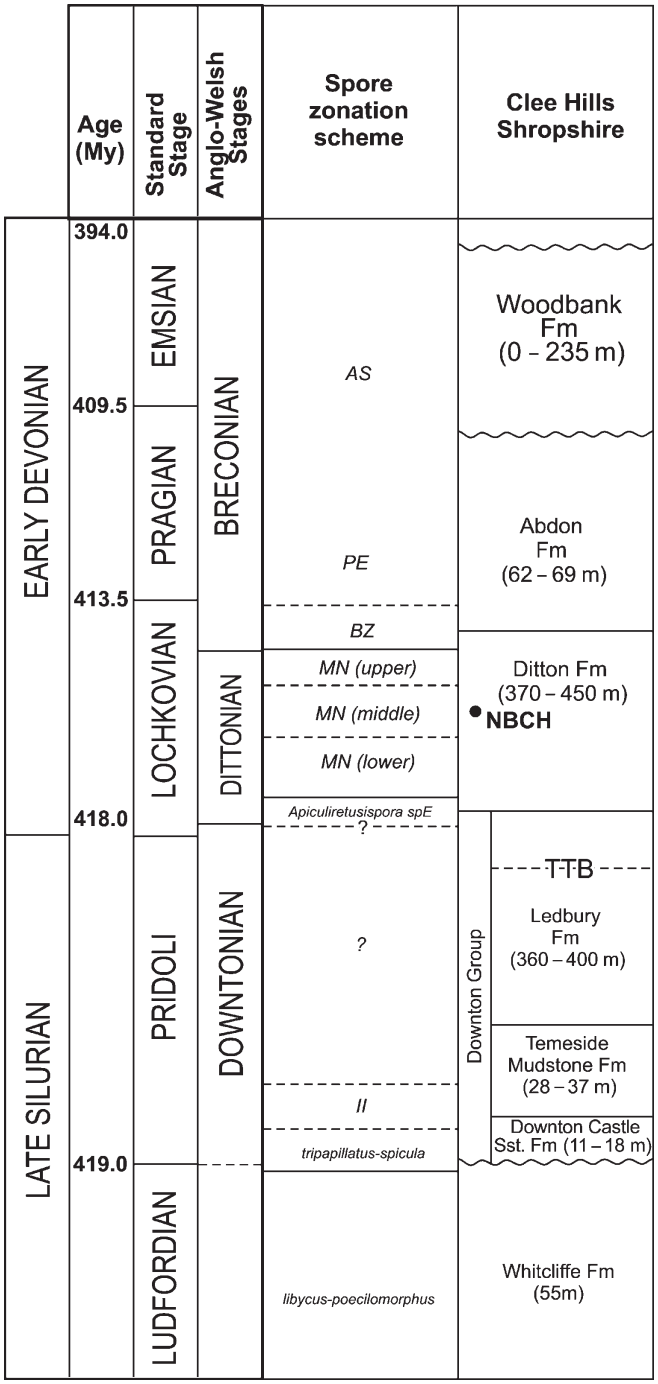

FIGURE 2—Stratigraphic log of the upper Silurian and Lower Devonian in the Welsh Borderland.

continuous, very narrow, limiting, homogenized layer which does not appear to be a section through a cuticle (Fig. 7A).

Content of Segmented Forms

It is apparent from the above that no two specimens are identical in surface features and this variation is also seen when specimens are cut or broken open for further analyses. For ease of description, we have divided them into four broad categories, which may intergrade but not within a single coprolite. We initially had to reallocate some specimens which, on breaking open, seemed to have no recognizable tissues, but these were revealed in microtome sections. Distinction is based on the degree of comminution of the ingested material, which affects our

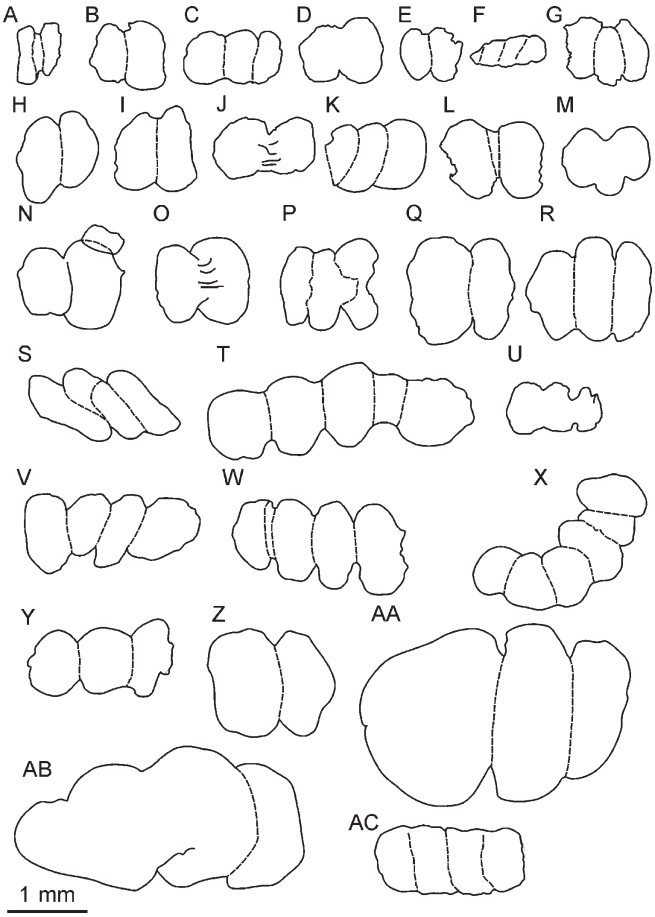

FIGURE 3—Outlines of coprolites drawn to same scale. Scale bar = 1 mm. A) NMW2012.21G.2. B) NMW2012.21G.3. C) NMW2012.21G.4. D) NMW2012.21 G.5. E) NMW2012.21G.6. F) NMW2012.21G.44. G) NMW2012.21G.7. H) NMW 2012.21G.8. I) NMW2012.21G.9. J) NMW2012.21G.10. K) NMW2012.21G.11. L) NMW2012.21G.12. M) NMW2012.21G.13. N) NMW2012.21G.14. O) NMW 2012.21G.15. P) NMW2012.21G.16. Q) NMW2012.21G.17. R) NMW2012.21G.18. S) NMW2012.21G.19. T) NMW2012.21G.20. U) NMW2012.21G.21. V) NMW 2012.21G.22. W) NMW2012.21G.1. X) NMW2012.21G.23. Y) NMW2012.21G. 24. Z) NMW2012.21G.25. AA) NMW2012.21G.26. AB) NMW2012.21G.40. AC) NMW2012.21G.41.

ability to recognize the original tissues, or its degree of compaction and homogenization. The deformation may have occurred during the growth of the original tissues, following ingestion, or during charring. In many of the less compacted examples, in addition to the regularly shaped spaces usually representing original lumina of cells/tubes, there are irregularly shaped voids which we suspect were once occupied by quartz grains which would have been dissolved during HF digestion.

Type 1.—Highly compacted content; no recognizable cells/tissues apart from unevenly thickened (banded) and smooth tubes or superficial cuticle. The cut surfaces in Figures 7A–C show small, irregularly shaped voids and occasional banded/smooth tubes. Fractured surfaces illustrate the high degree of disorganization in minute fragments and very rare examples of a limiting cuticular layer (?*Nematothallus*; Fig. 7D). Microtome sections of specimens viewed by light microscopy show homogenization of the content with some knife chattering and sections through irregularly thickened tubes (Fig. 11A).

Type 2.—Less compaction; increased number and size of voids; mostly of comminuted ± homogenized material with some cellular detail, particularly banded tubes and medullary spots. Material is highly comminuted but walls remain discrete with traces of cuticle and occasional to numerous banded tubes (Fig. 7E). Differing degrees of homogenization and voids of varying sizes are illustrated in Figure 7F. Occasional aggregations of tubes with small lumina are confirmed as medullary spots because they show detailed ultrastructure: a bilayered wall; the inner comprising a reticulum; the outer, homogeneous (Fig. 7G), as recorded in *Nematasketum* by Edwards and Axe (2012). Microtome sections show voids, homogenization, banded tubes, and aggregations of small tubes that characterize the medullary spots seen in *Prototaxites* and *Nematasketum* (Figs. 11B, C).

