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Evidence for an early terrestrial food web: coprolites from the Early Devonian Rhynie chert

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ABSTRACT: Fossils in the Pragian Rhynie cherts, Aberdeenshire, Scotland, are preserved with exquisite cellular detail, and provide much information on Early Devonian terrestrial and freshwater ecosystems. The fossils include abundant and diverse coprolites which demonstrate the existence of consumers differing in life-habit and diet. The coprolites are small (0.5–3 mm) and diverse in morphology and content, including groups of amorphous coprolites as well as coprolites with identifiable, particulate content. The present authors define three new ichnogenera to accommodate these coprolites:

- *Lancifaex* encompasses elongate coprolites with particulate content, and includes three ichnospecies, distinguished on morphology, *L. simplex*, *L. divisa* and *L. moniliforma*.
- *Rotundafaex* encompasses rotund coprolites with particulate content, and includes a single ichnospecies, *R. aggregata*.
- *Bacillafaex* encompasses rod-shaped coprolites with amorphous content, and includes two ichnospecies, distinguished on size, *B. constipatus* and *B. mina*.

Typically, plant spores do not dominate the content of these coprolites, but the population does include some spore-rich coprolites. The presence of spore-rich coprolites in this diverse assemblage adds evidence to the debate on spore-feeding as a nutritional strategy in early terrestrial ecosystems. The authors conclude that the coprolites described here indicate at least four types of consumer including detritivores and herbivores. Spore-rich coprolites might suggest sporivory; however, comparison with the faeces of modern millipedes demonstrates that they might equally well be the product of detritivores. The continuum observed here between spore-rich and spore-poor coprolites implies that, in this assemblage, spore-rich coprolites do not constitute a distinct group. Rather, they are part of a group of elongate, ellipsoidal coprolites with heterogeneous content that includes, at one extreme, coprolites which lack plant spores, and at the other, coprolites which contain abundant plant spores. Most coprolites in this group fall somewhere between the two extremes.

KEY WORDS: detritivory, ecosystems, energy-cycling, plant-animal interactions, sporivory.

The Rhynie chert is remarkable in that it provides some of the earliest unequivocal evidence for terrestrial ecosystems; its flora and fauna are well preserved, and contribute significantly to our knowledge and understanding of Early Devonian biotas. As well as body fossils, the chert preserves numerous small (<3 mm long) and diverse coprolites. Although the body fossils are a more common subject of study, the assemblage of coprolites is equally informative to an understanding of Early Devonian terrestrial and freshwater ecosystems.

During the Early Devonian, the Old Red Sandstone continent supported geographically varied floral communities of rhyniophytes, rhyniophytoids and zosterophylls (Powell *et al.* 2000). The fauna is dominated by arthropods (Trewin 1996; Anderson & Trewin 2003) and less geographical variation is evident.

Currently, we know much less of the food webs and ecosystems of the Old Red Sandstone continent than we do about its floral and faunal components. Our understanding comes largely from the functional morphology of arthropods (Rolfe 1980; Shear & Selden 2001; Anderson & Trewin 2003), plant wounds (Kevan *et al.* 1975), reports of coprolites from the Early Devonian (Edwards *et al.* 1995; Anderson & Trewin 2003), and most recently, the gut contents of the arthropod *Leverhulmia* from the Rhynie chert (Anderson & Trewin 2003). Previous studies have concluded variously that terrestrial Early Devonian food webs were dominated by predators, that they lacked herbivores, that herbivores existed and included 'piercing and sucking' herbivores (Kevan *et al.* 1975; Banks & Colthart 1993) and spore-feeders (Labandeira 1998), and that spore-feeders were a distinct and important functional feeding group (Chaloner 1976; Scott *et al.* 1985, 1992; Labandeira 1998; Collinson 1999). The assemblage of coprolites described here contributes new evidence for the nature of early terrestrial food webs that does not corroborate all of these assertions.

The present authors report a diverse assemblage of coprolites from the Rhynie cherts and place the fossils in an ichnotaxonomical framework. They examine the evidence for an early terrestrial food web and, with the aid of some modern analogues, consider the life-habits of the consumers which produced the coprolites and the possibility that spore-rich coprolites do not necessarily indicate a functional spore-feeding group.

1. The geological setting

The Rhynie chert occurs in discrete units of chert lenses within the fluvial, lacustrine and terrestrial lithologies (shales and sandstones) of the Dryden Flags Formation (Rice *et al.* 2002). The cherts are interpreted as deposits from siliceous hot springs in an area of fluvial and lacustrine sedimentation (Trewin 1994; Rice *et al.* 2002). The nearby Windyfield cherts are concluded to be near contemporaneous (Anderson &

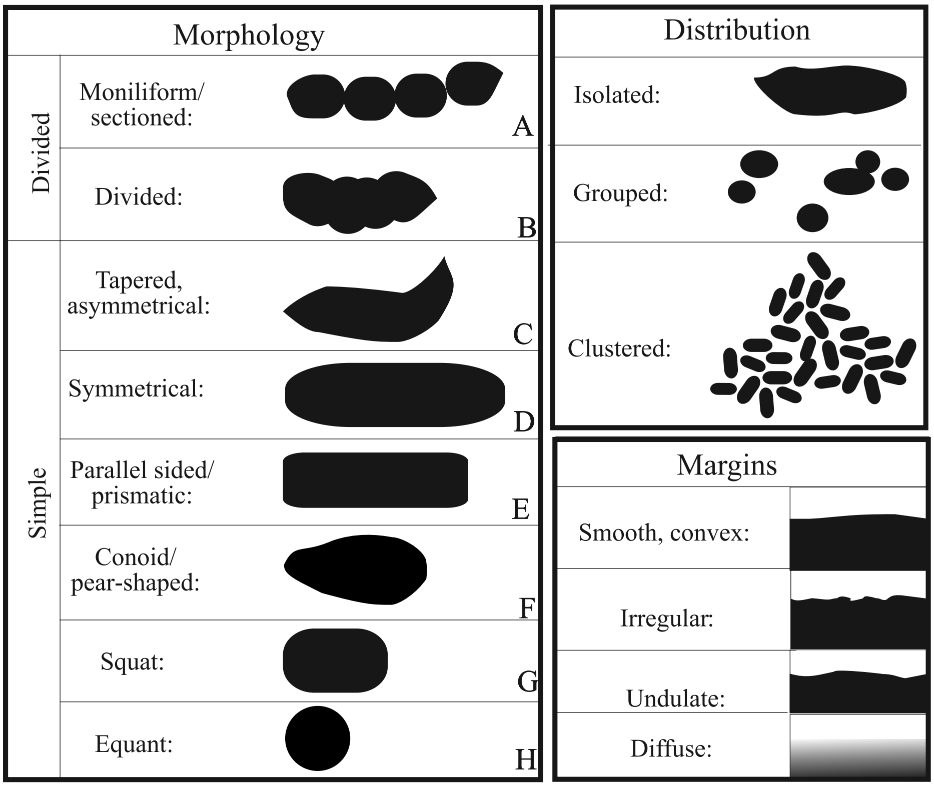


Figure 1 Variation in coprolites and terms used in their description.

Trewin 2003) and are associated with volcanic tuffs. Isotopic dating and palynological evidence place the cherts in the Pragian (Rice *et al.* 1995; Anderson & Trewin 2003; Rice & Ashcroft 2004). The Rhynie and Windyfield cherts have provided much evidence for the arthropods and plants present in Early Devonian terrestrial and freshwater ecosystems, and for plant–animal interactions (Powell *et al.* 2000; Anderson & Trewin 2003).

2. Material and methods

Like the flora and fauna preserved in the Rhynie chert, the faecal remains are silicified and most effectively examined in thin-section using both reflected and transmitted light microscopy; oil-immersion was used at high magnifications. Thin-sections are up to 1 mm thick. The material described here originates from loose blocks of the Rhynie chert collected as float and housed at Münster, Germany (prepared by Hagen Hass), and from the Lyon collection housed at the Cardiff University Department of Earth Sciences, Cardiff, Wales. Specimens referenced here are identified by thin-section slide number. All referenced thin-sections are housed at Münster, and holotypes are identified within the thin-sections by an arrow. Cherts in which coprolites have been recorded also contain abundant plant fossils and rarer arthropod fossils. However, this association is biased; cherts rich in plant fossils are preferentially sectioned and studied.

The coprolites described in this study occur in *c.* 100 thin-sections taken from 11 blocks of chert, and are abundant within many individual slides; 202 coprolites where included in this study. The coprolites described here come from isolated blocks of chert; thus, nothing is known of their original distribution within the sequence of chert beds.

3. The fossils

Coprolites have been noted to be concentrated at specific horizons in the Windyfield chert (Anderson & Trewin 2003) and are common in the Rhynie chert. These coprolites are dispersed through the chert rather than concentrated in bands or lenses; they are most abundant or most recognisable among plant axes in cherts where plant preservation is good. The context and nature of coprolites varies both between and within blocks. The coprolites are diverse in content and morphology, and range in maximum length between 0·5 and 3 mm. Figure 1 illustrates the terminology used in describing their morphology and distribution.

The coprolites preserved in the Rhynie chert fall into discrete morphological groups which form the basis for an ichnotaxonomical system defined in section 4:

(1) group A: coprolites with curved margins and heterogeneous content (Figs 2–5); and
(2) group B: coprolites with straight, smooth and parallel margins and homogeneous content (Fig. 6).

The latter group is less diverse, but comprises two clearly distinct forms on the basis of size and context.

3.1. Group A: coprolites with curved margins

This group comprises coprolites with curved margins and heterogeneous content, and encompasses coprolites diverse in morphology, content and context (Figs 2–5). Particles within the coprolites are recognisable and often identifiable; coprolite content is taxonomically diverse, as well as varied in particle size and degradation. For the group as a whole, content includes plant tissues and spores, mineral grains, amorphous organic matter, unidentifiable organic grains, fungal spores and hyphae, bacteria, and (rarely) undulate membranes most similar in appearance to arthropod membranes (Fig. 2F). The mineral grains are abraded quartz grains and are interpreted to be sedimentary in origin. Individual coprolites differ in content; in some, content is diverse, and in others, it is dominated by a single type of particle; for example, plant spores, degraded organic matter or membranes.

