

INTERRELATIONSHIPS OF EARLY TERRESTRIAL ARTHROPODS AND PLANTS

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ABSTRACT. At the dawn of terrestrial life some remarkably close interrelationships between arthropods, vascular plants, and fungi existed and promoted co-evolutionary developments which, in the same or analogous forms, have since remained fundamental in the functioning of ecosystems. The fossil record and hypotheses on phylogenies are examined in terms of functional morphology. Spore-eating and disseminating arthropods existed at the same time as the spores of terrestrial plants and fungi became more diverse and obtained characters indicative of protection from and/or dissemination by arthropods. An appendix discusses other aspects of the functional morphology of spores. Arborecence and structures on the stems of plants precede the arrival of alate arthropods, and may have been initially protective. Subsequent events indicate a dispersal role of those features for the insects and the spores they carried. Further evidence suggests that the first terrestrial arthropods were the cause of lesions described from Devonian plants. Such lesions could then have become sites for fungal and other infections. The parasitic, first terrestrial fungi show similar protective and dispersal relations with arthropods as those shown by vascular plants.

'It would seem probable that the first step in the evolution of true insects from some marine form of Arthropod was taken through an ecological association with the special group of plants which first made good their footing on the dry earth; most probably the Arthropods fed on the plants, and evolved with them, changing their mode of life and their forms as their food plants changed theirs' (Tillyard 1928). And, in reference to the earliest known fossil arthropods of the Devonian, 'one can conceive of forms like *Peripatus* living under rocks . . ., one can admit that scorpions may have lurked in the crevices, Thysanura may have run or jumped about there, and Collembola and Acarina may have worked amongst the debris as they do today' (Tillyard 1931, p. 82).

These two quotations were chosen as they point out the speculative nature of endeavours such as this work, suggest a possible close interrelationship of the terrestrial arthropods and the plants on which they lived (1928), and, paradoxically a non-specific dependence of these arthropods on detritus (1931), while at the same time suggesting that ecological connections of arthropods and plants were established as soon as the former started colonizing dry land.

Other workers, notably Bekker (1947), Taugourdeau Lantz (1971), Smart and Hughes (1973), have indicated similar relationships of early terrestrial arthropods, particularly Collembola, with detritus and with spore feeding. It is even suggested that those arthropods had an important role in spore dispersal, not only for vascular plants (Taugourdeau Lantz 1971) but also for fungi (Bekker 1947).

This paper explores in greater detail the possible interrelationships of arthropods, vascular plants, and fungi at the time when the process of the colonization of the land was just beginning, about 400×10^6 years ago. Evidence to suggest some complex interactions at the advent of co-evolution in terrestrial organisms is drawn from functional interpretations of structure found in Devonian fossils, from analogous modern phenomena, and from assessments of proposed phylogenies.

ARTHROPODA

Ghilyarov (1956, 1959, and earlier) and Manton (1973) propose that the origins of terrestrial Atelocerata (myriapod-insect line) was through minute skin-breathing annelids, or possibly Onychophora which left the water to inhabit damp soil litter. An onychophoran, *Aysheaia pedunculata* Walcott, which grew to about 50 mm is known from marine deposits of the middle Cambrian (Walcott 1911; Hutchinson 1930), and the possibility of even earlier Onychophora exists (cf. Moore 1959). In the soil, increased abrasion and friction necessitated the development of a tougher integument and strong locomotory appendages. This led to the myriapod condition, which was modified by the reduction in the number of legs in accordance with the greater importance of the forelimbs in crawling through narrow passages in the soil. No matter whether the origins of the terrestrial Atelocerata was through Crustacea (Sharov 1966, p. 60) or as described above through Annelida and Onychophora (Tiegs and Manton 1958; Manton 1964, 1969, 1973; Mackerras 1970), myriapods are considered closely related to the hexapods.

Evolution of Chelicerata to the terrestrial habit presumably took place independently of that of Atelocerata. They first appear to have been marine scorpion-like creatures (Aglaspida) which seem closely related to the Eurypterida (sea scorpions) known from Cambrian time. The origins of terrestrial Chelicerata (Arachnida) seem equally ancient (Størmer 1955).

The early arrival of apparently predatory chelicerates on land in the Devonian (see p. 393) indicates that there was probably terrestrial prey at that time. Presumably there were numerous subterranean annelids, other metazoa, and protozoa on which early air-breathing arthropods preyed, and of which we have no fossil record. Another possibility is that at least some early air-breathing arthropods were amphibious, or that at least some were not predators. More will be said of this later.

