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Coprolites as evidence for plant–animal interaction in Siluro–Devonian terrestrial ecosystems

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A FEW remarkable finds document the colonization of land by animals and plants in the mid-Palaeozoic^{1–3}, but much rarer is unequivocal evidence for plant–animal interaction^{4,5}. Here we announce the discovery of coprolites (fossil faeces) in Upper Silurian (412 Myr) and Lower Devonian (390 Myr) rocks from the Welsh Borderland that pre-date examples of similar composition in the Carboniferous by about 90 million years^{6,7}. The majority consist predominantly of undigested land-plant spores with varying proportions of cuticles, tubes and less readily identifiable (presumably plant) material. Because coeval animal fossils of suitable size are carnivores⁸, direct evidence for the coprolite producers is lacking, but we speculate that they could have been spore eaters (and hence the earliest example of herbivory of higher plants) or detritivores similar to modern millipedes. In either case, they demonstrate the cycling of primary productivity in early terrestrial ecosystems.

The majority of coprolites were recovered by hydrofluoric acid bulk maceration of fluvial siltstones (overbank flood deposit) from a Lower Devonian stream-side locality (Mid Lochkovian: mid *micromnatus-newportensis* Spore Biozone) on North Brown Clee Hill, renowned for its excellent cellular preservation in plant mesofossils⁹. The three Silurian examples occurred in marginal marine facies (Ludford Lane (1) and Perton Lane (2)), of Přídolí age. Ludford Lane has yielded the earliest terrestrial animals¹

and Perton Lane has a diverse rhyniophytoid assemblage¹⁰. At all localities, macerates also include axial, commonly fertile, higher plant fossils, and cuticles of higher plants, '*Nematothallus*', eurypterids and 'myriapods'.

In that they contain spores, the coprolites (Fig. 1) were initially thought to be isolated sporangia, but their regular shape, lack of an enclosing sporangial wall, presence of more than one spore type (up to nine in some specimens: 25 different spore types in total; Table 1), varying proportions of cuticles, tubes and less readily identifiable plant debris, rule out this possibility. As sedimentological evidence shows that the coprolites have drifted from near or far into these marine and fluvial depositional environments, were they produced by terrestrial or aquatic animals? Evidence favouring aquatic ones is the presence of cuticles of possible aquatic animals (eurypterids, scorpions and kampecarid 'myriapods') in the same sequence, though some or all of these may have been terrestrial or amphibious in the Devonian^{11,13}. Evidence for a land origin is considered more compelling in that the coprolites are consistently associated in both marine and freshwater facies with predominantly land-derived debris of the same preservation characteristics.

Were the coprolite producers feeding on living plants (herbivores) or on dead plant material (detritivores)? Considering the first possibility, extant herbivores exploit gut fungi and bacteria to degrade cellulose, but even with the assistance of such 'biochemical brokers'¹⁴, the nutrient value of living vegetative tissues would have been low. Sporangia and spores would have provided an energy-rich diet of presumably relatively high nitrogen content^{15,16}, and thus spore feeding becomes an attractive possibility. Indeed, it has already been suggested that pollen feeding preceded herbivory in insect evolution^{7,14}. This would explain why large numbers of a single spore type dominate many coprolites, whereas the higher frequency of tetrads (in comparison with dispersed spore assemblages) suggests that immature sporangia were eaten. It would also account for the presence of spines on sporangia¹⁰. The question then arises as to whether spores and pollen are directly comparable in availability of spore contents because sporopollenin itself is unlikely to have been digested. Extant pollen feeders obtain such nutrients by either mechanical lysis (for example, maceration in beetles) or chemical means (such as secretion of enzymes and/or simple diffusion in flies¹⁷). The first seems unlikely for our animal as so few spores are incomplete or broken and often remain in tetrads. Those that are cracked open are larger, usually smooth, ones (Fig. 1j), suggesting accidental breakage on passage through the animal or during post-depositional compression rather than deliberate lysis. Considering diffusion, our ultrastructural studies show¹⁸ that the fossil spores lack any areas of wall without sporopollenin (compare colpi and sulci of pollen) and that in *in situ* spores the trilete mark consists of a fold in the exospore, a slit presumably developing before germination. Diffusion would have had to occur through microcapillaries in the sporopollenin-impregnated wall. The limited available experimental data (on green mature *Onoclea* spores¹⁹) indicate that only very small molecules (smaller than glycerol) can pass through, and not macromolecules such as enzymes, although permeability increases with age of mature spore and proximity to germination. Thus, extraction of nutrients by diffusion alone seems unlikely, and diet might have been supplemented with extra-exospore material such as perispore or locular fluids. However, as sporangial walls were composed of thick-walled cells and were highly cuticularized, it is puzzling that they are not found more commonly, in coprolites (Fig. 1q) if the animals were spore feeders.