Type 3.—As for 2, but with occasional longer intact tubes and fragments of cuticle. Figure 7I shows a highly comminuted matrix, with both smooth and banded tubes. Cuticular fragments include *Nematothallus* (Fig. 7J), *Cosmochlaina* (Fig. 7K) together with sheets of cells (Fig. 8A). The specimen illustrated in Figure 7L resembles a section through the outermost layer of the sporangium wall in ?*Sporathylacium* and, if correct, would be the only embryophyte fragment recorded in the coprolites. The possible spores (arrowed) associated with smooth cuticle (Fig. 8B) show none of the haptotypic features that characterize embryophytes. A microtome section of specimen NMW.2012.21G.20 (National Museum Wales) shows voids, homogenization of tissues and a fragment of either a cuticle of *Nematothallus* or the remains of a single layer of cells. (Fig. 11D). The latter dominate one specimen (Figs. 11E, F).

Type 4.—Loosely consolidated contents with compacted smooth walled and irregularly thickened tubes, with occasional homogenized areas. This type is extremely rare compared with the remainder. Segmentation is less regular, but bears comparison to the preservation of tissue in some of the less regular forms described below. Tissues are somewhat disorganized and dominated by compressed, larger, thick-walled tubes, but the unevenly thickened tubes that characterize *Nematasketum* are present (Fig. 8C, D).

Nonsegmented Forms

Six specimens are united in their possession of banded tubes and comminuted material, and in lacking well-defined segmentation. Figures 9A, H show two almost cylindrical examples with similar, almost smooth surfaces (Fig. 9C)—one (Fig. 9A; 1930 µm long, 840 µm wide) with traces of oblique depressions, and the other (Fig. 9H; 1290 µm long, 1040 µm wide) looking like a fragment of the first. Their contents are very different. The second is unique among all the coprolites examined in that it shows no signs of homogenization, the bulk of it being comminuted, remarkably thin-walled tissues, with the only recognizable component being fragmented banded tubes (Figs. 9I, J). A few of the latter are directly comparable with those of *Nematasketum,* but others have much thinner sidewalls with evidence of degradation between the thickenings (Fig. 9J). By contrast, it is impossible to identify any tissues in the comminuted and compacted material in the first example (Fig. 9D), which lacks any gaps indicative of original sediment, although banded tubes are occasionally seen on the surface (Fig. 9F). A teardrop-shaped specimen (Fig. 9B) has the same surface features (Fig. 9E) and similar content, although it is slightly less compacted and has some voids (Fig. 9G). The gross morphology of specimen NMW.2012.21G.44 (Fig. 9K) more closely resembles that of spore-containing coprolites (Edwards et al., 1995), but the homogenized content, although masked by abundant pyrite, is close to the Type 1 described here (Fig. 9L). In marked contrast are the contents of specimen NMW.2012.21G.45, which is superficially less regular, with broad lobation (Fig. 10A). These are Type 4, comprising loose aggregations of wide and banded tubes, interspersed with very finely comminuted material but no small tubes (Figs. 10B, C). The latter are preserved in an almost spherical specimen dominated on one surface by smooth, wide tubes (Fig. 10D) and on fractured surfaces by masses of small tubes some showing a network of microfibrils (Figs. 10E, F)

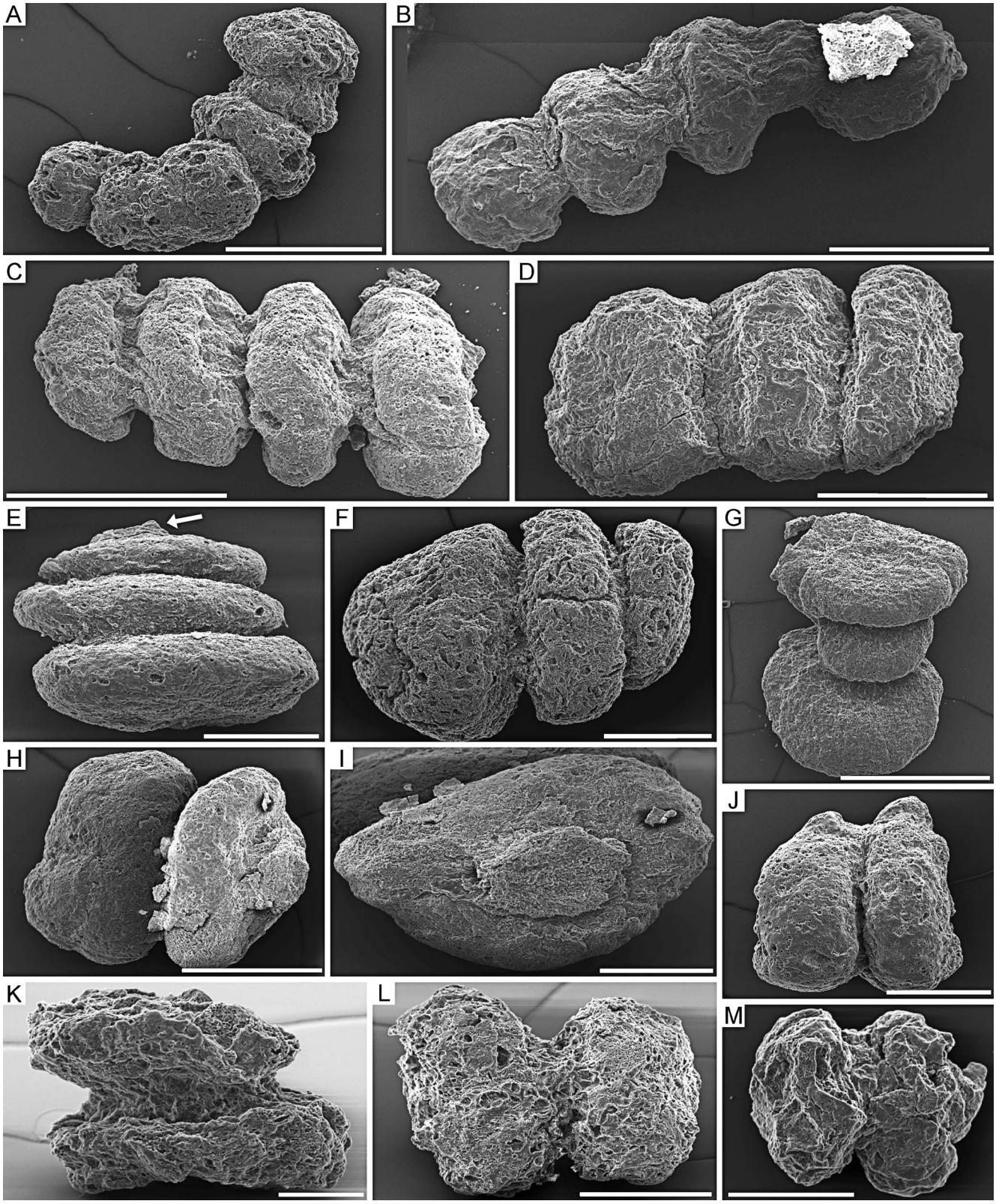

FIGURE 4—SEMs. Gross morphology of selected representatives. Scale bars = 1 mm (except where stated). A) Most segmented specimen, with irregularly shaped units and irregular surface. NMW2012.21G.23. B) Smooth surface with large particles of adhering cuticle. NMW2012.21G.20. C), D) Irregular outline on right hand edges suggest originally part of a longer coprolite. C) NMW2012.21G.1 (type). D) NMW2012.21G.4. Scale bar = 500 µm. E) Markedly flattened units and decrease in length. Arrow indicates attachment site of further unit. NMW2012.21G.11. Scale bar = 500 µm. F) Specimen exhibiting considerable variations in size and shape of individual units, with irregular surface. Note large overall size. NMW2012.21G.26. G) As for (F), but surface smooth. NMW2012.21G.27. H), I) Two units with small attachment sites, seen in face view in I. NMW2012.21G.25. (I, scale bar = 500 µm). J) Broader but short attachment between two units, with almost smooth surfaces. NMW2012.21G.9. Scale bar = 500 µm. K) More extended junctions; surfaces of discs very irregular. NMW2012.21G.2. Scale bar = 200 µm. L) As for (K) but units almost spherical. NMW2012.21G.12. Scale bar = 500 µm. M) Extremely irregular surface, largely due to folded cuticles. NMW2012.21G.6. Scale bar = 500 µm.