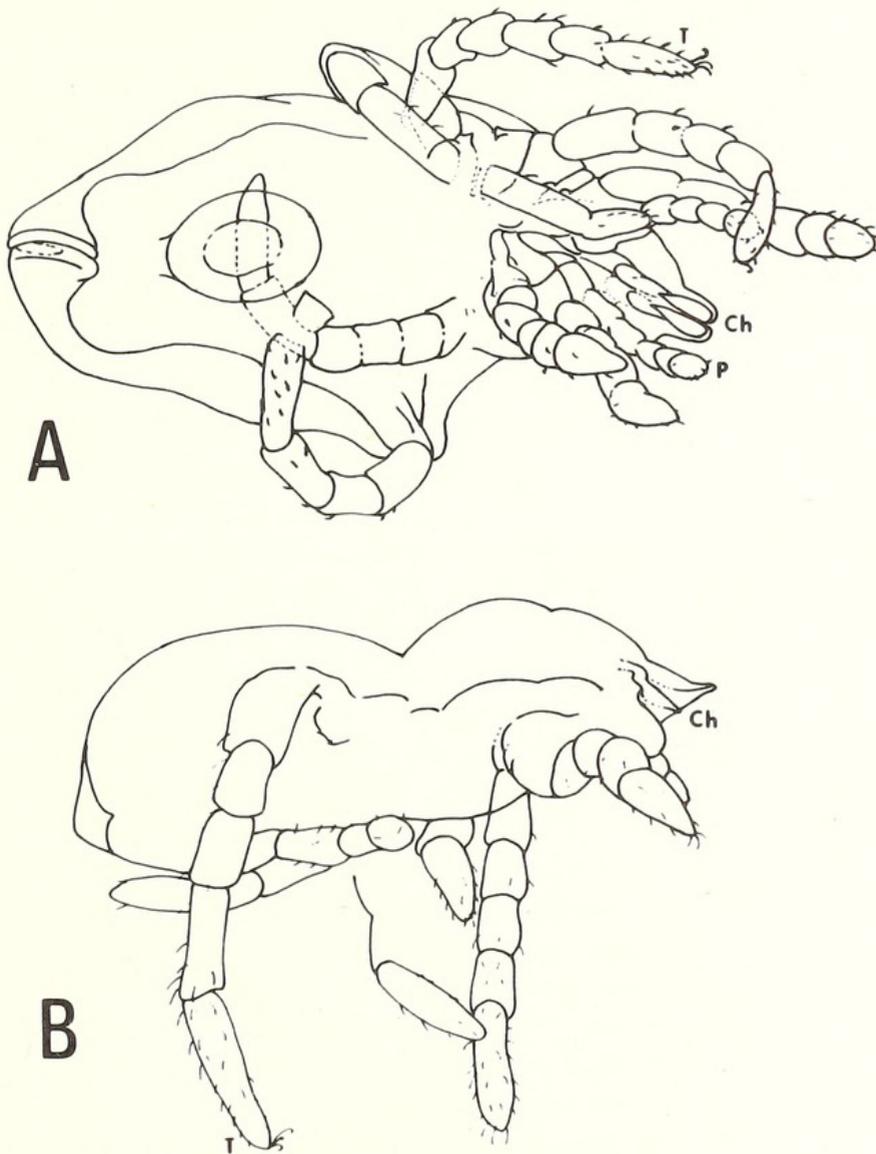
Fossil record and plant relationships

Unfortunately, the fossil record for terrestrial animals in the Devonian and earlier is very sparse. The earliest record is that of myriapods: *Archidesmus loganensis* from the Llandovery/Wenlock (Silurian) and *A. macnicoli* and *Kampecaris* spp. from the Lower Devonian Old Red Sandstone (Peach 1882, 1898; Crowson *et al.* 1967) (text-fig. 4*m*). Hoffman (1969) suggests that there is reason to suspect that some Palaeozoic myriapods were aquatic or semi-aquatic. On the basis of fragmented specimens it is known that the first genus grew in excess of 5 cm and the second 2 cm. Sharov (1966, p. 61) and Hoffman (1969) indicate that these animals (Archipolypoda) are close to Diplopoda, Pauropoda, and Chilopoda, but they provide no additional clue to their relationships with the Hexapoda. Most myriapods (Symphyla, Pauropoda, and Diplopoda) feed on plant debris; only the Chilopoda (centipedes) are carnivorous, and almost exclusively so, being equipped with poison fangs. It is logical to suppose that the fangs developed by specialization of a pair of segmental appendages of the ancestral group to which the above-mentioned fossils seem to belong (Sharov 1966, pp. 61-67; Manton 1969; Hoffman 1969).

What little we know of other Devonian terrestrial arthropods is mainly derived from the Rhynie Chert of early Old Red Sandstone age in Aberdeenshire, Scotland.

The age of this important occurrence is probably Siegenian/Emsian (see discussion in Chaloner 1970). Arthropod fossils have been described by Hirst (1923), Hirst and Maulik (1926), Tillyard (1928, 1931), Scourfield (1940*a*, *b*), Petrunkevitch (1953, 1955), Crowson *et al.* (1967), and others. Tasch (1957) has discussed aspects of the palaeoecology of the aquatic arthropods.

Hirst (1923) describes an assemblage of Chelicerata of which *Palaeocteniza crassipes* (Araneae?) and *Palaeocharinus* spp. and *Palaeocharinoides hornei* (now referred to Trigonotarbida: Palaeocharinidae) are all small (less than 3 mm), apparently predatory terrestrial animals (see also Petrunkevitch 1953, 1955). Hirst also described a mite (text-fig. 1), *Protacarus crani*, which was thought to resemble



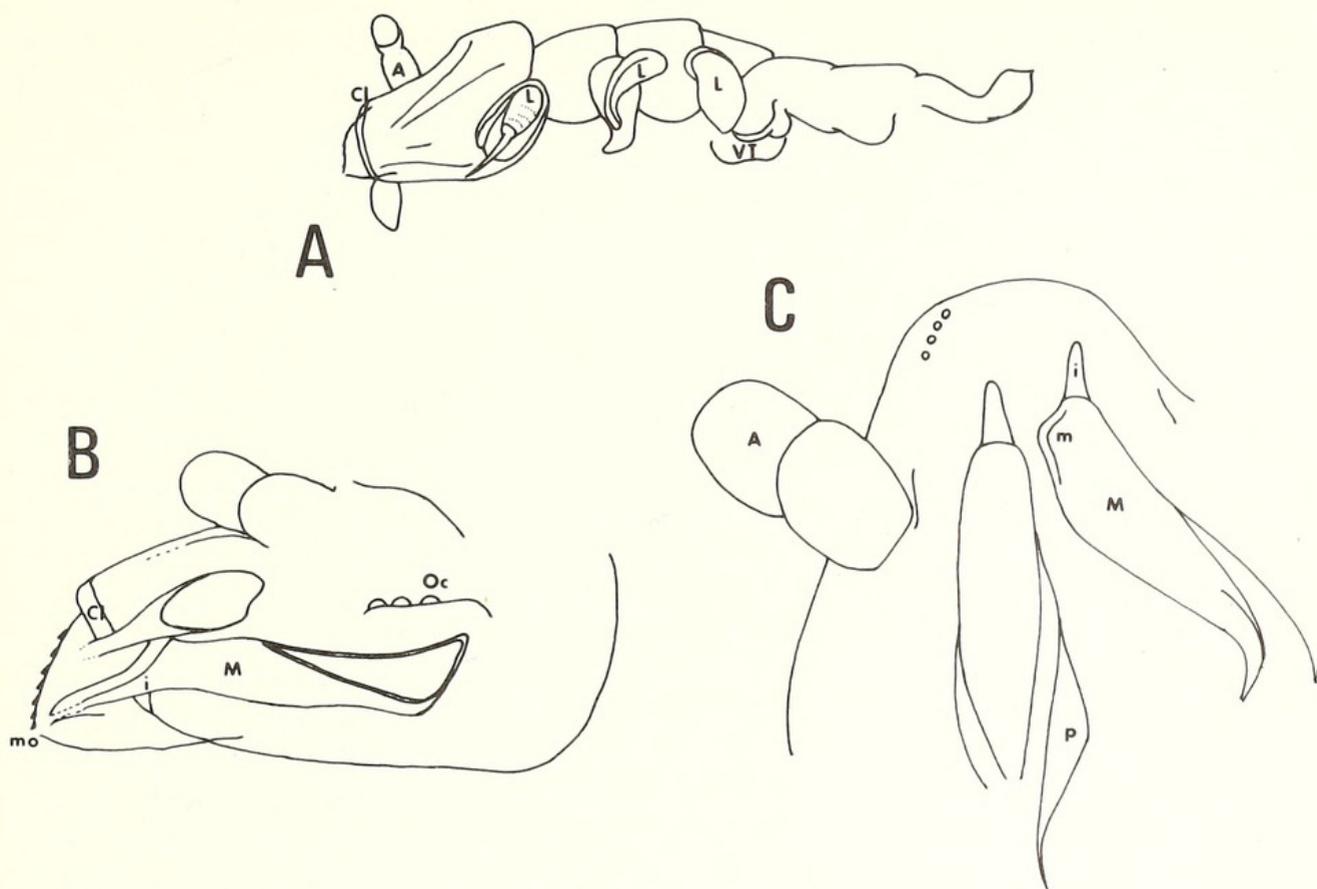
TEXT-FIG. 1. *Protacarus crani* Hirst. A, ventral aspect of *P. crani* (?) (from Hirst 1923) body length 448 μm . B, lateral aspect (from Hirst 1923) body length 310 μm . (By permission of the *Journal of Natural History*, Taylor and Francis, Ltd., London.) Explanation of lettering: Ch, chelicerae; P, pedipalp; T, tarsus showing the three well-developed claw-like setae.