Another explanation is that the animals were feeding on litter rich in spores and spore masses. The former would explain the diversity in the spores found in very small numbers, and the latter might reflect dispersal in clumps in certain taxa (for example, *Cooksonia pertoni*⁹) or production of sporangia at ground level (for example, certain extant hepatics, where spores also sometime occur in tetrads). The high spore concentration

FIG. 1 All examples Devonian (HD) except a and l (Přidolí: LL and PL). a–e, Range in shape of more regular and complete coprolites (40% of assemblage): 3.3×1.27 to 0.53×0.22 mm. a, Elliptical, with mainly cuticle and occasional spores (LL1 $\times 87$). b, Elongate with slight asymmetry, mainly spores (HD1 $\times 17$). c–d, Obliquely truncated (compare with modern millipedes), outline varying with degree of compression and composition. Spore-dominated forms have smooth outlines except when impregnated by pyrite, when they are three-dimensional and knobbly. (d, HD4 $\times 24$; p, HD16 $\times 185$). Cuticle- and unidentifiable-plant-debris-dominated forms are usually less regular, with numerous voids separated by draped debris (c, HD3 $\times 18$; e, HD5 $\times 32$). Many are partly compacted and show broad, ill-defined, oblique, shallow depressions (d, e). e, Contains mangled tissue from new tetrad-containing plant. f, *Laevolancis divellomedia* (of dyad origin), with amorphous slime (possibly anal-gland glue) and some cuticle (HD6 $\times 190$). g, *Pero-trilites* sp. with wrinkled outer layer and adhering apiculate forms (HD7 $\times 490$). h, Apiculate monads including *Streelispora newportensis*, *Aneurospora* sp. and ?*Emphanisporites* sp. (HD8 $\times 668$). i, Undescribed spore of dyad origin (HD9 $\times 615$). j, Large laevigate, split disk, intact *Streelispora newportensis* (papillate) and example of rare piece of indeterminate, probably higher plant, tissue (sterome?) (HD10 $\times 500$). k, Undescribed apiculate spore (dyad origin) with small apiculate tetrad (HD11 $\times 780$). l, Extremely well-preserved *Apiculiretusispora*; cf. *synorea* (PL1 $\times 1,660$). m, Possibly *Retusotriletes warringtonii* (HD13 $\times 950$). n, *Archaeozonotriletes* sp. with plant debris (HD14 $\times 455$). o, Indeterminate laevigate spores with interspersed cuticular sheets; latter are commonly stacked, fibrillar but rarely powdery; stomata have not been seen (HD15 $\times 235$). p, Laevigate tetrads filled with pyrite (HD16 $\times 190$). q, Fragments of sporangial cuticle (HD17 $\times 190$). r, Unique example of lumen cast of tracheid, grooves marking positions of spiral secondary thickening (HD18 $\times 1,880$).