Coprolites from this group commonly contain plant spores, but relatively few (*c.* 8%) are spore-dominated (with greater than 80% of the content accounted for by spores). The spores

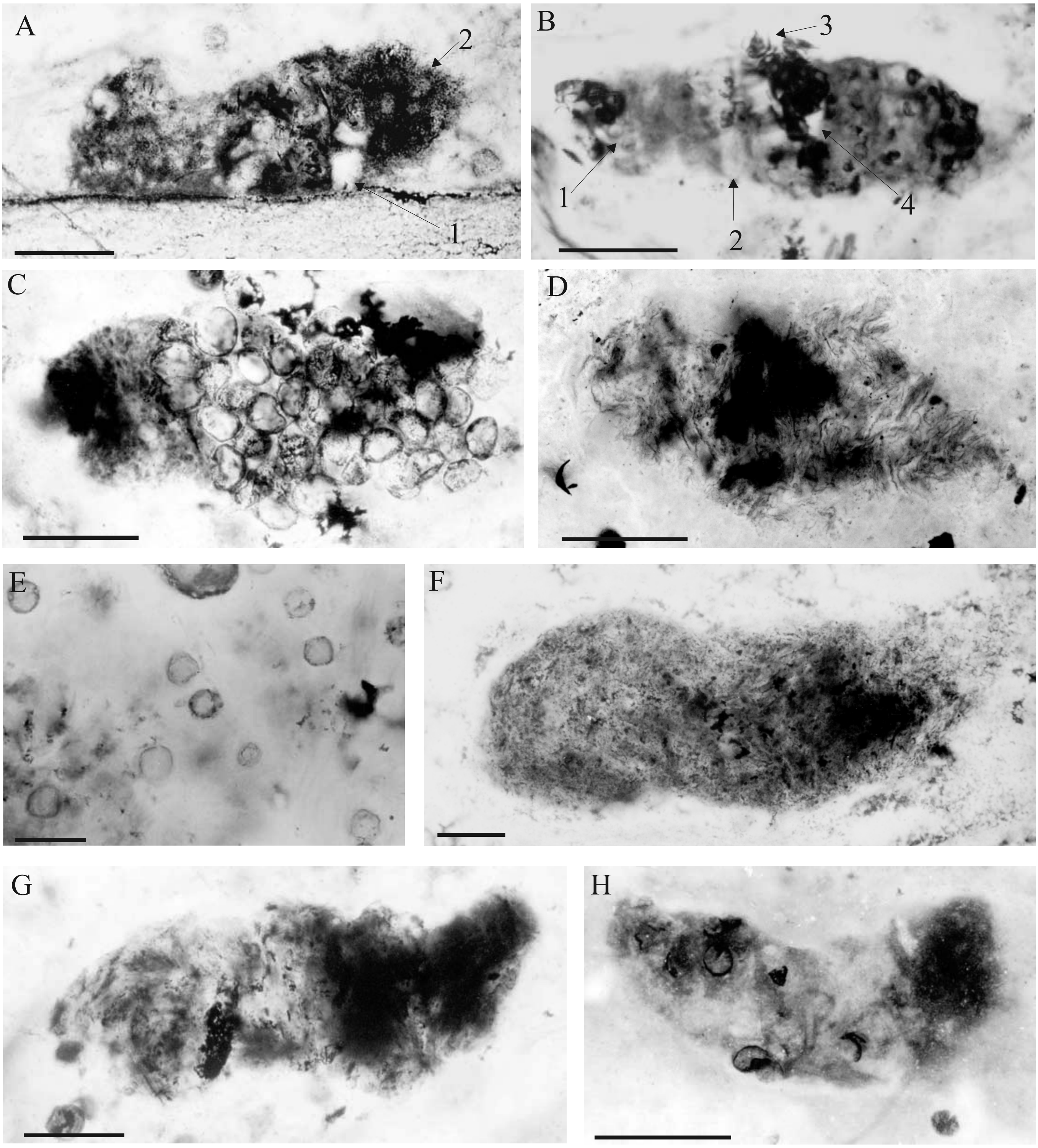


Figure 2 Group A(i) *Lancifaex simplex*: (A) *Lancifaex simplex* contents: quartz grains (arrow 1), amorphous organic matter (arrow 2) and cuticle. RC-3216. Transmitted light. Scale bar=300 µm; (B) *Lancifaex simplex* holotype RC-1928. Note the banded content. Contents: fungal spores (arrow 1), amorphous organic matter (arrow 2), degraded plant spores (arrow 3) and mineral grains (arrow 4). Reflected light. Scale bar=400 µm; (C) *Lancifaex simplex* with divided content. Contents: plant spores and amorphous organic matter. Transmitted light. RC-450. Scale bar=300 µm; (D) *Lancifaex simplex* content: sinuous organic sheets, presumably arthropod cuticles. RC-441. Reflected light. Scale bar=200 µm; (E) Detail of (D), small fungal spores. Transmitted light. Scale bar=10 µm; (F) *Lancifaex simplex* with predominantly amorphous content. RC-3216. Reflected light. Scale bar=300 µm; (G) *Lancifaex simplex* contents: densely packed degraded cuticle, amorphous organic matter and plant spores. RC-2365. Transmitted light. Scale bar=200 µm; (H) *Lancifaex simplex* contents: amorphous organic matter, rare plant and fungal spores. RC-564 Reflected light. Scale bar=400 µm.

are predominantly dark and opaque (Fig. 3); spore-wall degradation is varied in extent and nature, but is not dissimilar to the degradation seen in spores in the surrounding chert. On average, 54% of the spores in these coprolites are damaged (ratios of fragmented to complete spores, in populations of 20–50 spores, were measured in 15 Rhynie chert coprolites), compared with 50% in the chert (150 spores were surveyed in five chert samples). This difference is not statistically significant. The type and distribution of spores in coprolites is described in greater detail below.

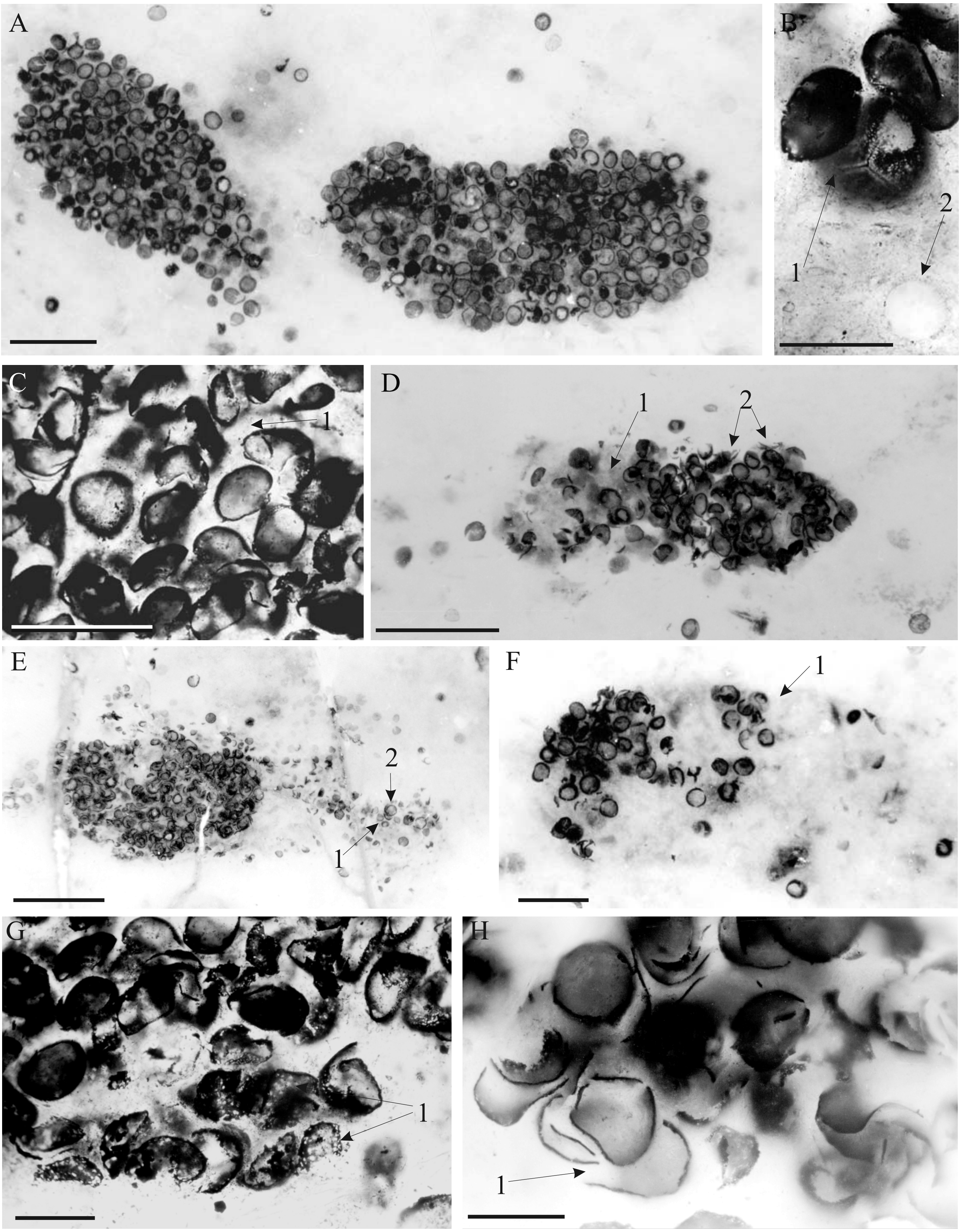


Figure 3 Group A(i) *Lancifaex simplex* with a high plant spore content: (A) Two *L. simplex*. Content: one type of laevigate spore, amorphous organic matter. RC-463-A. Reflected light. Scale bar = 1 mm; (B) Detail of *L. simplex* showing trilete, laevigate plant spores (arrow 1) and a fungal spore (arrow 2) in an amorphous matrix. RC-1966. Transmitted light. Scale bar = 50 µm; (C) Spores from a *L. simplex*, illustrating amorphous organic matter between spores (arrow 1). RC-1966. Transmitted light. Scale bar = 50 µm; (D) *Lancifaex simplex* with high degree of amorphous organic matter (arrow 1) and fragmented plant spores (arrow 2). RC-463. Reflected light. Scale bar = 400 µm; (E) Disintegrating *L. simplex* with two plant spore populations (arrows 1 and 2). RC-441. Reflected light. Scale bar = 400 µm; (F) *Lancifaex simplex* with indistinct margins (arrow 1) and predominantly amorphous content. RC-1632. Reflected light. Scale bar = 200 µm; (G) Detail of (E) showing dissolution texture in spore walls (arrow 1). RC-441. Scale bar = 50 µm; (H) Detail of (E) showing mechanically fragmented spore walls (arrow 1). RC-441. Scale bar = 50 µm.

Morphology is varied (Figs 2–5) and forms the chief basis for subdivision of this group. The length to width ratio (L:W) of intact coprolites varies between 1 (equidimensional) and 3. The coprolites fall into distinct groups in terms of L:W and common characteristics between these morphologically defined groups suggest that the distinction based on variation in L:W is real. Morphology also varies in terms of the shape of the coprolite ends, the shape and texture of their longitudinal margins, and the presence or absence of morphological features such as division and twisting (Figs 2–5).

Such coprolites are predominantly preserved isolated between fossilised plant tissues and sedimentary grains. Some examples are clustered in small groups (up to four coprolites), and in one subset, they always occur clustered among plant axes and sporangia, and are occasionally fused together (Fig. 5A).

3.1.1. Correlation between content, morphology and context. Coprolites with a low L:W differ from elongate coprolites in context and content, as well as morphology. These occur most commonly in loose clusters, sometimes partially fused together. Pale amorphous (non-particulate) organic matter is a common and often dominant component, isolated plant spores are often present and fungal spores are usually embedded within the coprolites. Sedimentary mineral grains are common.

Elongate coprolites (L:W = 2–3) are most often isolated, only occasionally occurring in small groups. Content is usually particulate and diverse, and there is little consistent variation between content and morphology. Morphologically diverse coprolites contain plant spores and remnants of spore walls, but few (only five specimens) are dominated by plant spores. There is some suggestion of a relationship between morphology and spore-dominated content. Four of the five spore-rich specimens share a similar morphology: slightly elongate, with simple longitudinal margins and rounded ends (Fig. 3A). This morphology is not confined to spore dominated coprolites (Fig. 2B–D), and the low numbers of spore-dominated coprolites make it impossible to determine the significance of this correlation. In terms of content, coprolites in which plant spores are the chief component do not form a separate population; there is a continuum between coprolites lacking spores and those dominated by spores (Habgood 2000). Consequently, spore-dominated coprolites are not treated as a separate population here.

The group can be split into four subsets on the basis of morphology, context and content. Briefly, the coprolites within this group fall into the following four categories:

[A(i)] isolated elongate coprolites with no morphological divisions;
[A(ii)] isolated elongate coprolites with morphological divisions or constrictions;
[A(iii)] isolated elongate coprolites comprising a line of rotund, conjoined sections; and
[A(iv)] rotund coprolites.

3.1.2. Group A(i): isolated elongate coprolites with no divisions. These coprolites (Figs 2 & 3) account for 27% of all the coprolites included in this study. They are distinguishable from other elongate coprolites by the lack of morphological division. Figures 2 and 3 illustrate the variation in gross morphology; it is common for these coprolites to have an asymmetrical and tapered outline (Fig. 2A). Individual coprolites are distributed through the thin-sections and usually isolated. Length varies between 440 and 1250 μm, and width between 280 and 490 μm.