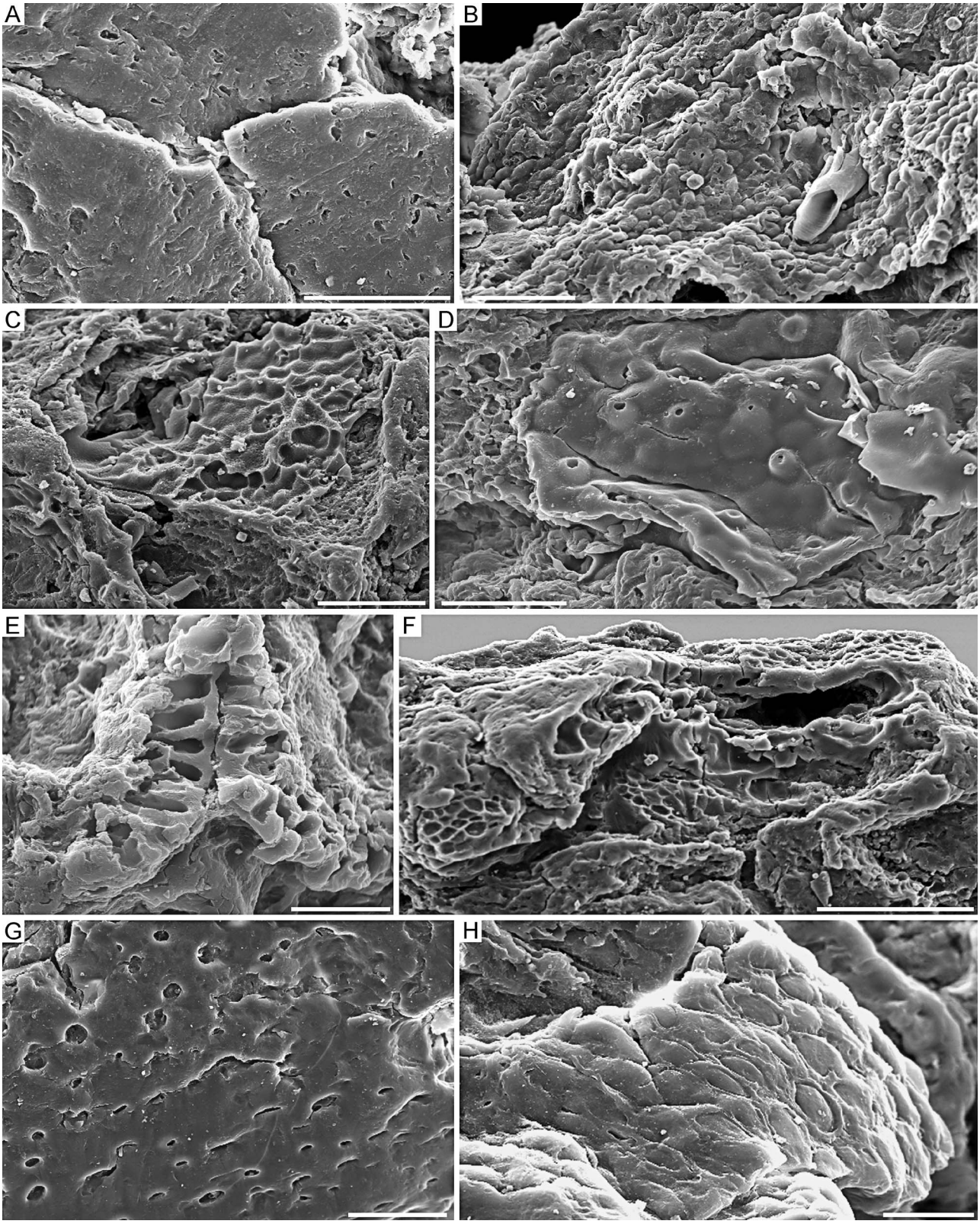

FIGURE 5—SEMs. Surface and cuticular features. Scale bars = 50 µm (except where stated). A) Smooth surface with irregular depression produced by homogenization of comminuted material. NMW2012.21G.28. B) C) Sheets of cells and adhering nonidentifiable material. NMW2012.21G.5, NMW2012.21G.29. D) Fragment of cuticle with hemispherical projections, some appearing apically perforated. NMW2012.21G.25. E) Fractured cellular layer or more likely *Nematothallus*. NMW2012.21G.2. Scale bar = 20 µm. F) Folded cuticles of predominantly *Nematothallus*. NMW2012.21G.6. Scale bar = 100 µm. G) Perforated cuticle, ?*Cosmochlaina*. NMW2012.21G.16. H) New type of cuticle with elliptical indentations. NMW2012.21G.16. Scale bar = 20 µm.

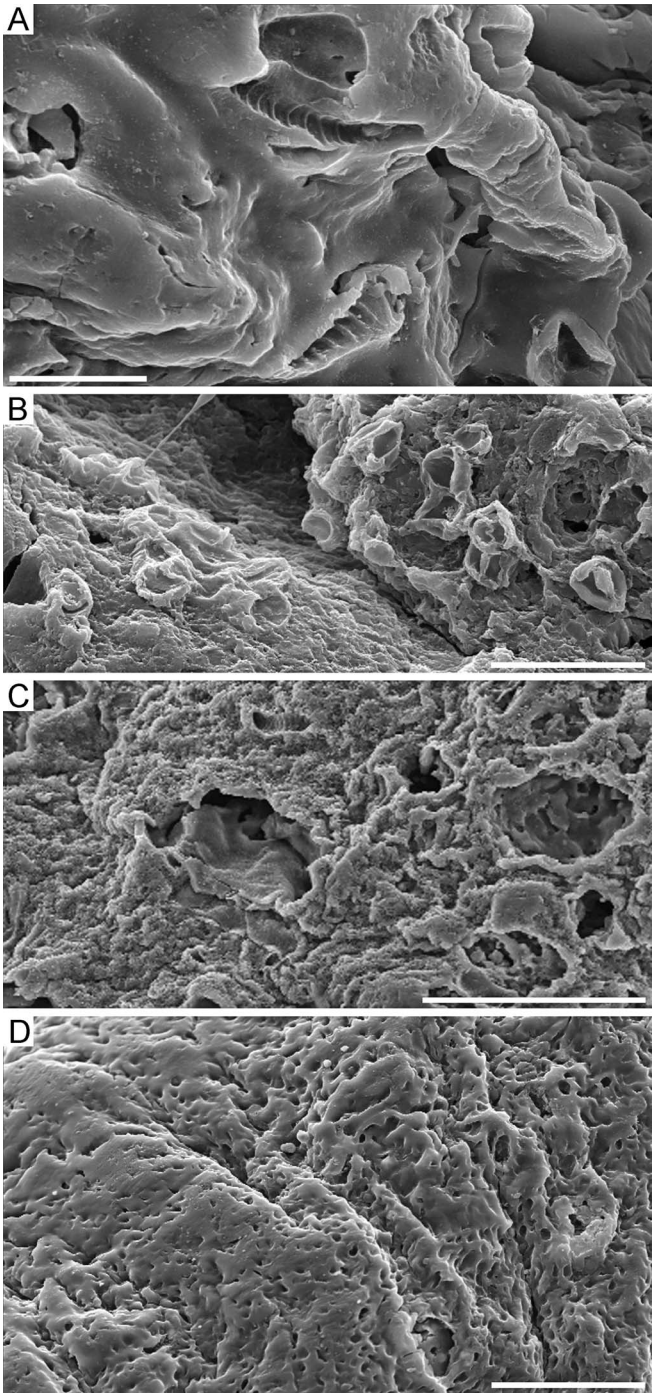

FIGURE 6—SEMs of surfaces of coprolites. A) Short lengths of longitudinally fractured banded tubes. Depressions are surface expressions of voids in homogenized tissue. NMW2012.21G.9. Scale bar = 20 µm. B) Adhering featureless spores. NMW2012.21G.30. Scale bar = 20 µm. C) Granular surface with depressions. NMW2012.21G.23. Scale bar = 100 µm. D) Irregular surface with depressions marking voids in homogenized material. NMW2012.21G.17. Scale bar = 50 µm.