modern running mites (Eupodidae) (Petrunkevitch 1955), but which is now regarded as being most closely attributable to the Pachygnathidae (cf. Krantz 1970, p. 144; Zakhvatkhin 1952), primitive mites which commonly live in forest litter. The fossils of *P. crani* range from 290 μm to 400 μm and apparently had strongly cutinized and pointed tips to their two-segmented chelicerae (see text-fig. 1A). Their pedipalpi were slender. These stylet-like mouthparts suggest that the animals fed on small particulate matter, or perhaps more likely pierced plant or animal tissue to imbibe liquid through the wound (see below). It is almost impossible to say more about their possible diet because of the lack of preservation of internal organs, and almost nothing is known of the diets of modern Pachygnathidae (Krantz 1970, p. 144). The body of *P. crani* may have been covered with fan-shaped setae and the legs had short, curved spines (text-fig. 1).

Hirst and Maulik (1926) described some other animals from the same formation, the first being a minute chelicerate, '*Crania*' *rhyniensis*. (It should be noted that '*Crania*' as used here requires a new name, and is not the inarticulate brachiopod genus.) The second description is of the collembolan, *Rhyniella praecursor* (text-fig. 2), which excited much interest as the oldest known fossil insect (although modern works separate Collembola from Insecta). *R. praecursor* was 1–2 mm long. Its mandibles are reminiscent of those of the Machilidae (*Thysanura s. l.*) in having well-separated molar and incisor regions. Text-figure 2B and C show the weakly developed molar region and the well-developed incisor region, which Scourfield (1940*b*) shows as more elongate than Tillyard (1928) indicates. Massoud (1967) shows some finer details of the mouthparts. Collembola are generally herbivorous or saprophagous (Christiansen 1964). The lack of a well-developed molar area indicates that *R. praecursor* did not eat material needing mastication. Possible foodstuffs include soil micro-organisms, spores, and plant juices obtained through puncture wounds (cf. *P. crani*) (see p. 400 below), although for the latter habit the mandibles do not resemble the piercing type of modern collembolan mandibles.

The affinities of *R. praecursor* are discussed by Tillyard (1928) on the basis of heads only. His conclusions are amended by Scourfield (1940*a, b*) on the basis of additional more complete specimens. *R. praecursor* has traits of both Hypogasturidae and Entomobryiidae, so Scourfield suggests that it be placed in the family Protentomobryiidae erected by Folsom (1937) for fossil Collembola from Cretaceous amber. Massoud (1967) and Delamare Deboutteville and Massoud (1967) remark on the similarity of *R. praecursor* to a modern family of Collembola, Neanuridae, which is sometimes considered as part of the Hypogasturidae. Crowson (1970) found this similarity so striking that he suggested that these 'Devonian' fossils of terrestrial animals could be 'modern contaminants'. Both Hypogasturidae and Entomobryiidae are well-known pollen (Kevan and Kevan 1970) and spore (Christiansen 1964) eaters.

Hirst and Maulik (1926) also illustrate some mandibles, which they do not name. Tillyard (1928) describes them under the name *Rhyniognatha hirsti*. Illustrations in both works are similar, but not identical. The mandibles are reminiscent of the sharp bladed and toothed jaws of a carnivore. Tillyard (1931) hints that they may be thysanuran and Hirst and Maulik suggest they may be larval. The former suggestion does not seem probable and the latter is unlikely as it would require the existence of holometabolous insects in the Devonian.



TEXT-FIG. 2. *Rhyiella praecursor* Hirst and Maulik. A, head, thorax with legs (L) and three abdominal segments; 'probably a cast skin' (from Scourfield 1940a, b). Length of entire animal probably about 1.5–2.0 mm. B, head capsule showing mandibles (M) and other features (from Scourfield 1940a, b). C, head capsule showing mandibles (M) with well-developed incisor region (i) and less-developed molar region (m). Length of head capsule from apex to end of the pedical of hypopharynx (p) is 314 μm (from Tillyard 1928). (A, B, by permission of *Nature*, Macmillan Journals Ltd., London and the *Proceedings of the Linnean Society*, London, Academic Press Inc., London. C, by permission of the Royal Entomology Society of London.) Explanation of lettering: A, antenna; Cl, clypeus; i, incisor region of mandible; L, leg; m, molar region of mandible; M, mandible; mo, mouth; Oc, ocelli; p, pedical of hypopharynx; VT, ventral tube.

It is curious that the preponderant fossil arthropods from the Rhynie Chert are apparently carnivores. These carnivores are also very small and presumably would be unable to tackle an animal as large as the myriapods which must have existed contemporaneously, if not in the same habitat (cf. Calman *in* Horne *et al.* 1920). It is unlikely that the assemblage of predators subsisted on Collembola and mites alone. Presumably a soil fauna of soft-bodied protozoa and small metazoans would have evolved in association with algae, fungi, and bacteria which must have preceded vascular plant colonization of the land. No fossil record of such fauna could be expected. It is reasonable to suppose that these perishable organisms may be the missing element in the food web (as it is represented in the fossil assemblage) on which the carnivorous arthropods were predators. If this is so, the arthropods preserved in the Rhynie Chert could be quite unrepresentative of the fauna which actually lived there at the time, in both numbers and species diversity. Possibly, at least some of the supposed predators were also facultative herbivores; presumably they could have fed

on plant saps and possibly spore protoplasts. Dr. W. D. I. Rolfe (pers. comm. May 1974) has discovered that 'a significant number of Rhynie trigonotarbid arachnids are preserved as fragments within empty sporangia of *Rhynia major* [see Pl. 56, fig. 3]. Another assemblage occurs within a stem fragment [Pl. 56, figs. 1, 2]. Whether such arthropods actively selected this micro-environment for feeding, as a temperature, humidity, or windspeed control, or whether they were swept in by post-mortem winnowing is unknown.' From the relatively unsorted state of the Rhynie plant material the latter mechanism seems the least plausible. We prefer to regard these arthropods within the sporangia and stem fragments as occupying a site into which they had moved in life, perhaps following spore-eating. This is of some interest, particularly because pollen and spore feeding is associated with the predatory habit, and evolution herefrom, in a large number of insect groups and in some mites. Another possibility is that some of the predators were amphibious, feeding in water and returning to land to evade the larger aquatic predators, i.e. the reverse of what happens now in most cases. In circumspection, it is reasonable to assume any combination of the above possibilities in considering the development of a diversity of ecological niches.