Content within individual coprolites is often diverse (Fig. 2A, B). Typically, content is varied in particle size, affinity and degradation. Identifiable particles include mineral grains (Fig. 2A, B), plant spores (Fig. 2C), plant cuticles, banded tubes, arthropod cuticles (Fig. 2D), fungal spores (Fig. 2E), hyphae and bacteria. Of these, fragments of plant and unidentifiable organic matter are most common. Rare examples are dominated by unidentified, macerated organic matter (Fig. 2F, G), or contain only plant spores and amorphous organic matter (Fig. 2H, 3). This group encompasses all of the spore-dominated coprolites (Fig. 3A).

Arthropod cuticles are recorded from only two coprolites, and in both cases, are folded, crenulate sheets of straw-coloured organic matter with a granular surface (Fig. 2D). Mineral grains are common: they are exclusively abraded quartz grains (Fig. 2A, B). Although morphological divisions are absent, contents are sometimes laterally differentiated or layered (Fig. 2B), and where mineral grains are present within coprolites, they often occur in bands perpendicular to the long axis of the coprolite.

Three types of spore, distinguishable by size and ornament, have been recognised within these coprolites. Only one coprolite contains all three types. The most common spores are trilete with a circular amb (i.e. circular in equatorial outline; for a definition of palynological terms, see Grebe 1971) and laevigate wall (Fig. 3B, arrow 1, Fig. 3C, D). Whether or not they are crassitate (with a thickened spore wall) is uncertain. Spore diameter is 51–58 μm. These are similar to those found *in situ* in *Aglaophyton major* (Bhutta 1973) and the dispersed spore genus *Ambitisporites*. A population of spores which are similar, but slightly smaller (40–50 μm in diameter), is present in some coprolites (Fig. 3E). These again resemble the spores of *Aglaophyton* and the dispersed spore genus *Ambitisporites*. They may represent a different species, or spores of the same species which originate from a different sporophyte or sporangium. A single spore-rich coprolite contains trilete spores bearing spinose-apiculate distal ornamentation.

Plant spores dominate the content of a small number of coprolites (Fig. 3A). In others, plant spores are confined to part of the coprolite (Fig. 3F), dispersed throughout the coprolite (Fig. 3D), loosely clustered (Fig. 3E) or isolated among other debris (Fig. 2H). Rare coprolites contain only fragments of spore wall (Fig. 2B). Plant spores are often entire with little evidence of degradation (Fig. 3A, C), but some appear partially dissolved (Fig. 3G) or fragmented (Fig. 3H). The percentage of spores damaged does not differ significantly from those recorded in dispersed spores in the Rhynie and Windyfield cherts. The five spore-dominated coprolites appear on first inspection to contain only spores, but closer examination reveals brown discoloration between spores (Fig. 3C), probably representing the amorphous organic matrix seen more extensively in other coprolite types (Fig. 3D).

3.1.3. Group A(ii): isolated elongate coprolites with morphological divisions. This group of coprolites (Fig. 4A, B) constitutes 10·1% of the coprolites included in this study. They are distinguished by their morphology; each is elongate with a series of lateral constrictions which divide the coprolite into sections (the morphology is illustrated in Fig. 1). Each section is morphologically distinct, but not separate. Sections vary in size and shape within and between coprolites, and decrease in size toward the ends of the coprolite. Individual coprolites typically possess three to six sections. Junctions between adjacent sections may be inclined (Fig. 4A), or perpendicular (Fig. 4B) with respect to the longitudinal axis, the former presumably indicating twisting. Margins vary between smooth and irregular, but are predominantly distinct. Individual coprolites are usually isolated. Length varies between 1200 and 1500 μm, and width between 350 and 600 μm.

In content, these coprolites are similar to group A(i). Content is diverse and includes amorphous organic matter,

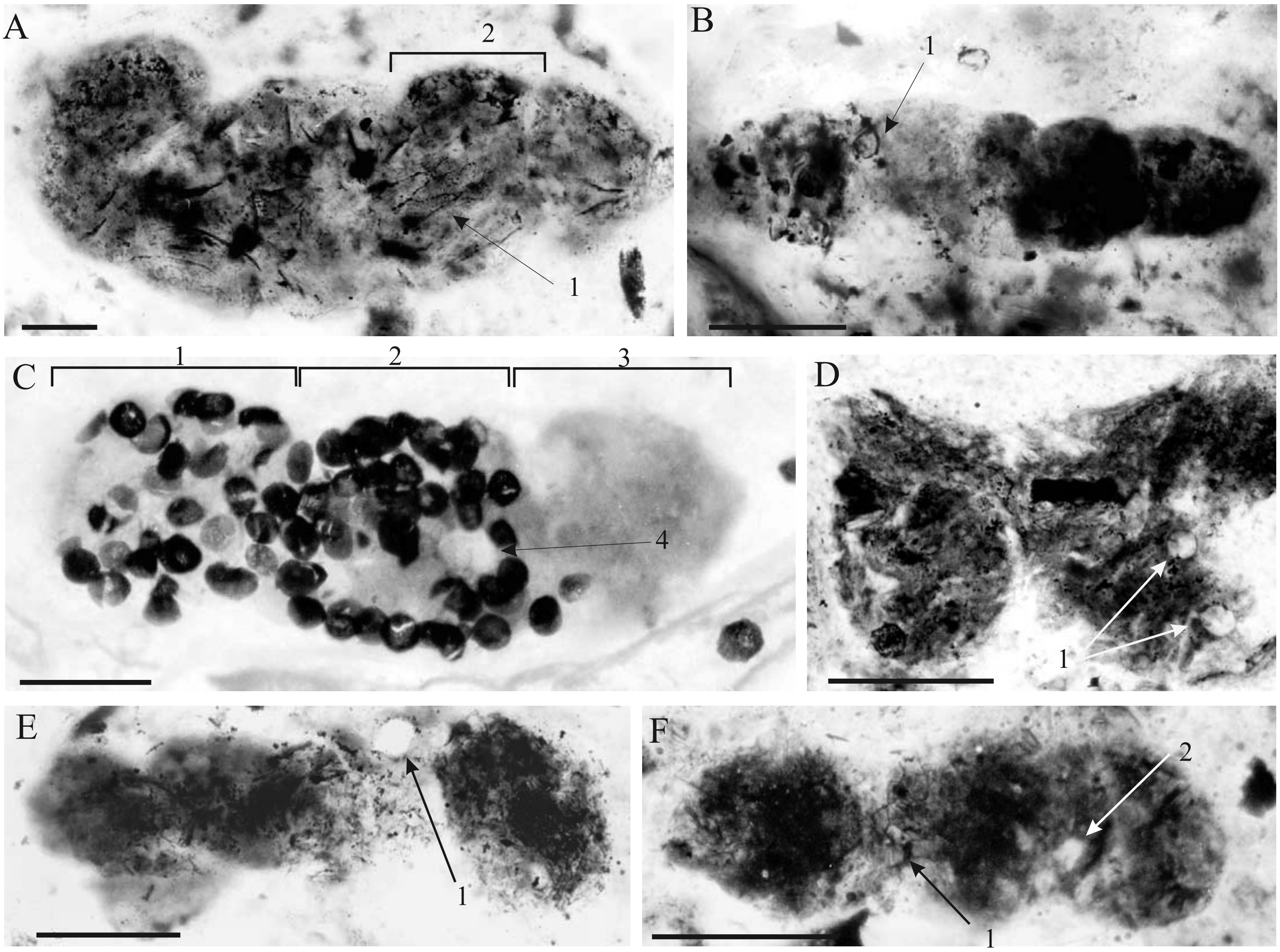


Figure 4 Group A(ii) *Lancifaex divisa* and group A (iii) *Lancifaex moniliforma*: (A) *Lancifaex divisa*. Contents: densely packed cuticle (arrow 1), amorphous organic matter, plant spores and mineral grains. RC-55-A. The '2' marks a single section of the coprolite. Transmitted light. Scale bar=200 μm; (B) *Lancifaex divisa* holotype. Contents: amorphous organic matter, plant (arrow 1) and fungal spores. RC-92-A. Transmitted light. Scale bar=400 μm; (C) *Lancifaex moniliforma*. Contents: amorphous organic matter, plant spores and mineral grains; '1', '2' and '3' are sections of the coprolite. Reflected light. RC-441-C. Scale bar=300 μm; (D) *Lancifaex moniliforma*. Contents: amorphous organic matter, fungal spores (arrow 1) and unidentified organic fragments. Reflected light. Scale bar=300 μm; (E) *Lancifaex moniliforma*. Contents: amorphous organic matter, mineral grains (arrow 1) and unidentified organic fragments. RC-1232-A. Reflected light. Scale bar=200 μm; (F) *Lancifaex moniliforma*. Holotype. Contents include amorphous organic matter, cuticle (arrow 1) and mineral grains (arrow 2). RC-1231-A. Reflected light. Scale bar=300 μm.

partially digested plant cuticles, plant spores, fungal spores and fungal hyphae. Isolated plant spores are common, spore clusters are less common and coprolites with abundant spores are rare. There are no examples for which the coprolite content is dominated by plant spores.

Content also varies in the degree of degradation and the size of particles. The most extremely degraded matter is amorphous, or otherwise unidentifiable, coalesced organic matter. Rare fragments of plant are greater than 300 μm in length and preserved with cellular detail (Fig. 4A).

3.1.4. Group A(iii): elongate coprolites comprising conjoined rotund sections. This group (Fig. 4C, F) constitutes 5·7% of the coprolites recorded in this study. They are distinguished in comprising a linear series of discrete, morphological units. Length ranges between 1200 and 1400 μm, and maximum width between 350 and 600 μm. The connection between units is often minimal; the ratio of maximum to minimum width is <0·6. Sections (Fig. 4C) may be separate, but remain in a linear configuration. These examples may be the product of an off-centre section of the coprolite.

Contents include amorphous (Fig. 4C) and macerated (Fig. 4D) organic matter, plant spores (Fig. 4C), fungal spores (Fig. 4D) and hyphae, fragments of plant cuticle (Fig. 4F), and mineral grains (Fig. 4C, E, F). Plant spores are rare, and are either isolated or in loose clusters, although one example contains approximately 55% spores (Fig. 4A) and the remaining content is amorphous organic matter, fungal spores and fungal hyphae. The spores within these coprolites are as for group A(i).

Sections in the same coprolite rarely differ in content (Fig. 4A is the only example), although some variation in colour density often occurs. This may be attributable to variations in thickness. Individual sections and occasionally whole coprolites are pale and have diffuse margins (Fig. 4C) and appear close to disintegration (Fig. 4E). There is a notable association between pale, diffuse coprolites and the presence of presumably secondary fungal spores and hyphae.