IDENTIFICATION

The compacted and comminuted nature of the content of the fossils indicates that they are coprolites. No other reasonable explanation is likely, and they are clearly assignable to the *Lancifaex* complex in Habgood et al.'s (2004) ichnotaxonomic framework. Most are closest to *L. moniliforma*, erected for coprolites divided into two or more discrete, equidimensional, rounded units, except that unit shape is predominantly discoidal in our material. A couple of specimens (Figs. 4A, 9A, H, K) are morphologically similar to *L. divisa* with less discrete units, and the remainder to undivided *L. simplex* (Fig. 9B, 10D). Here (see the Appendix), we erect a new ichnospecies, *Lancifaex nematophyta* sp. nov., for the segmented forms, the species distinction being based on the discoidal nature of the units and on their content.

IDENTITY OF CONTENT

Nematasketum sp.—Although the basic construction of the tissues of *Nematasketum* Burgess & Edwards 1988, *viz.* longitudinally aligned, wide, thick-walled, and irregularly thickened tubes embedded in a matrix of a narrower thin-walled system, has not been seen in the coprolites, the frequent presence of isolated tubes, particularly of the banded form, together with medullary spots (putative sites of branching; Figs. 7G, H; 10F; 11B, C) indicates that *Nematasketum* formed a major component of the producer's diet. It is possible that the banded tubes were individual living hyphae deriving nutrients from the coprolites postexcretion (coprophagy), because they have been recorded on the surface of coeval plant organs and within decaying tissues (Edwards and Axe, 2004). This is considered unlikely here because of their frequent occurrence in fragmented and often compressed states.

Cuticles.—Most resemble *Nematothallus*, where a reticulum of flanges occurs on one surface (Lang, 1937; Edwards, 1982) and *Cosmochlaina* with perforations (Edwards, 1986). The specimen with ± circular surface depressions (Fig. 5H) is currently being studied from macerations from the same locality, where it is associated with an underlying system of tubes.

Cellular layers.—Sheets of cells have not yet been isolated from the matrix. They are similar to the superficial layer (?cortex) of stratified aggregations of tubes that are currently under investigation as the fungal components of possible lichens (work in progress in Cardiff and Zürich). One example (Fig. 7L) broadly resembles part of the sporangium wall of a ?zosterophyll, *Sporathylacium salopense* (Edwards et al., 2001, fig. 29), but better material is needed to substantiate this. This is unfortunate because it would be the only evidence for higher plants in the coprolites, resilient (undigestible) tissues of tracheophytes, e.g., cuticle with stomata, tracheids, being absent.

Palynomorphs.—These are rare small monads lacking haptotypic features.

DISCUSSION

Affinities of Coprolite Content and Early Records of Mycophagy

The construction of *Nematasketum* is very similar to that in *Prototaxites* (Burgess and Edwards, 1988; Hueber, 2001) except that the former contains banded tubes. The affinities of *Prototaxites* have been much debated (Lang, 1937; Hueber, 2001; Graham et al., 2010a, 2010b) with suggestions including algae, liverworts, lichens, and fungi (Graham et al., 2010a, 2010b; Taylor et al., 2010). The last has recently been suggested for *Nematasketum*, based on similarities with the anatomy of basidiomycote cords (Edwards and Axe, 2012). In 1937, Lang erected *Nematothallus* for cuticles and underlying complexes of tubes and, because *Prototaxites* occurred in the same Pridoli (Silurian) and Lochkovian (Devonian) rocks, concluded that both were land plants that he united in a special class, Nematophytales. *Nematasketum* and *Cosmochlaina* have since been added and a similar affinity will be proposed for the new cuticles with ± circular markings (Fig. 5H, work in progress). Thus, it is concluded that the coprolites predominantly comprised members of the nematophytalean complex which, on balance of evidence, has closest affinity with the fungi, and thus provide evidence for mycophagy. Indeed, the latter had been hypothesized for nonsegmented forms containing degraded hyphae and ?undigested tissue fragments that were earlier recorded in meandering tunnels and galleries in Upper Devonian *Prototaxites*

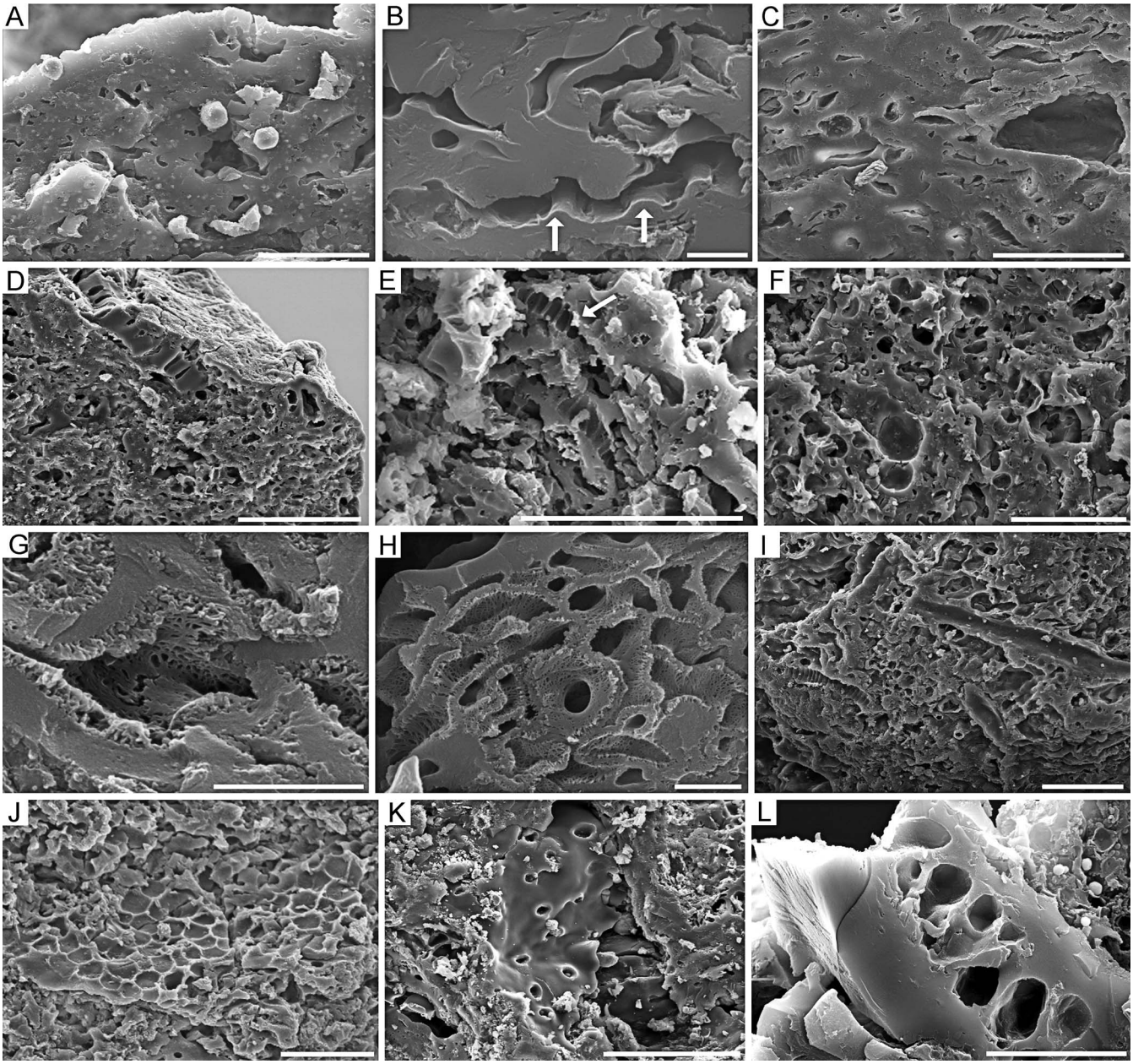

FIGURE 7—SEMs of contents of coprolites when broken open. Type I = (A–D); Type 2 = (E–G); Type 3 = (H–L). A) Fractured surface with ± complete homogenization at margin and some small voids. NMW2012.21G.11. Scale bar = 20 µm. B) Homogenization and compression with ridges of banded tube remaining (arrows). NMW2012.21G.27. Scale bar = 2 µm. C) Cut surface with occasional LS banded tubes. NMW2012.21G.24. Scale bar = 50 µm. D) Comminuted material continuous with cuticle on surface. NMW2012.21G.28. Scale bar = 100 µm. E) Loosely aggregated comminuted material with occasional banded tubes (arrow). NMW2012.21G.1 (type). Scale bar = 50 µm. F) Cut surface with variation in void size. NMW2012.21G.28. Scale bar = 50 µm. G), H) Cut surface through medullary spots with characteristic bilayered walls noted in *Nematasketum*. (G) = Type 2, NMW2012.21G.9; (H) = Type 3, NMW2012.21G.13. Scale bars = 2 µm. I) Fractured surface with smooth and banded tubes. NMW2012.21G.31. Scale bar = 50 µm. J) Fractured surface with *Nematathallus* cuticle. NMW2012.21G.25. Scale bar = 50 µm. K) Fractured surface revealing *Cosmochlaina*. NMW2012.21G.20. Scale bar = 100 µm. L) Section through ?sporangial wall of *Sporathylacium*. NMW2012.21G.2. Scale bar = 20 µm.