It appeared that the next stage of insectan evolution was exemplified by Rodendorf's (1961) finding of a fossil fragment from the late Devonian as a somewhat movable wing of an insect, which he called *Eopterum devonicum* (Eopteridae). The same author (Rodendorf 1970) described another Devonian fossil, *Eopteridium*, also in the Eopteridae, but later (Rodendorf 1972) he writes that eopterids are not insects but are eumalacostracan Crustacea. Despite this setback to a convenient theory it can be presumed that such primitive insects must have arisen at about the time indicated (text-fig. 4p) and that they were herbivores which climbed on to vegetation to feed (cf. Sharov 1966, pp. 117 *et seq.*; Crowson *et al.* 1967; Smart 1963, 1971; Smart and Hughes 1973). By the end of the Devonian, arborescent plants had become common (text-fig. 4l). Hocking (1957) writes that almost immediately, geologically speaking, following the development of tall plants the first winged insects appeared. Certainly increased humidity in the forests would have provided conditions more tolerable and more stable for evolution of above-ground dwelling arthropods. However, there is a gap of 50 million years from the upper Devonian until the base of the upper Carboniferous when 'winged' insects appear in the fossil record (cf. Riek 1970; Crowson *et al.* 1967). Those 'wings' or paranotal lobes could have functioned as gliding planes for descending insects (Hinton 1963; Flower 1964) either in escape or after feeding. Regarding the latter, Smart (1971) notes that a feature of plants of that time is stems with small up-pointed scale-like leaves or non-vascularized spines: such stems were probably easily ascended, but not easily descended. It is possible that spines and other enations which characterize several early land plant genera served to offer a readily climbed pathway for spore-gathering arthropods which would give such spines an adaptive significance beyond the mere increase in photosynthetic area, which is usually invoked. In contrast Chaloner (1970) suggests that spines on stems of some Devonian plants (e.g. *Psilophyton* spp.: Siegenian) may have been glandular, possibly with a secretion making them unpalatable to terrestrial invertebrates. These spines would afford protection for elevated sporangia from arthropods. The apparent paradox in the above reflects only that similar structures could have different functions

on different species or even in different stages of the same species. Other authors have suggested that such spines might have been an adaptation to a scrambling habit of growth. Spines generally are characteristic of at least two distinct groups of early Devonian plants, and they disappeared before the end of the Devonian (although glandular hairs with swollen tips are present in some Carboniferous pteridosperms); whereas scale-like leaves continue to modern times (text-fig. 4j). In the Carboniferous insect fossils become diverse, and their relationships with each other and with plants are beyond the scope of this paper (but see Hughes and Smart 1967; Smart and Hughes 1973).

TRACHEOPHYTA

The colonization of the land by plants is usually construed in terms of the rise of vascular plants. Although diversification of these tracheophytes must have affected the first major modification of the land as an environment for animal life, relatively simple plants (algae, fungi, bacteria) must have long preceded vascular plants at least in certain restricted habitats. All three of these groups have a long Pre-Cambrian history (Schopf 1970) and by the Devonian, as now, they must have constituted a significant microflora in suitable sites such as the intertidal zone, the sides of streams, and any terrestrial environments with impeded drainage. Presumably a soft-bodied microfauna of which we have no fossil record would have developed in such habitats. Early land-adapted arthropods might have been foragers on such a terrestrial fauna. The hypothesis of the existence of a pre-vascular land flora gains support from the diversity of early non-vascular land plants. The existence of stiff, upright plants apparently lacking vascular tissue is established for the early Silurian (Schopf *et al.* 1966) and possibly earlier (e.g. Fleming and Rigby 1972). There is a considerable diversity of non-vascular thalloid plants with a cuticle-like covering and resistant spores within the Devonian (*Foerstia*, *Parka*, *Spongiophyton*—see Lang 1945; Kräusel 1960). They are mentioned here merely to suggest that comparable non-vascular plants may have preceded the earliest tracheophytes, and that the pre-Devonian land surface was perhaps not as barren of plant life as the lack of fossil vascular plants might suggest.

Although some authors have claimed to recognize vascular plants in pre-Silurian rocks (e.g. Axelrod 1959) none of these show the criteria which are highly correlated with vascular plants (*viz.* xylem elements, cuticle with stomata, or spores with a triradiate suture) and as such, they are not generally accepted as vascular plants. It is still fair to say that no pre-Downtonian (pre-late Silurian) fossils are generally accepted as unequivocal vascular plants. None the less, it is clear that a number of Devonian plants showed adaptation to life on land (a cuticle, resistant spores) although lacking xylem, so that there was a sizeable element of non-vascular land plants accompanying the early tracheophytes.

In this review we are not concerned with all morphological features in which evolutionary changes can be traced in early terrestrial plants, but only with those which have a direct bearing on other organisms. These may be thought of in general terms as the production of erect vegetative organs, culminating in the arborescent habit; production of leaves or comparable organs in which phloem is accessible to

suitably adapted sap-feeding arthropods; and finally, spore-bearing organs and adaptations of spore size and sculpture in connection with arthropod feeding and transport of spores.

Vegetative organs, arthropods, and pathology

One of the earliest land floras of which we have detailed anatomical knowledge is still the Rhynie Chert flora, first described by Kidston and Lang (1917, *et seq.*). Recent additions to our knowledge of this flora, notably from the work of Lyon (1964) are reviewed in Høeg (1967) and Banks (1970). The probable age of this flora is now regarded as late lower Devonian (see discussion in Chaloner 1970) rather than the middle Devonian usually attributed to it. This flora shows at least two distinct lines of vascular plants (Psilopsida, and a Lycopsid forerunner) in addition to some non-vascular land plants (Lyon 1962) and both green and blue-green algae (Kidston and Lang 1921*b*; Croft and George 1959).