3.1.5. Group A(iv): squat coprolites. These coprolites (Fig. 5) are common within the Rhynie chert and constitute 17·6% of the coprolites. They occur predominantly in loose clusters in

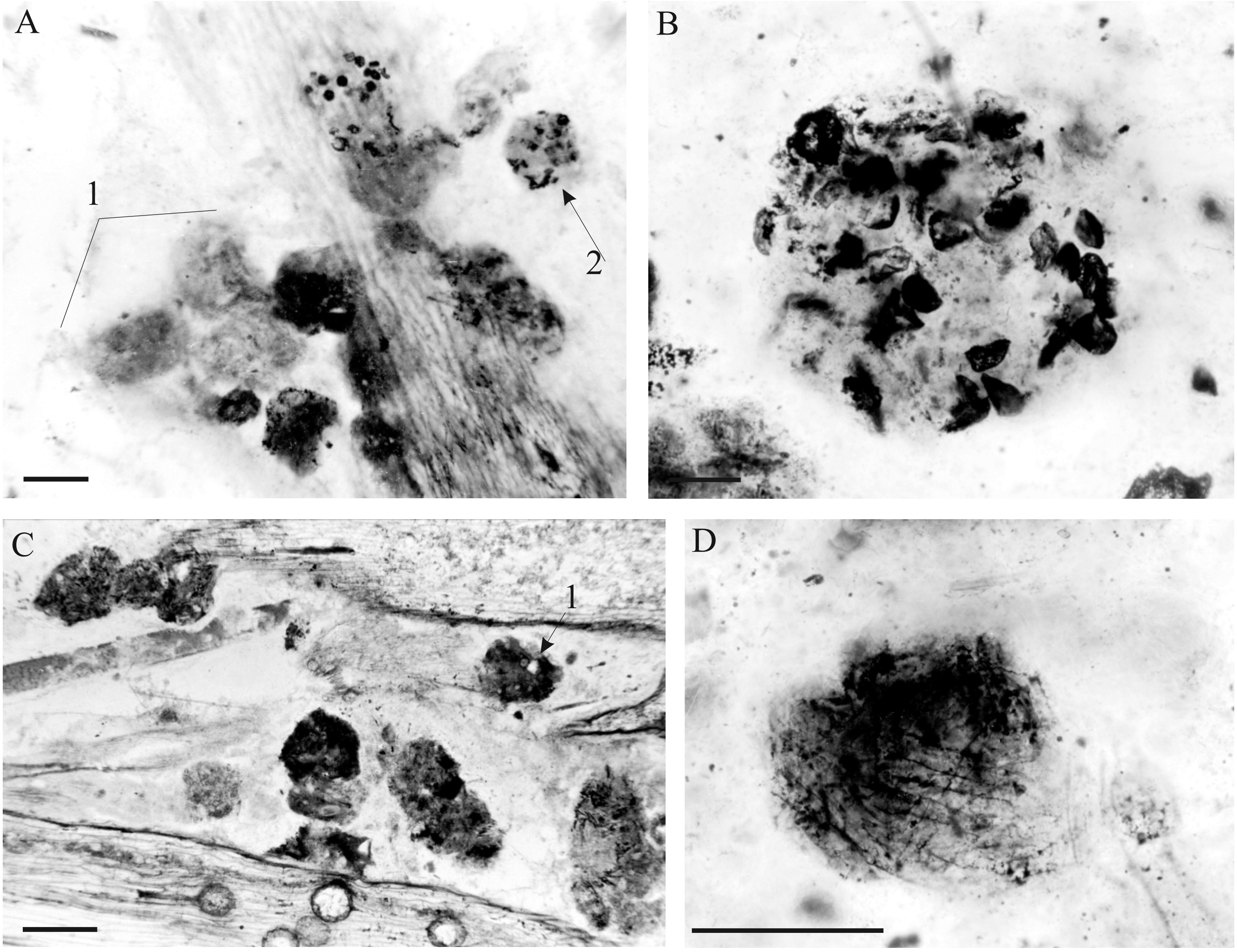


Figure 5 Group A(iv) *Rotundafaex aggregata*: (A) *Rotundafaex aggregata* clustered against a plant axis. Arrow 1 indicates coalescent individuals and the holotype (RC-1485-A) is indicated by arrow 2. RC-1485-A–F. Reflected light. Scale bar = 1 mm; (B) *Rotundafaex aggregata* contents: plant spore fragments, amorphous organic matter. RC-2325. Transmitted light. Scale bar = 200 µm; (C) *Rotundafaex aggregata* clustered amongst plant axes. Arrow 1 indicates mineral content. RC-1588-6A–C. Reflected light. Scale bar = 1 mm; (D) *Rotundafaex aggregata* in which content comprises cuticle, plant fragments. RC-1588-A. Transmitted light. Scale bar = 200 µm.

slides from the Münster collection, and scattered amongst *Aglaophyton* axes in thin-sections from the Lyon collection. Width ranges from 160 to 580 µm. Size varies slightly between clusters (Habgood 2000), although the number of coprolites in each cluster is too low to test the significance of these variations. Examples from the two collections are identical in shape and size, but vary slightly in fungal content. This group of coprolites is less varied in content than A(i), (ii) and (iii).

Content is dominated by light-brown to straw-coloured amorphous or coalesced unidentified organic matter (Fig. 5A). Plant spores are present in some coprolites (Fig. 5A–C), but do not completely dominate coprolites; fungal hyphae and spores are common. Fungal spores are much lighter in colour than plant spores and are simple spheres; within clustered coprolites, they are 27–49 µm in diameter (e.g. Fig. 3B). In the scattered coprolites from the Lyon collection, fungal spores are 15–25 µm in diameter (similar to those illustrated in Fig. 2E). A single example, from the Münster Collection, is dominated in content by fragments of plant cuticle (Fig. 5D).

These coprolites are morphologically simple, the margins are most often diffuse or welded (Fig. 5A), but may be smooth or irregular. Squat coprolites are sometimes found in association with more elongate and moniliform (Fig. 5C) specimens. It is difficult to be certain that they are not transverse-sections through elongate coprolites or separated sections of moniliform coprolites. The fact that clusters are not linear precludes the possibility that these are off-centre sections of moniliform coprolites.

However, there are reasons for considering these coprolites to be a separate population: they share features other than morphology; content is pale and amorphous with fungal spores; they are either clustered or scattered amongst plant axes, and they often have diffuse margins. These features are not common in elongate coprolites. The fact that clusters of elongate coprolites with similar content are not seen implies that these are a separate population.

3.2. Group B: coprolites with straight, parallel margins.

This is the less diverse of the two major groups of coprolites identified within this assemblage (Fig. 6). All have very straight, smooth, parallel longitudinal margins; content is always homogeneous, without identifiable particles. Diversity in morphology and content is very low, and even the distribution in size shows less variation. However, there are two distinct subdivisions within this group. The most abundant are the larger and occur in clusters of *c.* 30 coprolites. They are often welded together and in peripheral areas of the mass

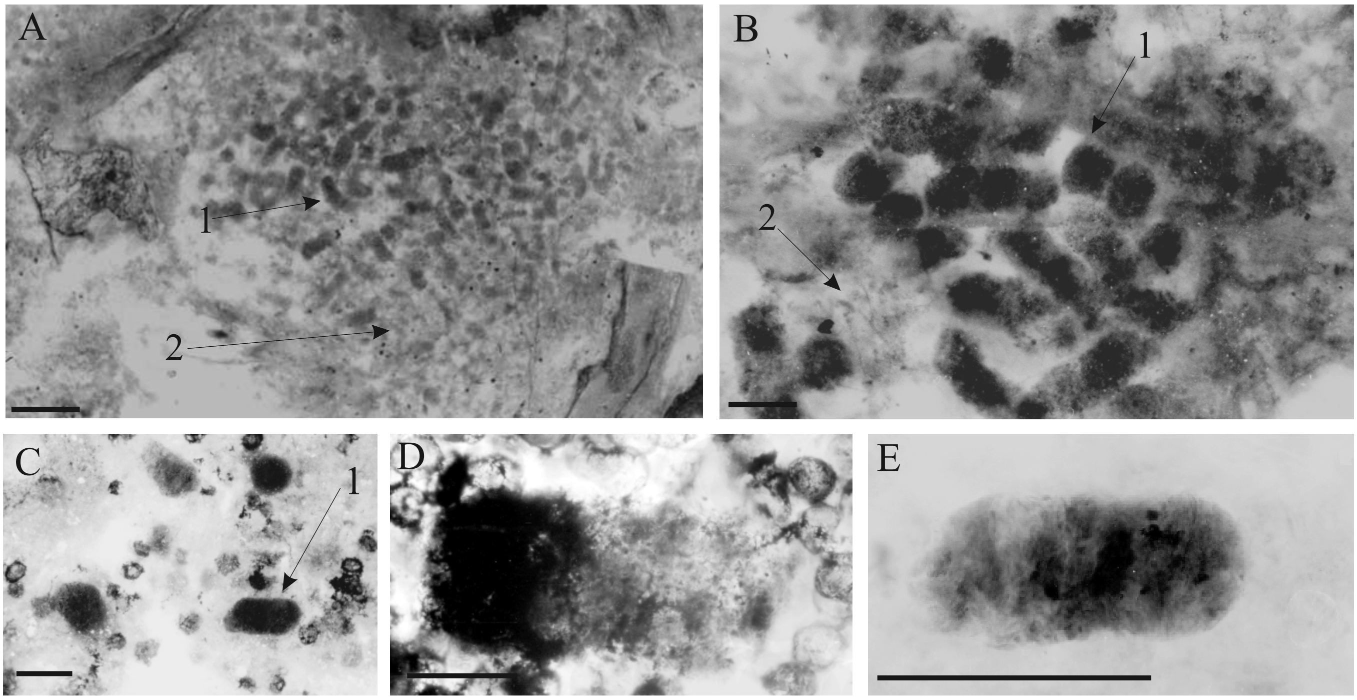


Figure 6 Group B(i) *Bacillafaex constipata* and group B(ii) *Bacillafaex mina*: (A) A mass of *B. constipata* including the holotype, RC-3233-A (arrow 1). In peripheral areas (arrow 2), individual coprolites have coalesced to form an amorphous mass. RC-3233. Reflected light. Scale bar=300 µm; (B) *Bacillafaex constipata* including transverse sections of coprolites (arrow 1) and associated fungal hyphae (arrow 2). RC-3234. Transmitted light. Scale bar=200 µm; (C) *Bacillafaex mina*. Holotype RC-1681-A, indicated by arrow 1. RC-1681-A–C. Reflected light. Scale bar=200 µm; (D) *Bacillafaex mina* inside sporangium. RC-2761-A. Transmitted light. Scale bar=200 µm; (E) *Bacillafaex mina*. RC-2765-A. Transmitted light. Scale bar=200 µm.

welded to the extent that individual coprolites are unrecognisable (Fig. 6A, B). Only identifiable coprolites were counted in the statistical aspect of this study; strongly welded material at the edge of these masses is not included in calculating coprolite percentages. The second type are rare small coprolites which occur in isolation, or in groups of four or fewer (Fig. 6C–E).

3.2.1. Group B(i): clustered prismatic coprolites. These coprolites occur in separate areas of three slides, and recognisable coprolites belonging to this group constitute 37.5% of the coprolites included in this study. Indistinct coprolites are discounted from this figure. Coprolites are always closely packed and their outline is typically parallel-sided with rounded ends (Fig. 6A). The coprolites occur in two masses of 30 or more coprolites, and a smaller mass (21 identifiable coprolites). Masses are irregular in outline, and coprolites become more widely spaced, lighter in colour and more diffuse toward the margins of the mass (Fig. 6A). Their width is constant within masses, but varies slightly between the three masses. Despite their abundance, the size range is low. These coprolites are 120–300 µm in diameter, the mode is 140–160 µm and the distribution is left-skewed. The orientation of coprolites in the clusters is also variable. A number of coprolites within masses are equant (Fig. 6B). These are approximately circular in outline and are presumably cross-sections of coprolites. Thus, these coprolites are interpreted as cylindrical in shape and uncompressed.

Contents are amorphous and dark to light brown. Variation in colour occurs within the same mass (Fig. 6B), and is at least partially caused by the angle and position of section. However, one mass is dominated by light-coloured coprolites, and where coprolites are indistinct (with diffuse or welded margins), they are also lighter in colour. This suggests that colour variation may be related to decomposition. Amorphous organic material close to the masses is optically identical to the contents of the coprolites, but occurs in chaotic 'clumps' (Fig. 6A). Fungal hyphae are abundant, especially at the diffuse margins, and where coprolites appear to be partially decomposed (Fig. 6B). Where decomposition is advanced, individual coprolites cannot be recognised.