southworthii (Hotton et al., 1996; Labandeira, 2006a, 2006b). In contrast, the segmented coprolites described by Habgood et al. (2004) from the Pragian Rhynie Chert, contained short fragments of diverse origin including fungal spores and hyphae in addition to macerated plant fragments, plant spores, mineral grains, and amorphous (?homogenized) organic matter. Nematophytes were not recorded. The earliest equivocal evidence for mycophagy on land comes from upper Silurian ovoid, cylindrical, heterogeneous bodies composed of hyphal fragments interpreted as the coprolites produced by mycophagous microarthropods (Sherwood-Pike and Gray, 1985). The very different morphology of the segmented and nonsegmented coprolites suggests that by the Early Devonian at least two types of animals were selectively mycophagous.

Identification of the Consumers

Early Devonian terrestrial animals are mostly carnivores, including arachnids such as scorpions, trigonotarbids, Opiliones and pseudoscorpions, as well as centipedes (Shear et al., 1984; Shear and Selden, 2001; Dunlop et al., 2004). The detritivorous and parasitic fauna consists of nematodes (Poinar et al., 2008), mites (Subías and Arillo, 2002; Schaefer et al., 2010), millipedes (including arthropleurids) (Shear

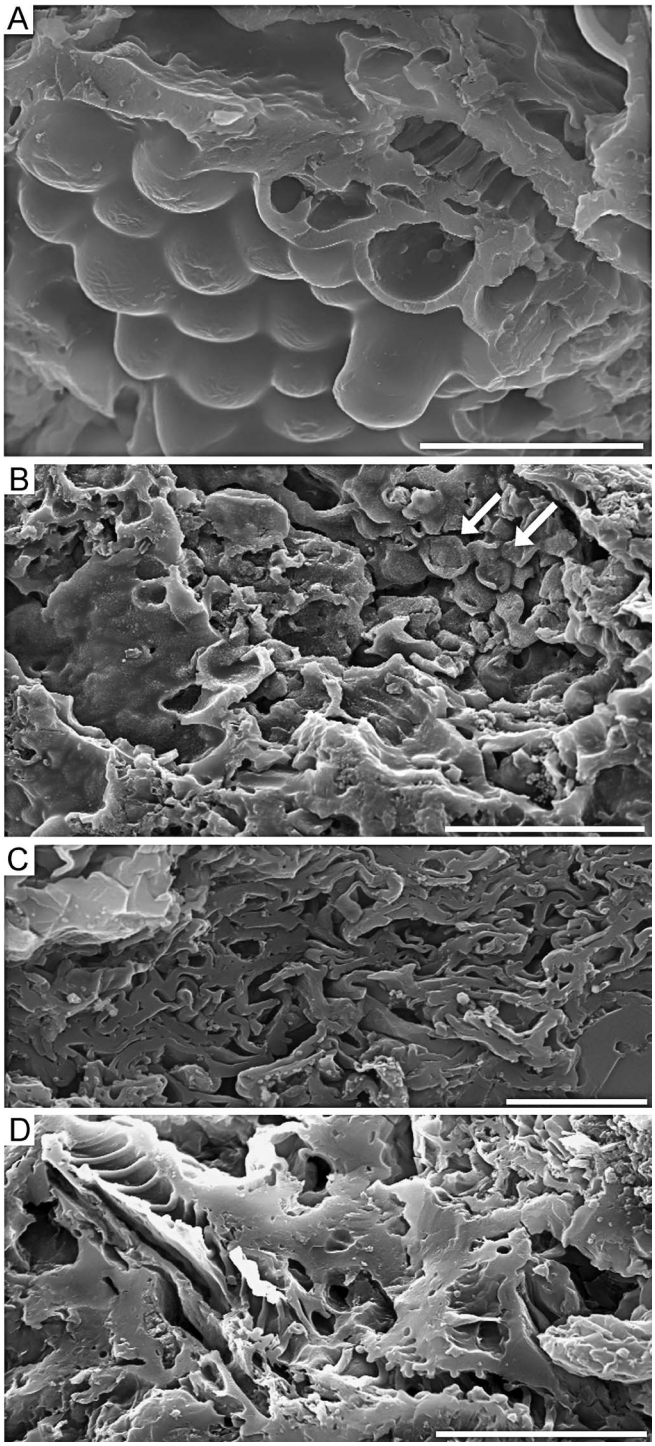

FIGURE 8—SEMs of coprolite content. Type 3 = (A, B); Type 4 = (C, D). A) Fractured surface with layer of bulbous cells and LS banded tube. NMW2012.21G.13. Scale bar = 20 μm. B) Fragmented surface with cuticles and cluster of possible spores (arrows). NMW2012.21G.26. Scale bar = 50 μm. C), D) NMW2012.21G.32. Fractured surfaces with compressed, free, wide tubes (C, scale bar = 5 μm) and LS banded tube (D, scale bar = 20 μm).

and Edgecombe, 2010), and collembolans (Whalley and Jarzembowski, 1981; Greenslade and Whalley, 1986; Labandeira et al., 1988), one of which may have been the producer of the coprolites.

Based on our recent work on *Nematasketum* (Edwards and Axe, 2012) and Hueber's conclusions on *Prototaxites* (Hueber, 2001) showing that these organisms were fungi, we make the assumption that the animals that produced the coprolites were mycetobionts. In the absence of direct evidence of megafossils with gut contents, the producer(s) of coprolites can be deduced from size, shape, content, and consistent associations of the coprolites. Based on the size of the coprolites, myriapods seem the most logical because Collembola range in body size from about 1 to 5 mm (Poole, 1959; Hopkin, 1997), and most mites show a similar order of body size: 0.8 to 1 mm (Babel, 1975). Both groups, therefore, are smaller in body size than the coprolites. Millipedes, on the other hand, range from a body thickness of 100 μm upward to more than 200,000 μm, and are, of course, many times longer than their thickness.

The earliest terrestrial animal fossils known are zosterogrammid and archipolypod millipedes from the middle Silurian of Scotland (Wilson and Anderson, 2004; Wilson, 2005). Supposed millipede burrows in Ordovician rocks of Pennsylvania (Retallack, 2001) have been comprehensively disproven (Shear and Edgecombe, 2010; Davies et al., 2010). Arthropleurid millipedes are known from the upper Silurian of England (Shear and Selden, 1995). So, by Devonian times, a diverse millipede fauna was present in terrestrial ecosystems (Shear and Edgecombe, 2010), including arthropleurids (Shear and Selden, 1995), archipolypods (Wilson and Anderson, 2004; Wilson, 2005; Wilson et al., 2005), and helminthomorphs (Wilson, 2006).

Feeding Habits of the Consumers

We have no direct evidence here whether the coprolite producers were detritivores or consumers of living tissues. However, Hotton et al. (1996) mentioned wound responses, associated with the galleries in *Prototaxites*, interpreted as created by fungivores. They gave no descriptions of the *Prototaxites*-filled coprolites in the galleries, but we conclude that they were probably different from the producers, because boring animals would have occupied a very specialized niche and hence were very unlikely to have consumed superficial coverings such as cuticles.

The nature of the material in the coprolites suggests that the consumer probably broke its food into very small fragments on mastication, while the degree of compaction may be indicative of residence time in the gut. Segmentation suggests presence of feeding episodes.

Homogenization/compaction prevents satisfactory assessment of selective digestion of the tissues of *Nematasketum*. Banded tubes and cuticles are the most common identifiable elements in the coprolites, followed by wider tubes and medullary spots. The narrow tubes that are a major component of *Nematasketum* are not visible, but this could be due to their greater susceptibility to compaction than the remaining elements (or less likely, greater palatibility and/or digestibility). Apart from homogenization, there is little evidence of wall alteration. Exceptions include the four specimens illustrated in Figures 7G, H; 9J, 10F, where the internal surfaces of banded and smooth tubes show unevenness. However, such data should be treated with caution as the specimens have been exposed to concentrated nitric acid. On the other hand, the majority of specimens so treated show no signs of corrosion.