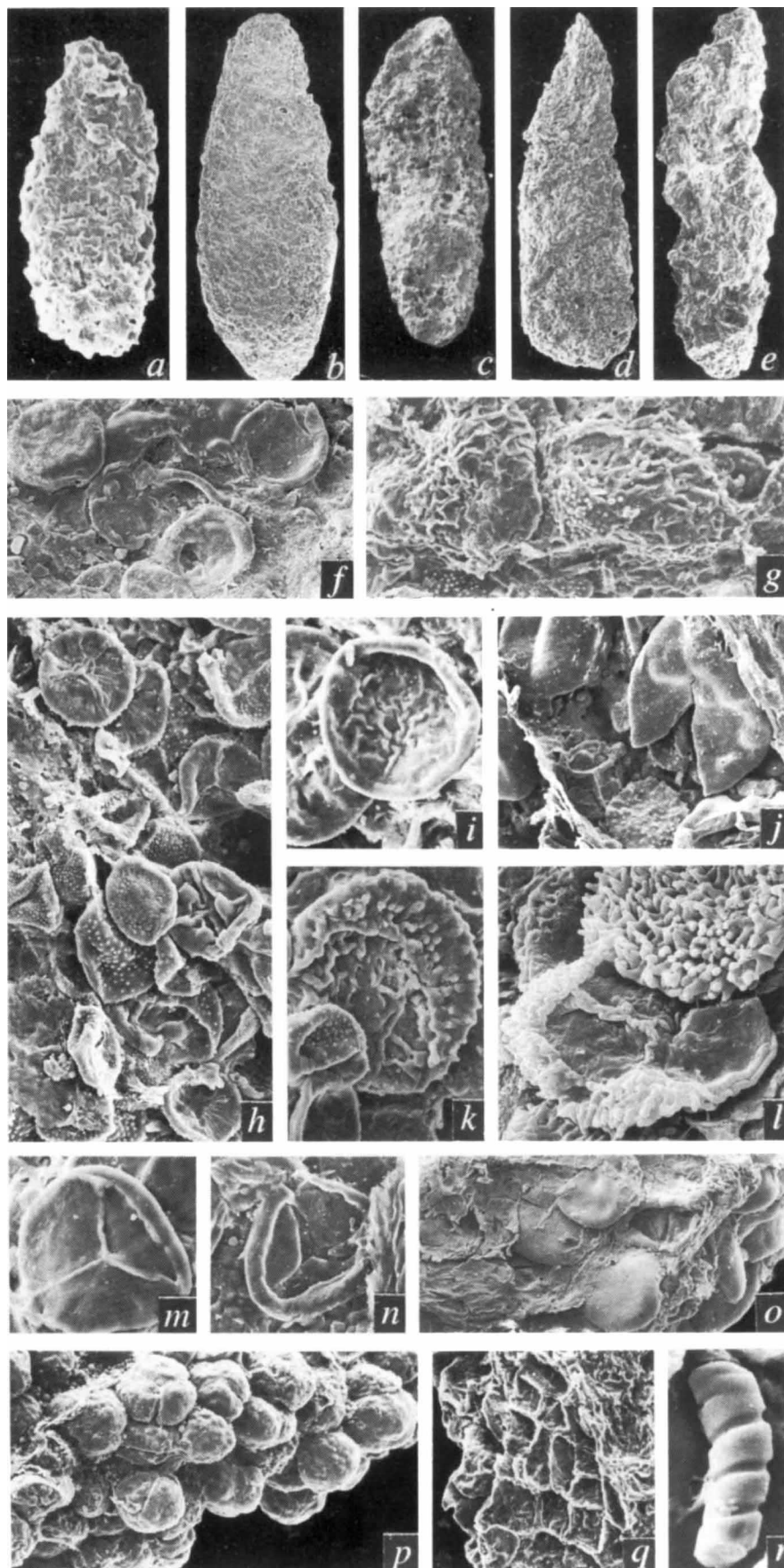


TABLE 1 Dispersed spore taxa recorded in coprolites and possible parent plants

Spore taxon	Frequency	Occurrence	Source	Fig.
<i>Ambitisporites avitus</i>	r	mt		1o
<i>Ambitisporites dilutus</i>	c	m	? <i>Cooksonia pertoni</i>	1m
<i>Ambitisporites</i> sp. (S)	r	m	? <i>Cooksonia pertoni</i>	
<i>Aneurospora</i> sp. (many varieties)	c	m	<i>Cooksonia pertoni</i> / <i>Salopella</i> sp.	1h
Apiculate cryptospores (4 new species)	c	d		1k
Apiculate/granulate tetrad	vr			1k
<i>Apiculiretusispora</i> cf. <i>synorea</i> (S)	c	mt	P (discoidal)	1l
<i>Archaeozonotriletes dubius</i>	r	mt		1n
<i>Artemopyra</i> sp. (cryptospore)	r			
<i>Chelinospora</i> sp.	vr	m	P	
<i>Cymbotrilletes</i> sp.	r	t		
<i>Emphanisporites micromnatus</i> ?	r	m		
<i>Emphanisporites</i> sp.	r	m	P	
<i>Hispanaediscus</i>	r?	d		
Laevigate tetrads, large	c			1j
Laevigate tetrads, small	r			
Laevigate tetrads with low ornament	c			1p
<i>Laevolancis divellomedia</i>	r	d	P	1f
<i>Perotrilletes</i> sp.	r	t	P	1g
? <i>Retusotrilletes warringtonii</i> n. sp?	vr	m	'Zosterophylls'	1m
<i>Streelisporea newportensis</i>	c		<i>Cooksonia pertoni</i>	1h,j
<i>Synorisporites verrucatus</i> (S)	c	m	P (discoidal)	
<i>Synorisporites</i> n. sp.	r	mt		