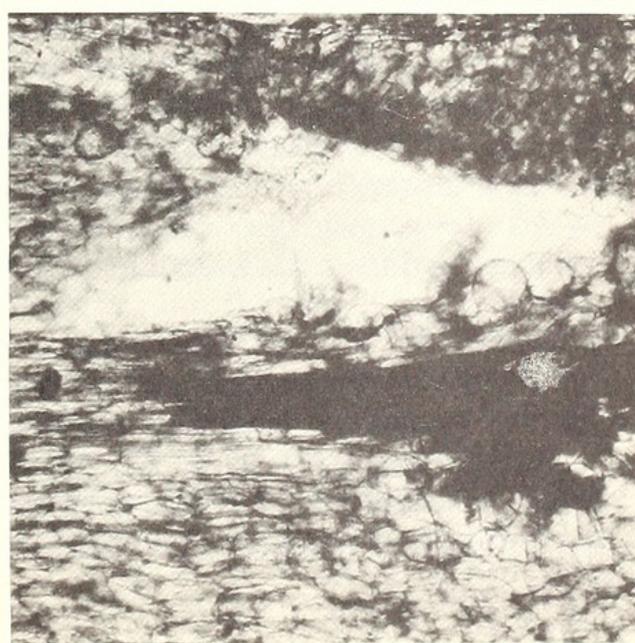
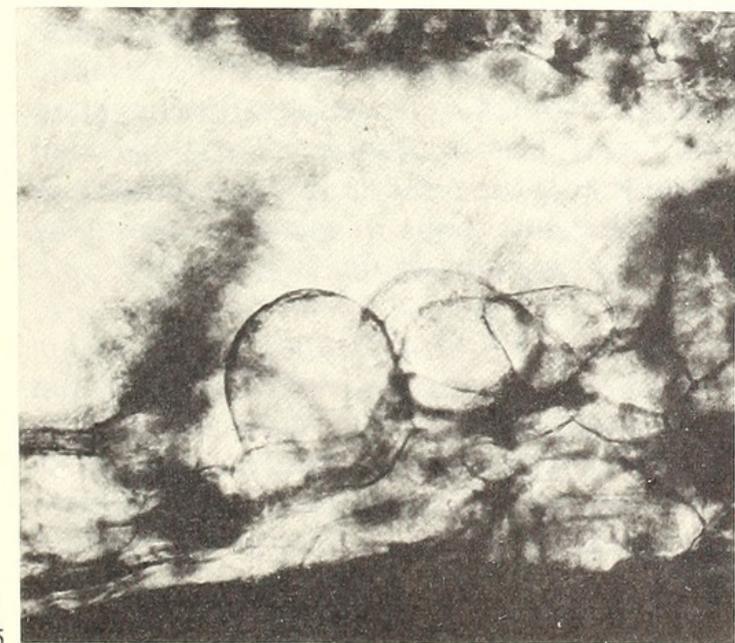
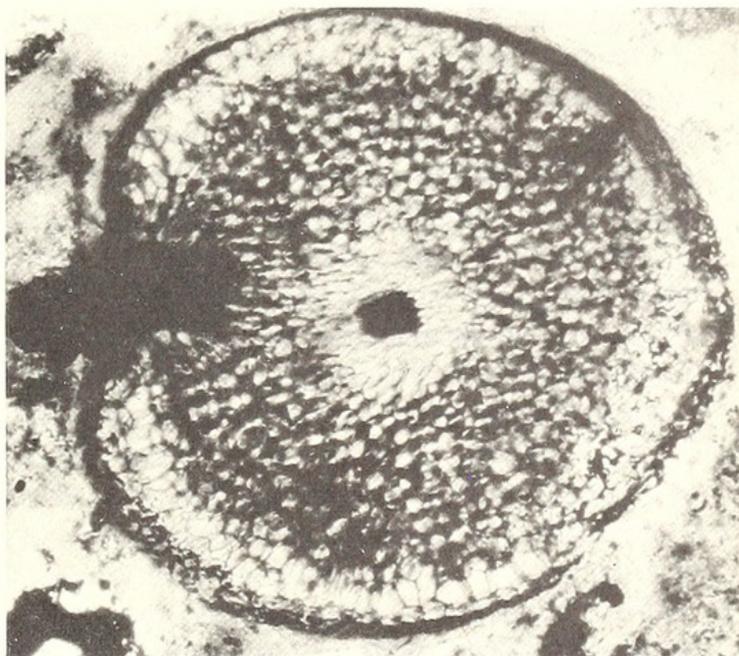
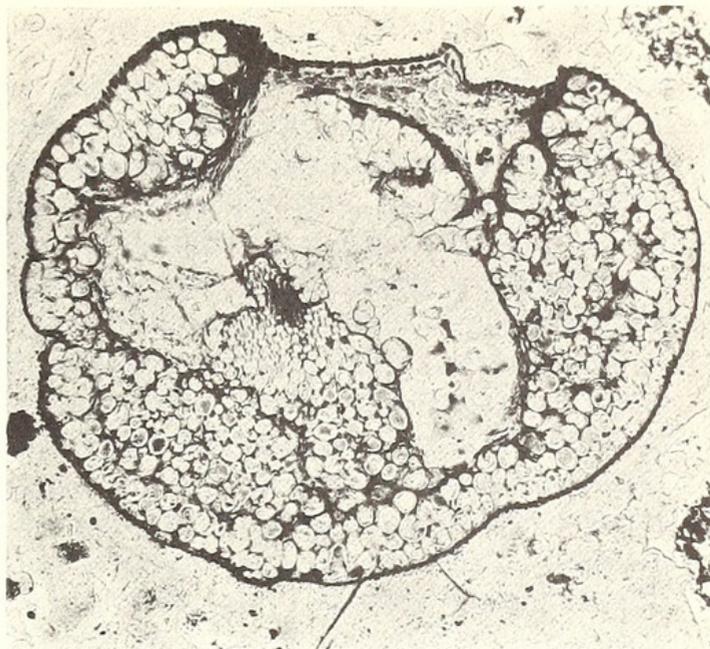
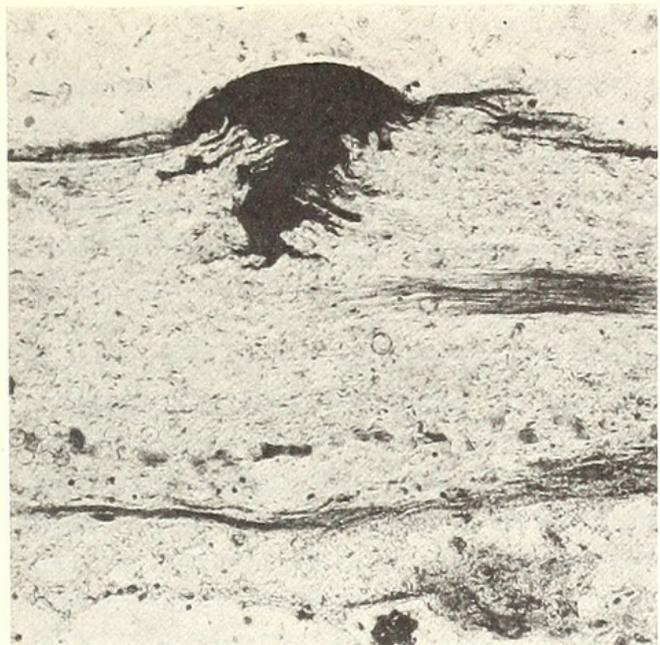
Foodstuffs synthesized in the subaerial chlorophyllous tissues of plants, and transported in the form of sap, represent a nutritive (and vulnerable) plant product from the standpoint of arthropod life. Recent work of Satterthwaite and Schopf (1972) has shown that tissue surrounding the xylem in *Rhynia* has features suggestive of sieve areas, thus supporting the supposition of Kidston and Lang and later authors that this tissue represents the site of phloem-equivalent (see text-fig. 4*k*). The relative proximity of this tissue to the plant surface and hence to sap-sucking arthropods (as discussed above) is evident. The Rhynie plants significantly show a number of lesions of the surface, evidently inflicted while they were alive (Pl. 54, figs. 1–4), since in some cases surrounding tissue shows growth response. Most show associated fungal activity (Pl. 54, figs. 5, 6), which seems more likely to have followed than to have caused the lesion, and which could well have been initiated by sap-sucking animals disseminating the spores (cf. modern examples in Leach 1940; Stakman and Harrar 1957).