Consequent on our conclusion that the *Nematophytales* had fungal affinities, we make the assumption that the cell walls of the ingested material contained chitin (noncellulosic β glucan) macromolecules that are nutritionally inaccessible to animals. We therefore propose that, as is the case of saprotrophic (detritivore) invertebrates such as millipedes, mites and collembolans, the consumers extracted the soluble fraction of the tissues (Martin, 1979) and possibly broke down storage material (Norton, 1985), but more likely utilized that made available by microorganisms. They could also have digested the microorganisms themselves, which are usually ubiquitous in decaying material (Christiansen, 1964). It is also possible that if the food were still living on ingestion, its own enzymes, including chitinases and glucanases, that were compartmentalized and isolated in the living organism, could have been employed to facilitate more efficient digestion (Poole, 1959; Martin, 1979; Norton, 1985).

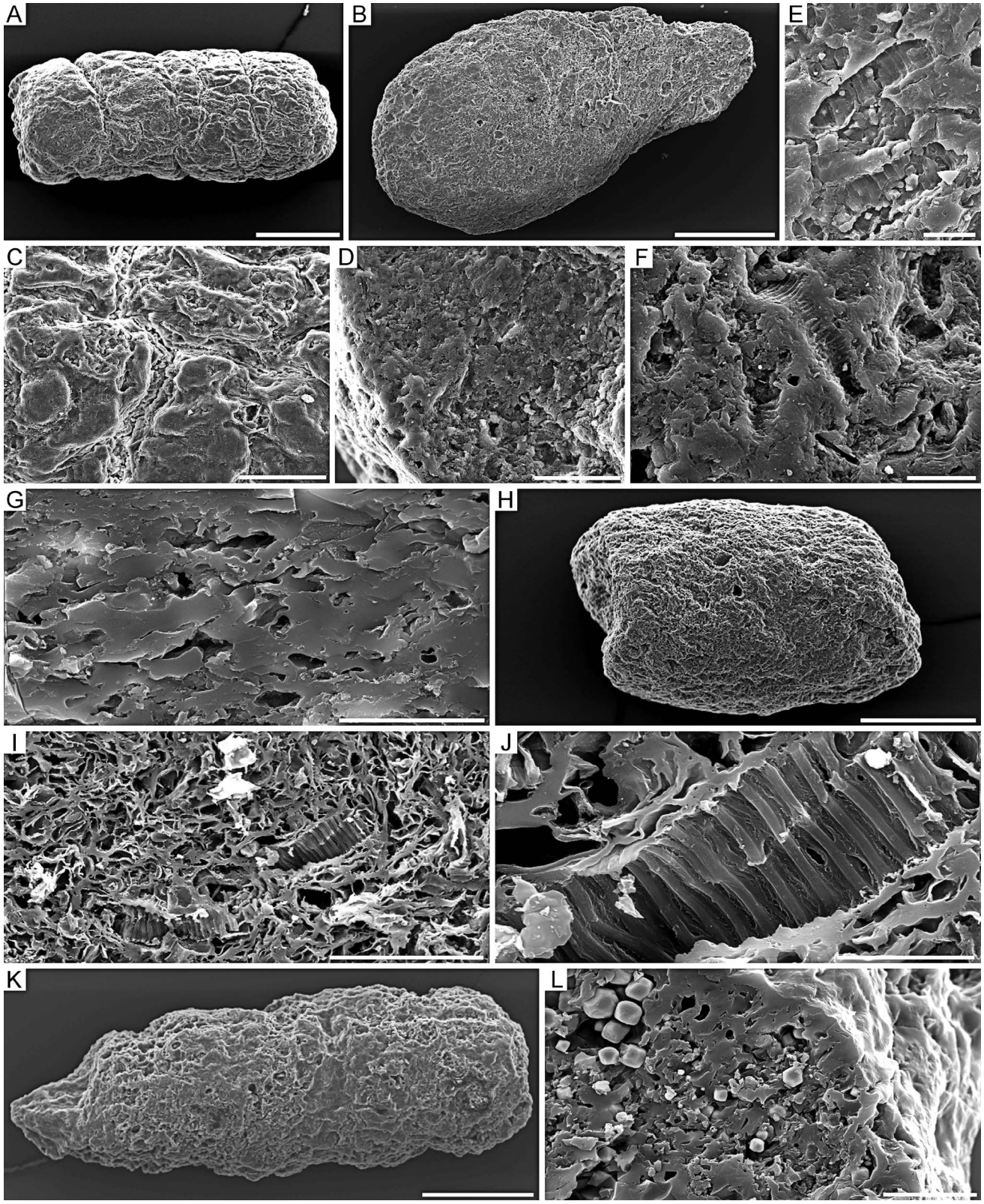

FIGURE 9—SEMs of nonsegmented coprolites. A) Cylindrical specimen before fracturing. Note oblique depressions. NMW2012.21G.41. Scale bar = 500 μm. B) Intact specimen. NMW2012.21G.42. Scale bar = 500 μm. C) Surface of (A) magnified. Scale bar = 100 μm. D) Fractured surface of (A) with compacted homogenized content (Type 1). Scale bar = 50 μm. E) Imprints of banded tubes on surface of (B). Scale bar = 20 μm. F) Imprints of banded tubes on surface of (A). Scale bar = 20 μm. G) Cut surface through (B), tissues homogenized, but small voids present. Scale bar = 20 μm. H) Intact specimen. NMW2012.21G.43. Scale bar = 500 μm. I) Fracture through (H) showing unique composition of thin discrete walls and banded tubes (Type 4). Scale bar = 50 μm. J) Longitudinally fractured banded tube with breakdown of wall between thickenings magnified from (I). Scale bar = 10 μm. K) Intact specimen with hint of spiraling and tapering end. NMW2012.21G.44. Scale bar = 200 μm. L) Fracture through (K) showing continuous margin and comminuted homogenized contents. Scale bar = 20 μm.