All Lower Devonian, except (S), which indicates Silurian. c, Common; r, rare; vr, very rare; m, monad; t, tetrad origin; d, dyad origin; P, present in as-yet unnamed sporangia. Not all spores can be matched with published dispersed spore taxa. This particularly applies to some of the commonest spores (apiculate monads in Fig. 1h) and laevigate tetrads (Fig. 1p), where details of distal and proximal surfaces are needed for identification. Difficulties also arise in identifying contorted or partially covered spores and those draped with a featureless film quite distinct from macerated cuticle (Fig. 1f).

in coprolites could result from digestive processes, coprophagy, or selective feeding. Litter feeders eat a variety of food: softer (for example, parenchymatous) tissues are more readily digested or compacted, and less recognizable in faeces. This might also account for the lack of identifiable fungal remains in the coprolites. Bacteria and fungi are important components of litter as both food sources and as endosymbionts for detritivores. Bacterium-sized particles in certain coprolites may be Recent, although precautions were taken to avoid contamination. Many litter arthropods ingest faeces, further concentrating more resistant items such as spores or cuticles. Selective feeding is perhaps the least plausible explanation, although 'leaky' spores might provide an energy source, as would the remains of extra-exosomal material and any saprotrophs living on it. However, apart from a few examples with roughened surfaces, the spores show no signs of bacterial or fungal damage²⁰, and are notable for the clarity of their surface detail—points in favour of sporangial feeding. Finally, overrepresentation of spore-bearing coprolites might result from choosing specimens for scanning electron microscopy. Feeding experiments with millipedes show that faecal pellets dominated by non-spore plant material are less regular in shape and so their fossils could be overlooked.

Whereas evidence for the feeding habits of the coprolite producers is equivocal, that for the animals themselves is even more obscure. Size of the coprolites would exclude most collembolans, mites and nematodes (too small), and earthworms (too large). Comparison with animals that are known or are likely to have evolved by Devonian times suggests that arthropods are the best contenders and that, for detritivores, 'myriapods' and large collembolans are the front runners. Although rather small kampeparid 'myriapods' occur in the same beds as the coprolites, little is known of their biology¹³. The oldest diplopod occurs in the late Silurian of Scotland, but the habitat (aquatic rather than terrestrial) of this and later Lower Devonian millipedes remains contentious²¹. Fossils of unequivocal herbivores are lacking from early terrestrial ecosystems, but indirect evidence for their activity comes from stems with wound response tissues, possibly due to chewing, and stained lesions, possibly a response to sap sucking which would leave no solid faeces. The few examples of appropriately sized extant embryophyte-spore feeders (such as ants²²

and moth caterpillars (D. Carter, personal communication)) come from groups not likely to have evolved by Silurian times.

In the light of such uncertainties, discussion on the relevance of our findings to the evolution of terrestrial ecosystems is perhaps premature. If the coprolite producers were detritivores, they demonstrate a logical extension of the microphytophagy first evidenced in the Silurian by faecal pellets of ascomycete hyphae^{23,24} and show that vegetation was being recycled through decomposer levels, as in soil and litter communities today. If herbivores, they add weight to the hypothesis that feeding on sporangia may have been more common and pre-dated that on vegetative organs¹². Given the sparse evidence for plant damage in the Devonian and Carboniferous¹⁷ and vertebrate herbivores until the Permian²⁵, it is possible that widespread herbivory did not arise until latest Palaeozoic times. □

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