3.2.2. Group B(ii): tiny isolated parallel coprolites. These tiny and rare coprolites (2·5% of the coprolites included in this study) have been observed only within three sporangia, where several coprolites occur together (Fig. 6C). The longitudinal margins are parallel and the ends blunt. Margins are distinct and smooth. Content is frequently dense and always amorphous, and colour ranges between a pale straw colour and opaque brown. Where coprolites are thinner because of the angle of section, a speckled appearance is created by opaque organic material within an amorphous organic matrix (Fig. 6D). Close examination reveals very faint lateral linear structures present wherever the coprolites are pale enough to allow such detailed examination (Fig. 6E). In one example, these coprolites occur within the same sporangium as a trigonotarbid.

4. Ichnotaxonomy

The coprolites described here represent several distinct groups of coprolites. The intent in erecting an ichnotaxonomical framework is to facilitate reference to these fossils, and to record the diversity recognised in this assemblage. For an overview of ichnotaxonomical convention, see Frey (1975). Figure 7 summarises the ichnospecies described here and the related groups described above.

Lancifaex Habgood, Hass and Kerp ichgen. nov.
Figs 2–4

Derivation of name. From the latin *lancea*, a spear, and *faecis*, meaning faeces (feminine).

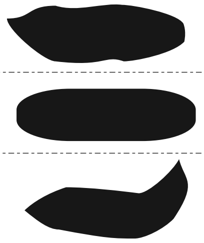
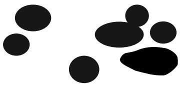
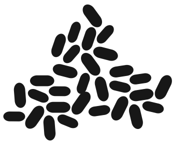
Ichnotaxonomy	Morphology	Content	Internal structure
Lancifaex simplex Group A(i)		Macerated plant cell including epidermis. Plant spores (isolated, clustered & fragmented). Fungal spores & hyphae. Mineral grain. Amorphous organic matter. 4 examples with simple morphology are dominated by plant spores.	Banded content in 1 example. Rare differentiation.
Lancifaex divisa Group A(ii)		Macerated plant cell including epidermis. Plant spores (isolated, clustered & fragmented). Fungal spores & hyphae. Mineral grain. Amorphous organic matter.	Rare differentiation. Sometimes twisted.
Lancifaex moniliforma Group A(iii)		Macerated plant cell including epidermis. Plant spores (isolated, clustered & fragmented). Fungal spores & hyphae. Mineral grain. Amorphous organic matter.	Occasional differentiation between sections.
Rotundafaex aggregata Group A(iv)		Amorphous organic matter. Fungal spores & hyphae. Plant spores. One example contains macerated plant cells. One contains undulate arthropod membranes.	None.
Bacillafaex constipata Group B(i)		Amorphous organic matter.	None.
Bacillafaex mina Group B(ii)		Amorphous organic matter.	None.

Figure 7 Summary of Rhynie chert coprolite groups and ichnotaxonomy.

Generic diagnosis. Elongate coprolites. Longitudinal margins curved. Ends rounded or tapered, rarely blunt. L:W = 1–4. Length = 500 µm to 3 mm, width = 200 µm to 1 mm. Contents include plant, fungal and animal tissues, bacteria, unidentifiable organic matter and mineral grains. Contents never exclusively amorphous.

Lancifaex simplex Habgood, Hass and Kerp ichsp. nov.
Figs 2, 3

Derivation of name. From the latin *simplex*, simple, describing undivided morphology.

Holotype. 1928 (Fig. 2B).

Paratypes. 33, 1558a, 1558d, 27, 2784, 1706, 1556, 1822, 565.

Location. Rhynie.

Age. Pragian.

Diagnosis. Simple, morphologically undivided coprolites. Contents include plant spores, cuticle, banded tubes, mineral grains and arthropod cuticles. Longitudinal margins are simple and convex. Poles rounded or tapered. Longitudinally and laterally asymmetrical.

Lancifaex divisa Habgood, Hass and Kerp ichsp. nov.
Fig. 3

Derivation of name. From the latin *divisus*, divided, describing the divided morphology.

Holotype. 92/1 (Fig. 4A).

Paratypes. 1969/6; -5; 1578.

Location. Rhynie.

Age. Pragian.

Diagnosis. Whole coprolites divided lengthwise into four or more rounded, but not necessarily equal or equant, morphological sections. Individual sections are distinct, but always joined. Maximum:minimum width $\geq 0{\cdot}6$.

Lancifaex moniliforma Habgood, Hass and Kerp ichsp. nov.
Fig. 4

Derivation of name. From the latin *monile*, necklace, describing the string of bead-like external morphology, and *forma*, in the shape of (feminine).

Holotype. 3240/1 (Fig. 4F).

Paratypes. 1286/2, 1526, 3240, 3216/1–3.

Location. Rhynie.

Age. Pragian.

Diagnosis. Whole coprolites divided along the length into two or more discrete, equidimensional rounded units. Individual units are approximately circular in outline, distinct and occasionally separate. Maximum:minimum width $<0{\cdot}6$.

Rotundafaex Habgood, Hass and Kerp ichgen. nov.
Fig. 4

Derivation of name. From the latin *rotundus*, spherical outline, describing the morphology, and *faecis*, meaning faeces (feminine).

Diagnosis. Equant to squat coprolites with convex margins and, where distinguishable, rounded ends. Contents may include plant tissues, unidentifiable organic matter and amorphous organic matter, but also include animal tissues and mineral grains. Simple morphology.

Rotundafaex aggregata Habgood, Hass and Kerp ichsp. nov.
Fig. 4

Derivation of name. From the latin *aggregatus*, grouped in clusters.

Holotype. 1485/1 (Fig. 5A, arrow 2).

Paratypes. 1882/1–7, 1678/1–6, 2667/1–4, 1485/2–8.

Location. Rhynie.

Age. Pragian.

Diagnosis. As for genus.

Bacillafaex Habgood, Hass and Kerp ichgen. nov.
Fig. 6

Derivation of name. From the latin *bacillus*, rod shaped, and *faecis* meaning faeces (feminine).

Diagnosis. Rod-shaped faeces, parallel longitudinal margins, and blunt or rounded poles. Contents are amorphous. L:W = 1–1·5, width = 50–300 µm.

There are two species, neither of which occurs as an isolated coprolite. These species of *Bacillafaex* are longitudinally and laterally symmetrical, and have a straight longitudinal axis.

Bacillafaex constipata Habgood, Hass and Kerp ichsp. nov.
Fig. 6A, B

Derivation of name. From the latin *constipatus*, crowded together.

Holotype. 3233/1 (Fig. 6B, arrow 1).

Paratype. 3234.

Location. Rhynie.

Age. Pragian.

Diagnosis. Length = 200–400 µm, width <100 µm. L:W = 1·2–3·2. Dense masses of >30 individual faeces. Ends are rounded.

Bacillafaex mina Habgood, Hass and Kerp ichsp. nov.
Fig. 6C, E

Derivation of name. From the latin *minus*, less, describing small size.

Holotype. 1696/1 (Fig 6E).

Paratype. 1689, 95.

Location. Rhynie.

Age. Pragian.

Diagnosis. Minute coprolites, length <100 µm. L:W = 1·5–2·5, straight and smooth longitudinal edges. These coprolites occur within sporangia, in small groups of up to four.

5. Taphonomy

Studies on modern faeces have identified several styles of post-depositional degradation (Bal 1973; Bullock *et al.* 1985). Mechanically induced changes include swelling and shrinkage caused by repeated wetting and drying, disintegration, the collapse of thin-walled cells, and compression. Chemical changes result in dissolution and the discoloration of organic material, associated with phenols, tannins and cellulose degradation (Nykvist 1963; Babel 1975), and biological agents also attack faecal material. Coprophagous fauna consume and so completely recycle faeces. Microbial digestion produces organic fine substances (Babel 1975) and 'slime' that is easily digested by saprovores. Fungal activity digests and mechanically breaks faecal material. As the faeces is penetrated by fungal hyphae, it is dissected into smaller parts, eventually leading to disintegration. Zachariae (1965) suggested fungal and microbial decomposition to be particularly important since many saprovores digest only the organic slime created by microbial activity, leaving organic particles largely intact.

The coprolites in this assemblage exhibit characteristics which can be attributed to taphonomic effects. Coalescence or amalgamation (Figs 5A, 6A), where faeces form an 'undifferentiated mass' (Bal 1973), is common in faeces deposited in clusters, and in which content is predominantly organic and amorphous or fine grained. Towards the edge of the mass the coprolites become amalgamated, and in some areas, only a mass of organic matter is preserved; fungal hyphae are common in these areas. In modern examples, this style of degradation eventually results in a mammillated soil horizon (Bal 1973). Coprolites are preserved in varying stages of disintegration in the Rhynie chert, including examples which are disintegrating into component particles (Fig. 3A, D) and those that are fractured. No examples have visible oxidation rims.

Internal ageing, where the faeces content tends towards amorphous (Bal 1973; Bullock *et al.* 1985), and morphological changes, where the original morphology is lost (Bal 1973), are difficult to identify in coprolites; it is not possible to differentiate between taphonomic and original features.

6. Penecontemporaneous assemblages

Coprolites of a similar age have been described from the Old Red Sandstone of the Welsh Borderlands (Edwards *et al.* 1995). Most similar in age (Lochkovian) are the coprolites recorded from north Brown Clee Hill. Like those of the Rhynie chert, these are preserved in deposits which include a significant floral assemblage. However, the two assemblages differ in taphonomy. The Rhynie chert coprolites are preserved close to their origin, those from north Brown Clee Hill have been transported and deposited in fluvial sediments, and are coalified (Edwards *et al.* 1995). The predominant method of examination (scanning electron microscopy and light microscopy) also differs.

The coprolites reported from north Brown Clee Hill are elongate ellipsoidal and ovoid, spore-rich coprolites with rounded or tapered ends (Edwards *et al.* 1995). These are morphologically similar to coprolites assigned to *L. simplex* and *L. divida* in this paper and are also comparable in size. Coprolites from north Brown Clee Hill with more diverse morphology and content (Habgood 2000) await description.

Spore-containing coprolites comprise a significant portion of both populations. However, the Rhynie chert assemblage includes more coprolites which lack plant spores, and fewer which contain greater than 80% plant spores. In both localities, the spore content of coprolites is comparable with the dispersed spore population in diversity, degradation and size.

6.1. Spore size, diversity and degradation

For spore populations in coprolites from north Brown Clee Hill, spore diameter ranges between 12 and 78 µm, with a mode between 20 and 35 µm. For Rhynie chert coprolites, spore diameter is larger, ranging between 30 and 90 µm, with a mode between 50 and 60 µm. These differences reflect differences in the size of dispersed spores in the two localities.

Of the 202 coprolites included in this study, 54% contain plant spores or fragments of plant spore-wall, only 8% are dominated by plant spores and only 3% contain more than one spore taxon. The maximum number of spore taxa identified in a single coprolite is three. Spores within north Brown Clee Hill coprolites are more diverse in size, configuration and ornamentation (Edwards *et al.* 1995; Habgood 2000). Again, this reflects differences in the dispersed spore populations of the two localities. The spore and sporophyte assemblage preserved at north Brown Clee Hill is diverse in comparison with other Early Devonian assemblages, including that preserved in the Rhynie chert (Edwards 1996).

Very little spore degradation was observed in the coprolites from north Brown Clee Hill (Edwards *et al.* 1995; Habgood 2000). In the Rhynie coprolites, it is difficult to differentiate between taphonomic spore damage and damage incurred by ingestion.

6.2. Taphonomic differences between the two localities

Taphonomic alteration of a coprolite assemblage depends on conditions in the initial depositional environment, transportation, preservation and the nature of the faeces.

In soils, the most significant control on degradation is biological activity. Degradation in biologically inactive soils is slower and largely caused by physical rather than biological degradation. Temperature and moisture affect the likelihood of disintegration or coalescence, and the re-assimilation of organic matter.