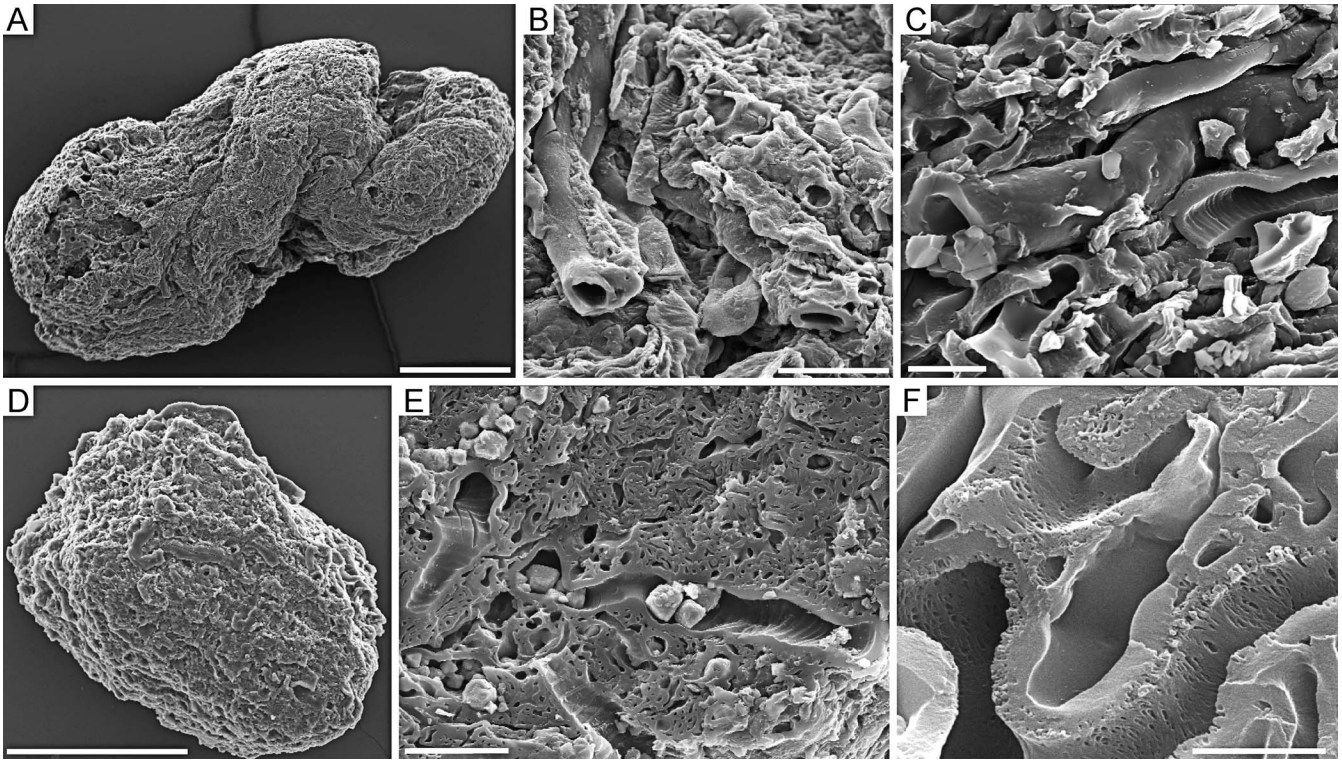

FIGURE 10—SEMs of nonsegmented coprolites. A) Irregular shape with possible terminal disc. NMW2012.21G.45. Scale bar = 500 µm. B) Surface of (A) revealing unconsolidated smooth tubes (Type 4). Scale bar = 50 µm. C) Fractured surface of (A) revealing unconsolidated smooth and banded tubes (Type 4). Scale bar = 20 µm. D) Fragment of probable coprolite with conspicuous isolated smooth tubes on one surface. NMW2012.21G.46. Scale bar = 200 µm. E) Section through a medullary spot from (D) comprising fused small tubes and occasional banded examples. Scale bar = 20 µm. F) Closeup of small tubes from (E) with bilayered wall noted in *Nematasketum*. Scale bar = 2 µm.

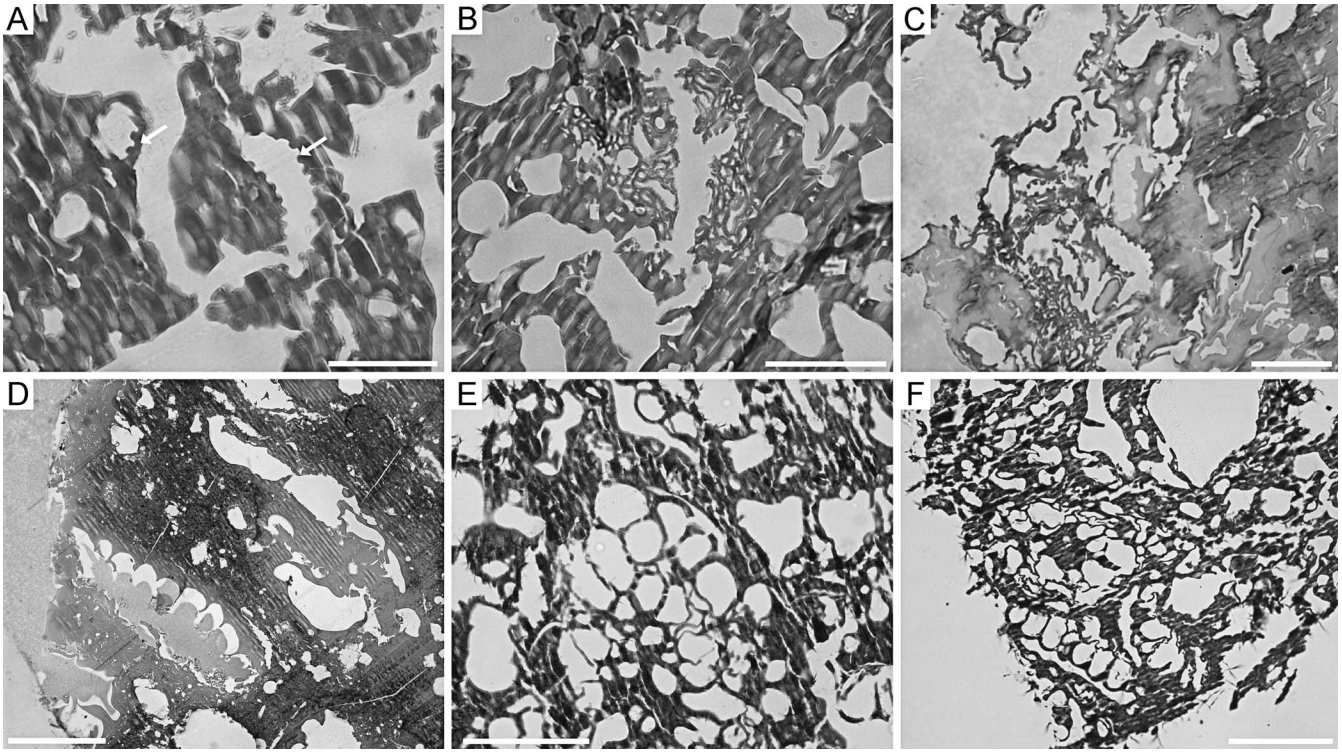

FIGURE 11—Light micrographs of resin-embedded microtome sections through coprolites. Scale bars = 20 µm. A) Complete homogenization of tissue, apart from banded tubes (arrows). Large jagged spaces were produced during sectioning. NMW2012.21G.4 (Type 1). B) Homogenized tissue with smaller voids and remains of a medullary spot. NMW2012.21G.9 (Type 2). C) Similar to (B), but banded tubes also present and fewer voids. NMW2012.21G.24 (Type 2). D) Homogenized tissue, irregular shaped voids and TS *Nematothallus*. NMW2012.21G.20 (Type 3). E), F) Limited homogenization, irregular voids, sections through tubes, *Nematothallus* and sheets of cells. NMW2012.21G.13 (Type 3).

We are aware that the contents of feces represent elements of the diet that were not the major energy source, the latter having been completely consumed during the digestion process (Christiansen, 1964). However, the consistency of the composition of the coprolites suggests selective feeding on nematophytaleans, and their size suggests consumption by millipedes, although relatively little is known on mycophagy in that group. Some millipedes are mycophagous (e.g., Bultman and Mathews, 1996; Crowther and A'Bear, 2012) and viable fungal spores can be dispersed by passing through millipede guts (Lilleskov and Bruns, 2005). Little is known about modern millipede fecal pellets; in *Glomeris,* the pellets are smooth, truncated cones approximately 2×0.5–1 mm (Nicholson et al., 1966): about the same size as the fossil fecal pellets. However, we know nothing about the size and shape of fecal pellets from the extinct millipede groups such as arthropleurids. These animals ranged in size from the minute, Devonian *Microdecemplex* (<10 mm body length, Wilson and Shear, 2000), through midsized, Silurian and Devonian *Eoarthropleura* (>20 mm body length, Shear and Selden, 1995), to giant Carboniferous *Arthropleura* (>2 m, Shear and Edgecombe, 2010). So, Siluro-Devonian arthropleurids were at least about the right size to have produced feces the same size as the fossil ones. What is known about arthropleurid feeding is that the Carboniferous forms were likely detritivorous (Rolfe and Ingham, 1967), as are most modern millipedes.

Most of the data on digestion comes from soil microarthropods such as mites and collembolans (Knight and Angel, 1967; Walter, 1988; Schneider et al., 2005; Bandyopadhyay et al., 2009). Ongoing *in vitro* studies in Cardiff by Lynne Boddy and co-workers on the interactions between millipedes and isopods (woodlice) and fungal mycelia (e.g., Crowther and A'Bear, 2012, and references therein) are providing an opportunity to analyze the fecal pellets of these animals when fed solely on fungi. To date, they show feces of appropriate size, but discrete shapes (millipedes ellipsoidal, isopods with distinctive groove) and ingestion of hyphae as well as mineral matter in the compressed soil substrate. The walls of the fungi show no evidence of degradation. Such experiments will now be extended to feeding the arthropods on cords similar in size to those we have described for *Nematasketum* (Edwards and Axe, 2012) and *in vivo* observations.

CONCLUSIONS

These coprolites show that the producers, probably millipedes, were showing selective feeding on nematophytes, and not on either vegetative parts or sporangia of higher plants, as evidenced by the coprolite contents. There is a growing body of evidence that Nematophytales have fungal affinities, although it has been impossible hitherto to allocate them with confidence to extant taxa. Thus, we conclude that these remains represent the feces of mycophagous animals, and are the earliest evidence of mycophagy in the fossil record in a terrestrial context.