Kidston and Lang (1921*a*, p. 834) noted these injuries to the axes, and commented: '... another feature which is clearly pathological must be briefly described. A considerable number of the stems show dark necrosed areas extending more or less deeply from the epidermis, in other specimens the dark necrosed mass is wanting or has more or less completely disappeared leaving a larger or smaller cavity. . . . The feature of special interest is the behaviour of the cells abutting on the necrosed area

EXPLANATION OF PLATE 54

Figs. 1–6. Axes of *Rhynia* showing various types of ?injury (lower Devonian, Scotland). 1, oblique longitudinal section of axis showing lesion extending to level of vascular tissue, more or less plugged with opaque organic matter, $\times 50$. 2, transverse section of axis showing more extensive damage extending to vascular strand, $\times 30$. 3, axis with enlarged (?traumatic) cortical cells, and associated opaque substance in the intercellular spaces, $\times 30$. 4, transverse section of axis showing peripheral ?lesion with plug of opaque matter, $\times 40$. 5, 6, cavity seen in longitudinal section of an axis, associated with growth of fungal hyphae and ?reproductive structures, 5×120 ; 6×40 .

All slides in the Palaeontology Department, British Museum (Natural History), London. Fig. 1, slide no. V.57834; figs. 2, 3, V.57833; fig. 4, V.57838; figs. 5, 6, V.57832.



or bounding the cavity; . . . the cells . . . frequently show evidence . . . of an active cell division that can without doubt be interpreted as a wound reaction.'

They speculate (1921*b*, p. 895) that these wounds may be 'a reaction to some prolonged external stimulus' and invoke 'the volcanic conditions that accompanied the supply of siliceous water'. Tasch's work (1957) casts doubt on this speculation. An alternative possibility is that the injury to the plant axes had an organic cause (attack by some animal—arthropod or otherwise).

Three rather different types of injury may be distinguished in *Rhynia* axes, which have no evident causal relationship with invasion by fungi (whether saprophytic, parasitic, or symbiotic—see Kidston and Lang 1921*b*; Boullard and Lemoigne 1971). Firstly, there are areas of disturbed tissue, in which some cells show abnormal enlargement associated with in-filling of intercellular spaces with opaque organic material (Pl. 54, fig. 3). This situation suggests a traumatic response by the plant to physical injury, which must, then, have occurred while the plant was still alive. Penetration of the plant tissue by an arthropod or other metazoan is one way in which this could have occurred.

The possibility that such injury could have been caused by toxic gases or other volcanic products, invoked by Kidston and Lang, seems inappropriate in this case, since damage is both internal (as seen in a single plane of section) and very local.

Rather different injuries (Pl. 54, figs. 1, 3) appear to represent plugs of opaque organic matter in fissures or lesions extending from the outer surface to the region of the phloem-like tissue at the periphery of the stele. In each of the two cases figured, black plugging material seems to be derived from (*Rhynia*) plant tissue, suggesting its formation while the axis was still alive. However, a fungal (or other, pathogenic) origin cannot be ruled out. Here again, however, the possibility of these lesions representing sites of attack by sap-feeding arthropods can reasonably be sustained.

Finally, there are cases of more extensive injury to axes which are hard to visualize as having been caused by any volcanic phenomenon. That shown in Plate 54, fig. 2 suggests injury possibly caused by some organism; at least, it is hard to reconcile such structure with some kind of physical event.

Whereas none of these three types of injury can be regarded as unambiguous evidence of damage by arthropods or other animal agency, all three could be more readily explained in these terms rather than as a result of any purely physical cause.

Smart and Hughes (1973) emphasize the role of bark thickness in controlling accessibility of sap to insects. 'Phloem close to the outer surface of plant stems suited to the hemipteran proboscis appeared only with the Cordaitales' (Carboniferous). It seems more likely that arthropods were able to gain access to phloem strands in leaves of Lycopods and soft (barkless and fibreless) stems of leafless psilosids as early as the Lower Devonian, as is suggested by the damaged *Rhynia* axes.

Spore structure and arthropods

Spores showing a clear triradiate germinal suture appear as fossils early in the Silurian period (Llandovery: see Owens and Richardson 1972). The triradiate mark on such Silurian spores (see Pl. 55, fig. 2; text-fig. 4*a*) can be regarded as evidence of spore formation in a tetrad, presumably following a meiosis; as such it indicates spore formation as part of a life cycle involving alternation of haploid and diploid

phases. It does not, of course, prove the existence of vascular plants, since bryophytes and certain extinct supposedly land-adapted algal groups (e.g. *Protosalvinia*, *Foerstia*) produced resistant triradiate spores. Even so, the diversification of spore types in the Silurian and Devonian closely parallels that of vascular plants (see Chaloner 1970) and the latter may reasonably be assumed to be the source of most triradiate spores of that period. Putative triradiate spores, showing this tetrad marking with varying degrees of clarity, have been claimed from pre-Silurian strata (see Chaloner 1960; Schopf 1969; Gray and Boucot 1971, 1972; and Boureau and Moreau-Benoit 1972). Late Silurian diversification of spore wall structure was fairly restricted, only eleven 'spore genera' being recognizable by the close of the Silurian (Chaloner 1970; Owens and Richardson 1972; Richardson and Ioannides 1973). Silurian spores show relatively simple development of exine ornament (text-fig. 4e, f, g), being either smooth with an equatorial thickening (Pl. 55, fig. 2) or having a papillate or ribbed ornament (see Silurian and early Devonian examples in Pl. 55, figs. 2, 4, and 9). Presumably these exine features are related to spore dispersal by physical forces such as wind or water, or to protection from harmful radiation or drying, or both dispersal and protection (see appendix).