Some characteristics of faeces influence their preservation potential. Faeces with high water content have high plasticity and low preservation potential. Dry faeces are more prone to disintegration. Content affects the rapidity of re-assimilation. Phloem tissues decay most rapidly, followed by collenchyma, parenchyma, lignified tissues, epidermis (and epidermal cuticle), and finally, the phlobaphene-containing tissues, sporopollenin and chitin, are extremely long-lived even in a biologically active environment (Babel 1975).

The greater diversity noted in Rhynie chert coprolites may signify that, although deposited in a biologically active soil, they were preserved rapidly. Some taphonomic effects are recognisable, but there has been little winnowing and coprolites with apparently low preservation potential are preserved. The Welsh assemblage is less diverse and dominated by coprolites rich in spores. This might result from a longer period of time in which faeces were degraded and assimilated (the Welsh coprolites were transported, hence, weak ones would be broken).

7. Deciphering coprolites

The coprolite assemblage described here records part of an Early Devonian food web. Determining the taxonomic identity of coprolite-producers is difficult; determining their origin in terms of functional feeding group or nutritional strategy is likely to be more accurate, and in terms of reconstructing a food web, more relevant. Modern faecal pellets can provide a key to understanding the origin of coprolites (Labandeira & Phillips 2002).

The relationships between consumer behaviour and faecal character are particularly useful. Faeces content, distribution and morphology are all controlled to some extent by consumer behaviour (Habgood 2000). The faeces produced by extant soil-dwelling consumers are illustrated in Figure 8 and summarised in Figure 9.

Faeces character is controlled by diverse variables. Those most consistently associated with diet are content diversity and identity, distribution is also associated with nutritional strategy. The following observations are helpful for interpreting coprolites in terms of feeding strategy:

(1) Sedimentary grains occur in the faecal matter of fauna which consume detritus, soils or sediment.
(2) Fauna for which food intake is diverse, such as detritivores, saprovores and some deposit feeders, produce varied faecal matter:
    (i) The faecal matter is diverse in shape, size and content.
    (ii) Individual faeces often, but not always, have diverse content.
(3) The faecal matter of fauna with a constrained intake, such as some herbivores, is more constant in shape, content and content degradation, although size may vary between individuals.
(4) Fauna which have little effect on consumed matter produce faecal matter that resembles closely their dietary intake.
(5) A component of intake that is hard to digest becomes concentrated in the faeces.
(6) Fauna with low assimilation efficiency for their intake produce abundant faecal matter, and *vice versa*.
(7) Clusters of faecal matter may arise from taphonomic effects; for example, concentrated targeted feeding, storage of faecal matter or feeding in large groups.
(8) Interpretation of faecal matter is dependant on the availability of a number of faeces. The characteristics of a single faecal pellet may be misleading.
(9) The faecal pellets of suspension and deposit feeders include aquatic organisms and large amounts of sediment. For the former, included sediment consists of clay to fine sand in grain size.

8. Producers of the Rhynie chert coprolites

8.1. *Lancifaex simplex*, *L. divisa* and *L. moniliforma*

Coprolites assigned to these ichnospecies share some significant characteristics, with each other and the faeces produced by modern detritivores:

- Faeces content is diverse in origin.
- Internal particle size and particle degradation are varied.
- Individual coprolites are dispersed rather than clustered.
- Mineral grains are common within the coprolites.

The faecal products of modern soil-dwelling herbivores differ. They usually contain only highly degraded matter, particle size and origin is homogeneous and unattributable, and the faeces tend to be clustered and morphologically similar. These coprolites contain diverse particulate matter, including plant tissues, fungal spores and mineral grains.

In some modern arthropod faeces, alternate bands of packing and loosening structures relate to separate feeding episodes (C. C. Labandeira, pers. comm. 2002). In these coprolites, banding is rare (Fig. 2B) and is recognisable as a variation in content (in colour or particle nature) – it is not clear whether they relate to changes in packing. The morphological divisions of *L. divisa* and *L. moniliforma* may also result from consecutive feeding episodes. In all three species, content occasionally varies between parts of the same coprolite. This variation presumably relates to changes in dietary intake and may result from an intentional feeding strategy or an indiscriminate dietary intake of poorly mixed, heterogeneous detritus.

The consumers which produced these coprolites were omnivorous, and mineral content suggests that intake included

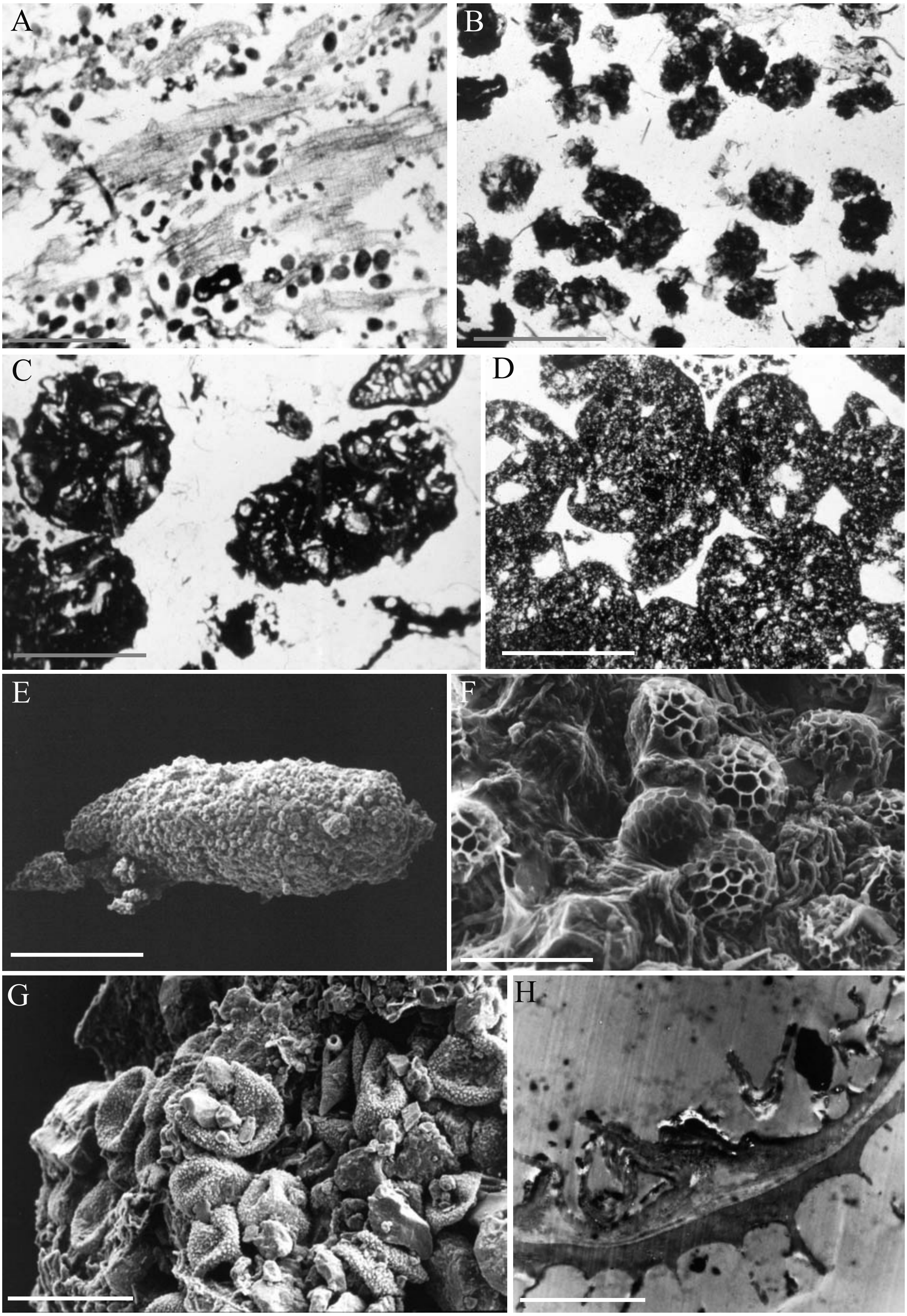


Figure 8 Faecal matter produced by modern soil-dwelling organisms: (A) Faecal pellets from oribitid mites feeding on plant tissues. Scale bar = 500 µm; (B) Faecal pellets from collembolans feeding on phytodebris. Scale bar = 300 µm; (C) Faecal pellets from tipulid fly larvae feeding on mixed detritus. Scale bar = 1 mm; (D) Faecal pellets from earthworms feeding on soil. Scale bar = 1 mm; (E) Faecal pellet from a millipede (*Julus scandinavius*) fed on mixed detritus that contained fern spores (*Lycopodium* sp.). Scale bar = 500 µm; (F) Detail of the faecal pellet pictured in (E). Scale bar = 50 µm; (G) Detail of a faecal pellet from *J. scandiavius* fed on mixed detritus that contained *Osmunda regalis* spores. Scale bar = 50 µm; (H) A section through an *Osmunda regalis* spore ingested by *J. scandiavius*. The spore walls remain intact. Scale bar = 5 µm; (A–D) Transmitted light. (E–G) Scanning electron microscope. (H) Transmitted electron microscope. A–D reproduced by permission of the Soil Society of America.

EXAMPLES RELEVANT TO THE LOWER DEVONIAN	FAECAL CONTENT	FAECAL DISTRIBUTION	REFERENCES
Detritivores: (Figures 8B & 8C)			
Diplopods Collembolans (Figure 8B) Millipedes (Julidae) (Figure 8E – 8H)	Diverse in origin, degradation & particle size. Includes: Plant tissues, Animal tissues (rare), fungi, bacteria and mineral grains Ingestion has little decompositional effect on intake, other than fragmentation and seeding with bacteria.	Distributed through the soil horizon Or Clustered in a storage area. Assimilation efficiency is low and feeding is continual.	Franz & Leitenberger 1948 Gere 1956 Van der Drift 1964 Zachariae 1965 Babel 1975 Fitzpatrick 1984
Other comments:	In experiments using modern millipedes (*Julus scandinavius*) and fern spores (*Lycopodium* sp., *Osmunda regalis* and *Anemia* sp.) the millipedes consumed spore-containing detritus and produced spore-rich faeces. The spores were unaffected by ingestion, and were only consumed when mixed with detritus. Spore-rich faeces can be the product of a non-selective, detritivorous diet (Figures 8E – 8H).		
Saprovores: (Figure 8D)			
Earth worms (Figure 8D) Enchytraeid worms	Amorphous with sedimentary grains. Moisture and bacterial content is high. Ingestion has little decompositional effect on intake, other than fragmentation and seeding with bacteria.	As for Detritivores.	Bal 1973 Babel 1975 Fitzpatrick 1984
Herbivores: (Figure 8A) encompasses a range of feeding strategies, e.g. Piercing and sucking, Foliage feeding, Surface fluid feeding, Tissue boring			
Oribatid mites (Figure 8A) Collembolans	Plant derived. Variation is low in terms of particle size, origin and degradation. Content is often predominantly amorphous.	Faeces are produced in abundance, and in some examples sporadically. Oribatids produce faeces concentrated at the site of feeding. Assimilation efficiency depends on the animals feeding strategy, but is not as high as for predators.	Van der Drift 1964 Labandeira *et al.* 1997
Palynivory and spore-feeding:			
Some modern insects are palynivores (Rasnitsyn & Krassilov 1996), pollen walls are often porous, possess permeable apertures and degrade over time (Rowley & Skvarla 1994). Spore-feeding in modern fauna is widely considered rare (Leschen & Lawrence 1991); however various modern arthropods and insects are reported as spore-feeders – see text section 9. The nature of their faeces is not well-documented.			Plitt 1907 Gerson 1969 Loria & Hernstadt 1980 Rasnitsyn & Krassilov 1996
Predators:			
Spiders	The content of spider faeces is dense, dry and amorphous or fine-grained.	Very little waste is produced and the pellets are small and dense. They are usually isolated or in small groups. Assimilation efficiency is very high.	Bal 1973 Babel 1975 Fitzpatrick 1984
Suspension feeders (Aquatic)			
Shrimps	Sedimentary grains Skeletal grains Calcite rhombs High inorganic content	Feeding is continual. The faecal pellets are abundant (40 pellets per minute for *C. major*) and concentrated in burrows or on fine sand surfaces.	Haven & Morales-Alamo 1968 Pryor 1975 Baltres & Medesan 1978 Beladjal *et al.* 1997
Deposit feeders and Aquatic Grazers:			
Gastropods Shrimps (*Palaemonetes pugio*)	Content and particle size is varied. Cellulose, Lignin, Chitin presumably originating from organic remains in the sediment. High inorganic content.	Faecal pellets are produced in great quantities and form a dense matt on the sediment surface. Recycling is rapid and predominantly by means of biological degradation.	Pohl 1946 Frankenberg *et al.* 1967 Frankenberg & Smith 1967 Kofoed 1975 Hyellberg & Gallucci 1975 Welsh 1975

Figure 9 Modern soil-dwelling and freshwater functional feeding groups, and the characteristics of the faeces produced.

detrital matter. Given the coprolite content, it seems likely that the consumers were unable to digest undecomposed plant cuticle, animal cuticles and sporopollenin. In distribution and the diversity of content, they are similar to the faeces produced by modern soil-dwelling detrivorous arthropods, and in size and morphology, they are similar to the faeces of modern British diplopods. These coprolites are inferred to be the product of detritivores.