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TABLE 1—Data and comments on coprolites. Key to table: segmented and nonsegmented forms. Numbers refer to columns. (1) ± segments; (2) Number of segments; (3) Maximum length (μm); (4) Minimum–maximum width (μm); (5) Surface: smooth = S, intermediate = I, uneven = U; (6) Type based on content; (7) ± banded tubes; (8) Segments: discoidal = D, spherical = S; (9) Attachments: broad = B, limited = L; (10) Uniformity of segments ±.

Museum number	1	2	3 (μm)	4 (μm)	5	6	7	Comments	8	9	10	Figures
Segmented forms												
NMW2012.21G.4	+	3	1270	690–705	S/I	1	+	Numerous banded tubes	D	B	+	3C,4D,11A
NMW2012.21G.8	+	2	2160	840–1140	S	1	+	Partial compression	D	L	+	3H
NMW2012.21G.10	+	2	1270	667–712	U	1	+	Partial compression	S	B	+	3J
NMW2012.21G.11	+	3	1200	800, 920	S/I	1	−	Surface smooth with craters	D	B	+	3K,4E,7A
NMW2012.21G.17	+	2	1600	1520, 1630	S	1	+	Continuous outer homogeneous layer	D	L	−	3Q,6D
NMW2012.21G.27	+	3	2000	790–1290	S	1	+	Very irregular widths	D	B	−	4G,7B
NMW2012.21G.33	+	3	1160	1010–1160	S	1	+	Surface with flakey cuticle	D	B	+	
NMW2012.21G.34	+	?3	c. 1000	800–875	S	1	−	Smooth with craters	D	B	±	
NMW2012.21G.1	+	4	3800	830–1000	S/I	2	+		D	L-B	+	3W,4C,7E
NMW2012.21G.9	+	2	955	455, 500	S	2	+	Adhering masses, one contaminant	D	B	−	3I,4J,6A,7G,11B
NMW2012.21G.14	+	2	1300	235, 300	S/I	2	+	Adhering masses, one contaminant	D	B	−	3N
NMW2012.21G.15	+	2	1160	990–1150	S	2	+	Cuticles on surface	D	B	−	3O
NMW2012.21G.19	+	3	1500	350	S/I	2	+	Lots of banded tubes	D	B	+	3S
NMW2012.21G.21	+	3	1180	340–473	S	2	−	Abundant pyrite	S	B	+	3U
NMW2012.21G.24	+	3	1900	830–1000	I	2	+	Numerous banded tubes in comminuted matrix	D/S	B	±	3Y,7C,11C
NMW2012.21G.28	+	2	1250	1000–1180	S	2	?	Surface + cuticle	D	?	−	5A,7D,7F
NMW2012.21G.30	?	?1	-	910 diam.	I	2	+	Odd shape (single disc plus fragments), spores on surface	D	n/a	n/a	6B
NMW2012.21G.35	+	2	1120	370	S	2	+			L	+	
NMW2012.21G.36	+	2	?	640, 950	I	2	−	Specimen obliquely flattened with overlapping discs	D	B	−	
NMW2012.21G.37	+	?3	1270	1017–1142	I	?2	−	Cosmochlaina plus undescribed cuticle	D	B	−	
NMW2012.21G.2	+	2	490	630, 695	U	3	−	?with Sporathylacium?	D	B	+	3A,4K,5E,7L
NMW2012.21G.5	+	2	1060	720, 860	U	3	+	Large void on surface	D	B	−	3D,5B
NMW2012.21G.6	+	2	850	650, 715	U	3	−		D	B	+	3E,4M,5F
NMW2012.21G.7	+	3	960	245–260	U	3	−	Not broken up	D	B	−	3G
NMW2012.21G.12	+	2	1170	970–1000	I	3	+	Nematothallus cuticle extends over junction between segments	D/S	B	+	3L,4L
NMW2012.21G.13	+	?3	1080	235, 300		3	+	Bulbous cell layers	D/S	B	−	3M,7H,8A,11E–F
NMW2012.21G.16	+	3	1270	1020–440	I	3	−	New cuticle and Cosmochlaina and homogenized areas	D	B	−	3P,5G–H
NMW2012.21G.18	+	3	1550	1130–1320	S	3	−	Nematothallus	D/S	L	−	3R
NMW2012.21G.20	+	?5	3800	860–1030	S	3	−	Perforated cuticle	± S	B	−	3T,4B,7K,11D
NMW2012.21G.22	+	4	2130	755–1000	U	3	+	Nice Nematothallus	D/S	B	−	3V
NMW2012.21G.23	+	?6	2600	450–870	U	3	+	Unusual surface	D/S	B	−	3X,4A,6C
NMW2012.21G.25	+	2	1550	1300–1350	S	3	−	Good Nematothallus, craters	D/S	L	+	3Z,4H–I,5D,7J
NMW2012.21G.26	+	3	3400	1800–2280	I	3	+	Comminuted material + cells	D/S	B	−	3AA,4F,8B
NMW2012.21G.29	+	?2+	1700	1480, 1600	I	3	?	Cuticles and cellular sheets on surface	D	B	−	5C

TABLE 1—Continued.

Museum number	1	2	3 (µm)	4 (µm)	5	6	7	Comments	8	9	10	Figures
NMW2012.21G.31	+	?3	2270	1600	S	3	+	Irregularly shaped lobe	D/?	B	–	7I
NMW2012.21G.38	+	2	1060	1303, 1340	S	3	+	Abundant tubes	D	B	+	
NMW2012.21G.40	+	4	3570	1250–1810	–	3	–	Nematothallus, present; spores on surface; segmentation less distinct	S	B	–	3AB
NMW2012.21G.32	+	?3	1070	500	U	4	+	Cuticles and tubes	D	B	–	8C–D
NMW2012.21G.3	+	2	1060	720, 860	S	?	–	Numerous cuticles on surface	D	B	–	3B
NMW2012.21G.39	+	2	?	1400	S	?		Overlapping discs	?	?	?	
Nonsegmented forms												
NMW2012.21G.41	–	n/a	1930	840	I	1	+	Cylindrical, ?oblique	n/a	n/a	n/a	3AC,9A,9C–D,9F
NMW2012.21G.42	–	n/a	2020	1125	S	1	+	Pear shaped	n/a	n/a	n/a	9B,9E,9G
NMW2012.21G.46	–	n/a	460	260	U	1	+	Conspicuous smooth and banded tubes and detritus	n/a	n/a	n/a	10D–F
NMW2012.21G.44	–	n/a	935	355	I	2	–		n/a	n/a	n/a	3F,9K–L
NMW2012.21G.43	–	n/a	1290	1040	S	4	+	Unique contents, very flakey	n/a	n/a	n/a	9H–J
NMW2012.21G.45	?	?	2330	1160	U	4	+	Very unusual: isolated tubes	n/a	n/a	n/a	10A–C

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APPENDIX
ICHNOTAXONOMY

Lancifaex Habgood, Hass, & Kerp, 2004

Lancifaex nematophyta Edwards, Selden, & Axe, ichsp. nov.

Etymology.—After the common component of the coprolite: Nematophytales.

Diagnosis.—Coprolite divided into two or more discrete, predominantly discoidal units composed of nematophyte remains. *L. nematophyta* differs from other species of *Lancifaex* based on the discoidal nature of the units and on their content which, in other species, does not include nematophytes.

Holotype.—NMW2012.21G.1. Figures 3W, 4C, 7E. Specimens are deposited at the Department of Geology, National Museum Wales, Cardiff.

Locality and Stratigraphy.—Stream section to the north of Brown Clee Hill, Shropshire; *micrornatus-newportensis* Sporomorph Assemblage Biozone, in the lower part of the Ditton Group, Lochkovian (Lower Devonian).

Description.—Specimens consist of 2–6 discrete units, commonly laterally compressed, discoidal structures (shorter forms possibly originally longer and lost units). Total length <3800 μm; width 235–2280 μm generally constant along length. Surfaces smooth with occasional small depressions; some less regular deeper depressions and occasional smooth areas. Few specimens show extremely irregular topography comprising sheets of cells and patches of cuticles. Content *Nematosketum* tubes, *Nematothallus* and *Cosmochlaina* cuticles, unidentified cellular layers.

Distribution.—Known only from the type locality.