Within the early Devonian spore morphology and sculpture types show increasing diversity so that by the end of the early Devonian (Emsian) fifty-five 'spore genera' are recognized (text-fig. 4). Within this period, mean spore size shows a steady increase so that the Silurian spores typically less than 50 μm diameter are succeeded by assemblages with individual spores rising to 100 μm by the Siegenian and to 200 μm by the end of the early Devonian (text-fig. 4b, c, d). This appears to represent the inception of heterospory, as a clear segregation of larger megaspores from smaller miospores follows in the middle and late Devonian (Chaloner 1967). Later Devonian spore exines show increasing elaborations in developing separation of exine layers (perinate, cavate, saccate, or pseudosaccate of various authors' usages: Pl. 55, figs. 1, 3, and 8) and sculpture types ranging from apiculate to reticulate ornamentation of various types (Pl. 55, figs. 5 and 8) and spines (Pl. 55, fig. 3) including forms with grapnel-like terminal hooks (Pl. 55, fig. 7; text-fig. 4e-i).

It is unlikely that such developments in spore structure were without function. Much energy is involved in the formation of a highly ornamented spore wall, at least in fungi where this has been studied by Savile (1954). Certainly all wall ornamentations increase the surface:volume ratio, and if close together, reduce over-all density by causing the formation of a thicker boundary-layer of air than in smooth spores, so increasing the buoyancy of the spore in air (Stokes's Law). Savile (1954) says that decoration on rust spores is clearly an aid to dispersal, and is often, at least, an advanced character (p. 705), and 'sculpturing serves both to give the spore added buoyancy when it is airborne and to increase its chances of being transported by insects or other small animals' (p. 738). He also points out that small spore-feeding animals must contend with nearly nutritively valueless wall material to assimilate nutritive protoplasm. Hence spines, wall thickening, etc., can function as protective structures against attack. Wall decoration can also be correlated with other features concerning dispersal (see appendix).

Many of the same arguments can be employed in ascribing function to exine sculpturing on pollen. Muller (1970) suggests evolutionary trends in angiosperm

pollen, starting from simple gymnosperm types as exemplified by *Cycas* and *Ginkgo* and retained in a few angiosperm (*Magnolia* and *Degeneria*) and proceeding to more and more complex types of grains. Although Muller does not consider the functional significance of ornamentation, the scheme he presents can be thought of as broadly paralleling those of Chaloner (1970) and Savile (1954). Anemophilous plants tend to have small, rounded, smooth, rather thin-walled, dry pollen grains with furrows shallow or absent; whereas pollen of zoophilous plants tends to have thicker, ornamented walls with associated oil or wax (Eames 1961). It is clear that elaborations of angiosperm pollen exines are also associated with their carrying highly labile substances, involved in the stigma reaction on arrival of the pollen at its destination (Mattson *et al.* 1974). These substances may have an incidental or derived role as attractants or 'reward' for insect vectors, as distinct from that of the flower bearing them, or the cytoplasmic contents of the grain. Compositae show the greatest amount of exine sculpturing, and in this group Wodehouse (1935) shows a series of retrograde simplifications of exine sculpturing correlated with the reversion to anemophily.

Spines on pollen grains can also be considered as protective as they make eating the pollen grain or its protoplast more difficult for small animals. Also decorations add structural support which would be more appropriate on a spore being manipulated and transported by animals.

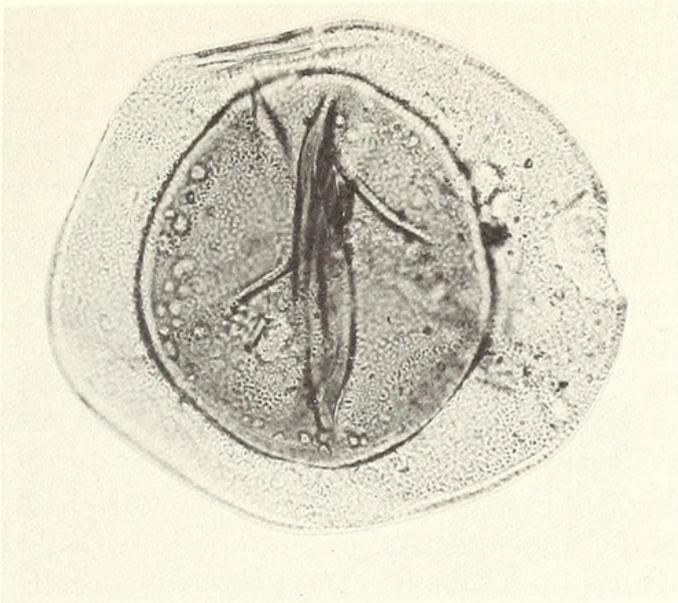
On a larger scale, similar adaptations can be seen on seeds: protective spiny sheaths, retrorse hooks, barbs, and spines for dispersal by animals; wings for wind dispersal, etc. (Stebbins 1971).

Returning to similar features of Devonian spores: long spines appeared on lower Devonian spores (Gedinnian) such as those of *Grandispora* and *Spinozonotriletes* (text-fig. 4h). Other processes and verrucosity may have functioned similarly and aided in dispersal. Of particular interest are the grapnel-hooked spores such as those of *Ancyrospora*, *Hystricosporites*, *Nikitinsporites*, and *Densosporites* (e.g. *D. devonicus* and *D. lysii*). It is noteworthy that these middle and upper Devonian spore genera, divergent in other aspects, all show these grapnel-shaped spines (cf. Pl. 55, fig. 7;