Support for the thesis that these coprolites are the product of detritivores comes from the arthropod (*Leverhulmia mariae*) reported from the Windyfield chert with intact gut contents (Anderson & Trewin 2003). The material preserved in the gut includes tightly packed fungal and plant spores, and finely macerated plant cells and the variety of material indicates a detritivorous intake. The animal is concluded to be a detritivore that inhabited the soil litter. The mixture of plant and fungal spores, and macerated plant tissues in the gut of *L. mariae* is comparable with the content of *Lancifaex* reported here.

8.2. *Rotundafaex aggregata*

The diverse content of these coprolites indicates that they are likely to be the product of detritivores. Their pale colour, diffuse margins and the abundance of fungal hyphae and spores suggest significant post-depositional changes. Either this taxon includes only coprolites in a more advanced stage of decay than others, or they are prone to rapid biological decay. It is possible that these coprolites are degraded versions of *Lancifaex monilifoma* or *L. divisa*, the clusters being separated sections. However, these clusters are not linearly arranged.

On the basis of coprolite size and content, *Rotundafaex* is likely to be the product of detritivorous collembolans, bristletails or small, burrowing diplopods. They appear to have decomposed more rapidly than *Lancifaex*. This may relate to the environment in which they were deposited, the porosity and water content of the faeces, or that the coprolites predominantly contained highly degradable matter.

8.3. *Bacillafaex constipata*

The uniformly amorphous content of these coprolites implies either that intake was amorphous, or that it was uniformly and effectively digested. It seems probable that intake was either carefully targeted or the consumer was able to digest a wide range of organic products. It is assumed that these coprolites were originally deposited in the clusters in which they are preserved. The uniformity in size, morphology and content of these coprolites is comparable to the faeces of modern herbivores, and distinguishes them from the faeces of detritivores. The abundance of these faeces suggests that consumers were inefficient in assimilating nutrients.

Modern terrestrial herbivores, as well as aquatic grazers, suspension feeders and deposit feeders, produce large clusters of faeces. The high organic content (deduced from coprolite colour) and lack of fine-grained sediment is not typical of faecal pellets produced by suspension feeders. Modern suspension feeders such as shrimp produce abundant rod-shaped pellets, often with internal structure, which contain abundant sedimentary and mineral matter (Haven & Morales-Alamo 1968; Baltres & Medesan 1978; Beladjal *et al*. 1995, 1997). The faecal pellets of deposit feeders have a similarly high inorganic content (Kofoed 1975). There are some morphological differences too; modern suspension and deposit feeders produce rod-shaped faecal pellets with blunt ends (Haven & Morales-Alamo 1968; Baltres & Medesan 1978; Beladjal *et al*. 1995, 1997) rather than the ellipsoidal morphology of *B. constipata*.

Soil-dwelling herbivores such as oribatid mites produce clustered faeces more similar in size, morphology and organic content to these coprolites. In modern examples and other fossil record assemblages, multi-modal size distributions are considered indicative of variation in consumer maturity (Labandeira *et al*. 1997). Such variation is not seen in clusters of *B. constipata*; each cluster is unimodal in terms of size. In terms of size, morphology and content, it is possible that these coprolites are the product of herbivorous mites. The diet of modern mites varies between species; Zachariae (1965) and Babel (1975) identified phloem and sap-feeding mites in modern soil ecosystems. These coprolites may be the product of freshwater consumers or soil-dwelling microherbivores.

8.4. *Bacillafaex mina*

These coprolites with amorphous contents are presumably the product of a consumer whose intake was discriminate and limited to a digestible food source. Their paucity may be a function of size and the difficulty of picking these coprolites out amongst other debris. However, their size and distribution in small groups suggests that the consumer produced a small amount of faecal matter.

Herbivores observed in modern soils produce abundant faeces either dispersed through the soil horizon or concentrated in clusters similar to *B. constipata*. The size and spatial distribution of *B. mina* is significantly different from this, although their presence within sporangia may intuitively suggest that sporangia provide the consumer with shelter, a food source or both. Tapetum or locular fluids within sporangia would provide a rich food source.

Sporangia which contain *B. mina* also contain, in one case, parts of a trigonotarbid, and in another, mite exuviae. Despite the size of trigonotarbids (usually less than 4 mm), it is possible that they produced these small faeces. Extant fluid-feeding arachnids store waste products before defecation, and the results are very few, small, amorphous faeces. Carnivorous trigonotarbids were presumably fluid-feeders which preyed on oribatid mites and other small arthropods. It has been suggested that the trigonotarbids found within sporangia were spore-feeders (Kevan *et al*. 1975; Rolfe 1980; Powell 1994). Spore-feeding has not been recorded in modern arachnids, although pollen feeding is documented in modern spiders (Carrel *et al*. 2000). The coprolites found in association with trigonotarbids do not provide evidence to support this and pierced spores are unknown from the Rhynie chert. However, spore cytoplasm, tapetum and locular fluid would provide an easily digestible, nutrient-rich food source. Thus, the contents of immature sporangia (locular fluid and tapetum) would have provided a good dietary source of nutrients. Since the content of these faeces is amorphous, it is ultimately impossible to determine the identity of the intake, although the size and sparseness (in comparison with faeces produced by modern herbivores) imply that the consumers had high nutrient assimilation efficiency. Two specimens are preserved in a sporangium that also contains a trigonotarbid; therefore it seems likely that *B. mina* may have been produced by trigonotarbids.

9. The origin of spore-rich faeces

There are documented examples of modern animals feeding on plant spores as well as pollen, although spore-feeding is generally considered to be uncommon (Leschen & Lawrence 1991). Species of Coeloptera, Lepidoptera and Hemiptera (Ottosson & Anderson 1983; Srivastava *et al*. 1997), as well as collembolans have been observed to feed on bracken (*Pteridium aquilinum*) spores in modern soils and experiments (Gerson 1979).

The richest source of nutrient in a spore is the cytoplasm in the spore lumina. In Early Devonian spores, this appears rather inaccessible; the spore walls are thick, without permeable areas and usually without aperture (unlike modern pollen grains, and many modern fern and bryophyte spores). For consumers to extract nutrient from spore lumina, it would be necessary to breach the spore wall, to consume the spore when the laesurae is gaping (when they are ready to germinate) or to remove the cytoplasm by diffusion, in the same way that modern pollen cytoplasm is removed by some consumers (Johnson & Nicholson 2001). The possibility that the Devonian fauna was able to extract nutrient from spores is difficult to test. Edwards *et al.* (1995) found that the size of molecule able to pass through an intact spore wall was significantly smaller than any enzyme, even when spore wall porosity had increased with maturity. Sporopollenin is an extremely robust biomolecule; the only known agents which degrade sporopollenin are bacteria (Havinga 1964, 1971, 1984) and hydrothermal fluids (Elsik 1971; Trewin 1996). The contents of immature sporangia (locular fluid and tapetum) may have provided an alternative food source.

Spores in coprolites from the Welsh borderlands (Edwards *et al.* 1995) and the Rhynie chert do not show significant degradation. External tapetally derived spore-wall layers and the locular fluids of sporangia may have offered nutrition. It has also been suggested that detritivores extract most nutrient from bacteria and liquid/amorphous products of bacterial decomposition on the surface of ingested particles such as spores (Zachariae 1965; Babel 1975). Experiments undertaken by Chaloner (1976) using locusts (*Locusta migratoria*) and *Pteridium* spores found that consumption reduced spore viability by about 50%, implying alteration during ingestion.

Spore-rich coprolites from the Welsh borderlands exhibit little damage to the spore walls and contain diverse spores. Small, ornate and thick-walled spores such as *Emphanisporites* are abundant (Habgood 2000); large, thin-walled, laevigate spores (although more prone to physical damage) are not. The diverse spores within the Welsh coprolites imply that consumers were ingesting dispersed spores and were not selective. In contrast, where Rhynie chert coprolites contain spores, they are usually mono-specific. This lack of diversity does not necessarily indicate that the spores were consumed while still in the sporangia: the dispersed spores in the Rhynie chert are distributed unevenly; and local spore populations are largely mono-specific and spore masses are common. An animal in this environment consuming *in situ* or dispersed spores would be likely to consume a mono-specific spore population.

There is a continuum in the Rhynie chert between coprolites rich in spores and those which lack spores. It seems probable that they originate from the same type of consumer. Coprolites with diverse content, which commonly include mineral grains, are the product of detritivores, and it seems probable that spore-rich coprolites were as well. In experiments using modern millipedes (*Julus scandinavius*) and fern spores (*Lycopodium* sp., *Osmunda regalis* and *Anemia* sp.), the millipedes consumed spore-containing detritus and produced spore-rich faeces. The spores were unaffected by ingestion, and were only consumed when mixed with detritus. Spore-rich faeces can be the product of a non-selective, detritivorous diet (Habgood 2000).

The uneven distribution of spores and spore masses in the Rhynie chert means that a consumer ingesting detritus here would occasionally consume spores and produce spore-dominated faeces. The low number of spore-rich coprolites, their similarity to coprolites with more diverse content (including mineral grains) and the varying abundance of spores in morphologically similar coprolites is consistent with this model. Had a group of sporivorous consumers existed, it seems likely that a more significant and distinct population of spore-rich coprolites would exist. The spore-rich coprolites reported in this paper are interpreted as the product of detritivores rather than sporivores or herbivores.

10. Nutrient cycling and functional feeding groups in early terrestrial ecosystems

10.1. Spore and sporangia feeding

Spore/sporangia feeding has been identified as a functional feeding group during the Late Carboniferous (Scott *et al.* 1992; Labandeira & Phillips 2002), and has been suggested for Early Devonian arthropods (Labandeira 1998). Previous reports of spore-consumers (Chaloner 1976; Labandeira 1998; Collinson 1999) have been based on the presence of spore-rich coprolites (Edwards *et al.* 1995). However, such coprolites do not necessarily demonstrate the existence of spore-feeders, but may be the product of detritivores (Edwards *et al.* 1995). The evidence for deliberately targeted spore-feeding in the Early Devonian is not conclusive.

10.2. Detritivores and saprovores

There is significant evidence for terrestrial detritivory in the Late Silurian and Early Devonian, and even as far back as the Late Ordovician. The earliest evidence comes from burrows with associated faecal pellets from the Upper Ordovician of Pennsylvania, USA; Retallack (2001) attributed these to soil-ingesting organisms. The Upper Silurian and Early Devonian diplopods *Archidesmus macnicoli* and flat-backed kampecarids are concluded, on the basis of functional morphology, to have been litter-splitters (Rolfe 1980, 1985) and detritivores (Almond 1985). Kampecarids are typically short, cylindrical diplopods, considered by some to be aquatic (Almond 1985) and by others to be terrestrial burrowers (Rolfe 1980). Fragments of a slender, cylindrical millipede from the Late Silurian are interpreted to represent a burrowing detritivore (Shear *et al.* 1995; Shear & Selden 2001). Eoarthropleurids (Shear *et al.* 1995) are again interpreted to have been detritivores. The most conclusive evidence for detritivores comes from the Rhynie chert arthropod, *Leverhulmia mariae* (Anderson & Trewin 2003), as noted above.

Collembolans and myriapods have been suggested as Early Devonian detritivores (Rolfe 1980; Anderson & Trewin 2003), although myriapods have also been suggested as sporivores (Labandeira 1998; Collinson 1999). Body morphology (Rolfe 1980; Shear *et al.* 1995; Anderson & Trewin 2003) and gut-content (Anderson & Trewin 2003) suggest that they were detritivores. The ichnogenera *Lancifaex* and *Rotundafaex*, described in this paper, are concluded to be further evidence for detritivores, and are of a suitable size to have been produced by collembolans or myriapods.

Coprolites and gut content indicate the presence of a group of omnivorous consumers, presumably detritivores and saprovores, whose dietary intake included plant and fungal resources, mineral grains and more rarely animal tissues. It seems likely that they would, to some extent, rely on the decomposition of tissues prior to ingestion. This is true of modern detritivores, and the common lack of degradation noted in the contents of ancient coprolites suggests that it is also true of ancient detritivores.

10.3. Sap-sucking, micro-herbivory and mycophagy

Modern mites are known to target soft tissues such as cortex and phloem (Zachariae 1965; Bal 1973; Babel 1975) and to extract phloem sap from plant axes (Rolfe 1980; Risebrow & Dixon 1987). Wounds observed on plant axes have been interpreted as evidence for arthropods having pierced the epidermis to suck sap from the phloem (Kevan *et al.* 1975; Banks 1981; Banks & Colthart 1993). Although not all damage is attributable to herbivory, degradation of cortex tissues, without reaction from the plant, in plant axes from the Rhynie chert has been interpreted as the product of natural collapse of the tissues once the plant has died (Trewin 1996).

Modern micro-herbivores produce copious amounts of clustered faecal pellets. Although it is difficult to prove that such consumers were present in early terrestrial systems, *Bacillafaex constipata* pellets are remarkably similar to the faecal matter produced by such herbivores. These coprolites suggest the presence of microherbivores, the most likely microherbivores in the Early Devonian terrestrial ecosystems are oribatid mites and possibly collembolans (Banks & Colthart 1993).

Arthropod–fungal associations are well documented in modern systems (Ananthakrishnan & Dhileepan 1984), and fungi are understood to have played an important role in early terrestrial nutrient cycling (Taylor & Osborne 1996). Fungal spores, and to a lesser extent hyphae, are common in these coprolites, but only occur in coprolites with diverse content. While they presumably contributed to the diet of omnivorous consumers, these coprolites do not demonstrate the presence of consumers which targeted fungal resources as a food source.

10.4. Predators

Evidence for animals with a predatory feeding strategy and carnivorous diet comes from the morphology of jaw parts (Rolfe 1980; Dunlop 1996) and comparison with modern counterparts. A number of early terrestrial arthropods are interpreted on this basis to be carnivorous. However, the only coprolites which contain animal remains also contain plant remains, suggesting that the consumer was omnivorous and possibly a detritivore. Rare, small and amorphous coprolites are possibly the product of carnivores. These (*Bacillafaex mina*) are comparable with the rare, tiny faecal products of modern spiders. Carnivorous arthropods are efficient in nutrient assimilation and it is unsurprising that the faeces of carnivores are rare.

Possible carnivores and predators include trigonotarbids, arachnids, scorpions and centipedes. The only coprolites which are suggestive of carnivores are small, amorphous coprolites (*B. mina*). Rare heterogeneous coprolites include arthropod cuticles. Since these coprolites also include mineral grains and plant matter, they are interpreted as the product of detritivores.

Dunlop (1996) observed that predators dominated the early terrestrial arthropod scene. However, there is significant evidence for herbivores and detritivores (see previous discussion), and the coprolites reported here suggest that detritivores were active in early terrestrial ecosystems.

Figure 10 illustrates a probable early terrestrial food web. The interpretation of coprolites in terms of trophic level (detritivore, herbivore, predator) is confident. However, the interpretation of the same fossils in terms of producer identity is less certain. The most common coprolites are those of detritivores. This is likely to be in part because detritivores produce more faecal material than carnivores. On the basis of the coprolite assemblage described here, it is concluded that, in this community, detritivores were common and selectively feeding herbivores were present. There is a high degree of interconnectivity in the reconstructed foodweb, and in an ecosystem dominated by primitive arthropods consuming plant debris and tissues, fungi and bacteria would play important roles both as food and as decomposers.

11. Conclusions

Soils and detritus clearly played an important role in ancient terrestrial ecosystems, and the Rhynie cherts and associated sediment, rapidly preserved *in situ*, provide examples of early terrestrial 'soils' (Trewin 1994, 1996; Anderson & Trewin 2003). It seems likely that early terrestrial soils were spatially varied in content and degradation, and as noted by Wright (1985), poorly mixed and aerated, thin veneers susceptible to removal by erosion. The fossils preserved in the Rhynie chert suggest that the organic soil component was predominantly of plant origin and that distinct floral communities existed (Powell *et al.* 2000).

As in modern soils, organic matter varies in digestibility and the rapidity with which it is re-assimilated into the nutrient cycle. Plant spores are very resilient to degradation, while at the other extreme, the inner cortex of plant axes and parenchyma offer an easily degraded, accessible food source. Fungi are believed to have played a major role in decomposition (Taylor & Osborne 1996; Taylor *et al.* 2004), but the role of bacteria is uncertain; they are rarely fossilised.

Spore-rich coprolites are present in small numbers. A possible interpretation of this is that they indicate the presence of spore-feeders, spore-feeding being a known strategy in some modern arthropods and insects. However, spore-rich faeces are not exclusively produced by spore-feeders; detrivores feeding on debris that contains spores also produce spore-rich faeces. Spores, often dispersed in masses or clusters, contributed significantly to the organic detritus in the Rhynie chert. An animal ingesting such detritus would consume spores and spore masses, and produce diverse faecal matter: faeces rich in spores, faeces with some spore content and faeces without spores at all. Spore-rich coprolites cannot be assumed to indicate a spore-feeding group. Given their rarity and the presence of plant spores in varying abundance in coprolites with diverse content, the spore-rich coprolites in this assemblage are interpreted to be the product of detritivores.

The coprolites preserved here indicate two broad feeding strategies:

(1) Indiscriminant feeding on (presumably) detrital matter. Ingestion has little effect other than mastication, and the resulting faeces contain pristine particles of plant tissue as well as degraded material. The state of the faecal content depends on its state prior to ingestion more than changes which take place during its passage through the gut. These consumers were presumably dependant on microbial or fungal decomposition prior to ingestion, in order to extract nutrient. The diversity of coprolites attributed to this group suggests that at least two separate groups of consumers used this feeding strategy. The most likely producers are collembolans and myriapods.

(2) Discriminant feeding on digestible material results in faecal products which are amorphous and rarely contain identifiable fragments. Since the faecal content is amorphous, it is not possible to ascertain its origin or how digestive processes altered the intake. The coprolites indicative of this feeding strategy were produced by two types of consumer. Microherbivores, concluded to be oribatid mites, produced clusters of coprolites, and selective consumers, possibly trigonotarbids, produced minute faeces.

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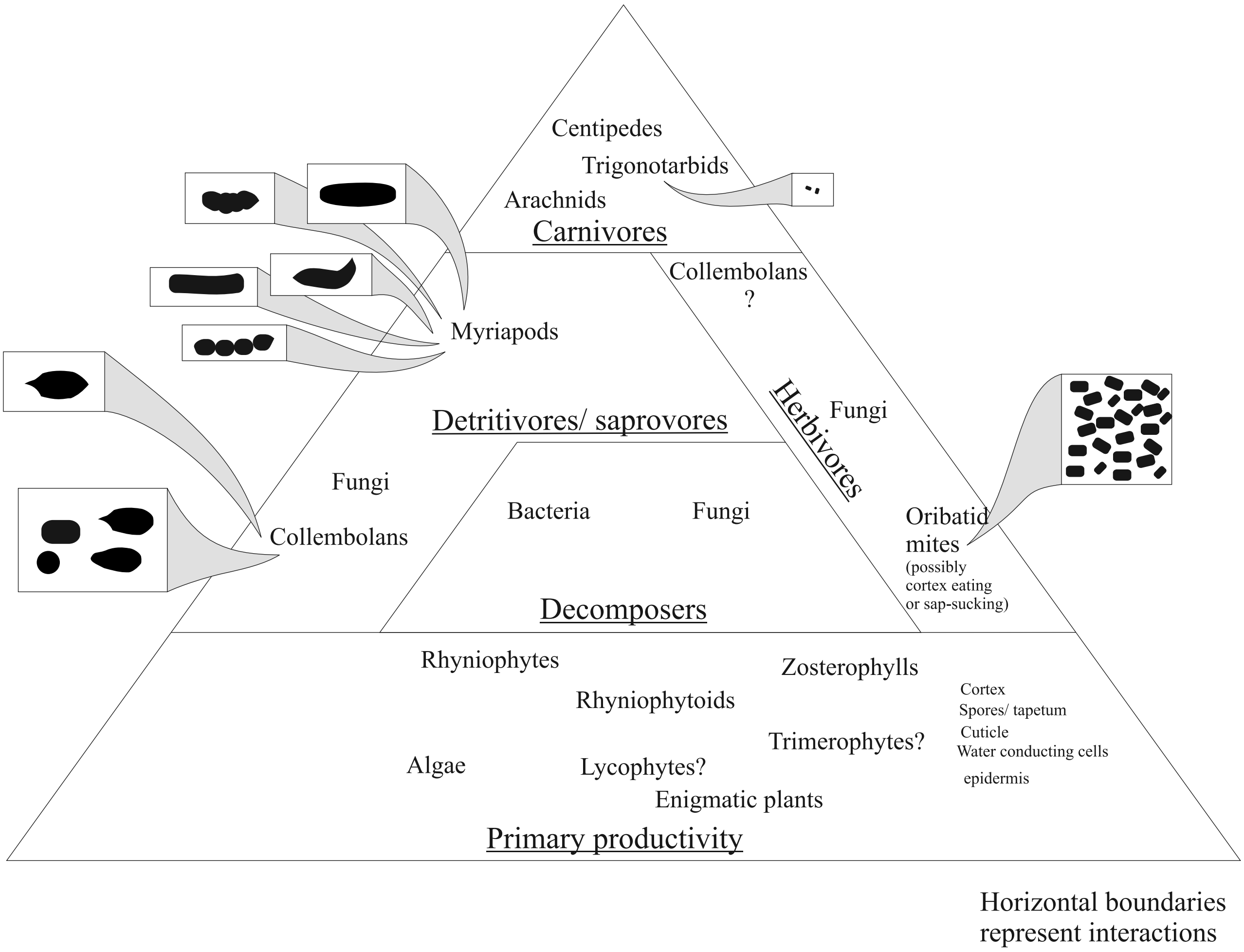

Figure 10 A reconstructed foodweb for the Rhynie chert terrestrial community.

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