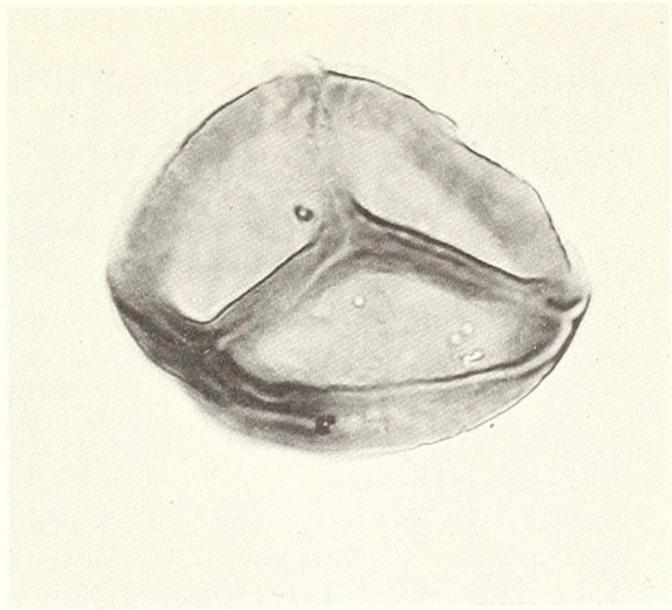
EXPLANATION OF PLATE 55

Figs. 1-9. Devonian and Silurian spores, illustrating various types of morphology and sculpture. 1, *Rhabdosporites langi* Richardson (middle Devonian, Russian platform). Saccate, with fine sculpture on the saccus surface, $\times 500$. 2, *Ambitisporites avitus* Hoffmeister (Silurian (?Downtonian), North Africa). Smooth, with an equatorial thickening, $\times 1000$. 3, cf. *Grandispora* sp. (middle Devonian, southern England). Spiny ornament on outer layer of a cavate exine, $\times 500$. 4, *Streelispora newportensis* (Chaloner and Streel) Richardson and Lister (early Devonian, South Wales). Papillate sculpture, $\times 1350$. 5, *Dictyotriletes perlotus* Naumova (upper Devonian, Turnford Borehole, southern England). Reticulate ornament, $\times 650$. 6, *Hymenozonotriletes* sp. (middle Devonian, Russian platform). Broad equatorial flange ('zona'), with ornament, $\times 250$. 7, scanning micrograph of grapnel-shaped spine of *Hystricosporites* (upper Devonian, Wyboston, England), $\times 1500$. 8, *Geminospora* sp. (middle Devonian, Russian platform). Minute conical spines on outer layer of cavate exine, $\times 1000$. 9, *Emphanisporites pseudoerraticus* Richardson and Ioannides (Silurian (?Downtonian), North Africa). Proximal annular thickening and radiating ribs, $\times 1260$.

Figs. 1, 2, 6, 8, 9, slides in Palaeontology Department, British Museum (Natural History), London. 1, 6, 8, V.57835; 2, V.57836; 9, V.57837. 4, 5, slides in the Palynological Collection of the Institute of Geological Sciences, Leeds. 4, PF3239; 5, MPK 521. 3, slide in the Mortimer Collection (Geology Department, University College, London) RE 276/4. 7, specimen stub not preserved.



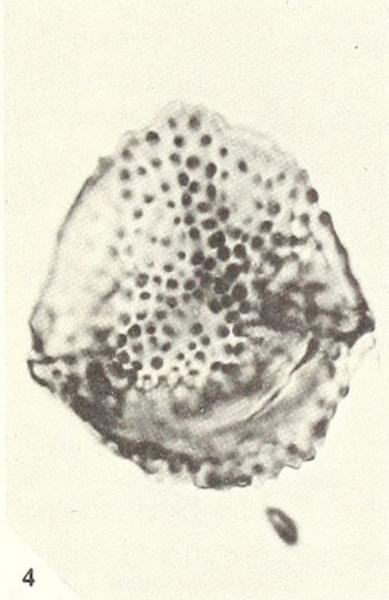
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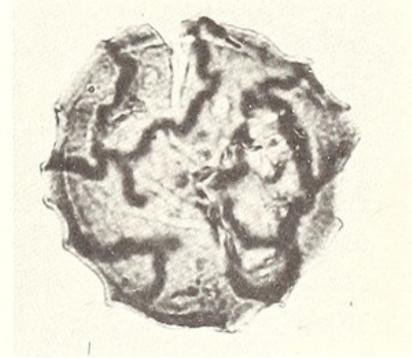
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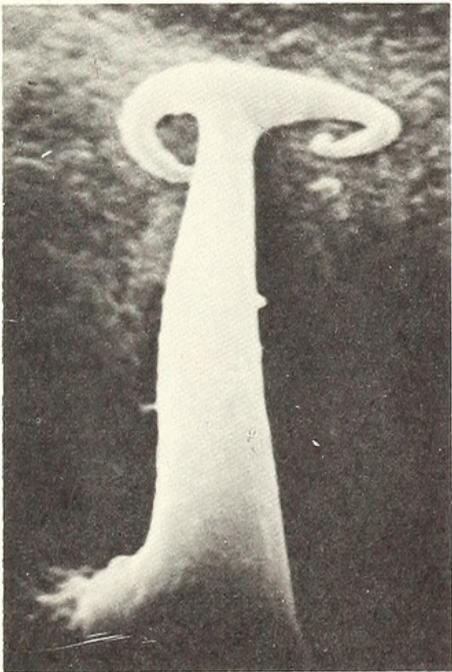
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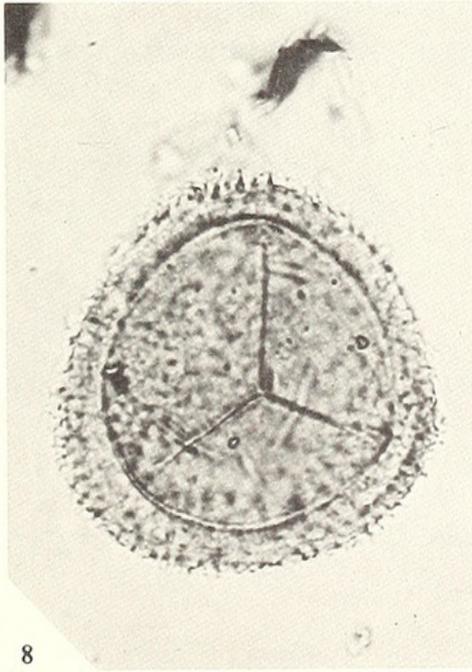
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6



7



8



9

KEVAN, CHALONER and SAVILE, Devonian and Silurian spores

text-fig. 4i). This strongly suggests some common selective pressure. The processes are quite far apart in proportion to the (relatively large) diameter of the spores. Such processes could afford protection but would seem to add little buoyancy. The most evident explanation is that these spores were dispersed by arthropods by becoming attached to the setae by the retrorse hooked processes. As has been shown, arthropods likely to have effected such dispersal are known from considerably earlier formations. In fact, Taugourdeau Lantz (1971) writes on the role of insects in Devonian spore dispersal saying: '... Ils (Les Collemboles) trouvaient donc leur pâture dans le sous-bois dévoniens et leur rôle pour la dispersion de spores et la colonisation d'espaces vierges est probable, et a dû s'exercer dans des régions variées puisque à l'heure actuelle, ils supportent des températures extrêmes de -13° à $+38^{\circ}$ C et qu'ils vivent aussi bien dans la zone de balancement des marées qu'à plus de 5000 m d'altitude...' (p. 63). Taugourdeau Lantz shows that spores with grapnel spines show a maximum diversity (in species number) at about the Frasnian stage (late Devonian).

Modern Collembola have been shown to carry spores (Collinge 1910), and to defecate undigested and viable fungal spores (Bekker 1947) similarly as have mites (Griffiths *et al.* 1959; Mignolet 1971) and other soil animals (Talbot 1952) (see p. 395). Occasionally Devonian spores are found showing globules of tapetal residue adhering to the exine, and not apparently forming part of the regularly arranged sculptural elements (cf. Chaloner 1963). It is possible that these represent tapetal material analogous to the 'pollen kit' of entomophilous angiosperms and having some role in relation to insect transport. Normally one might not expect to find spores so freshly preserved as to display such droplets.

Heterospory and arthropods

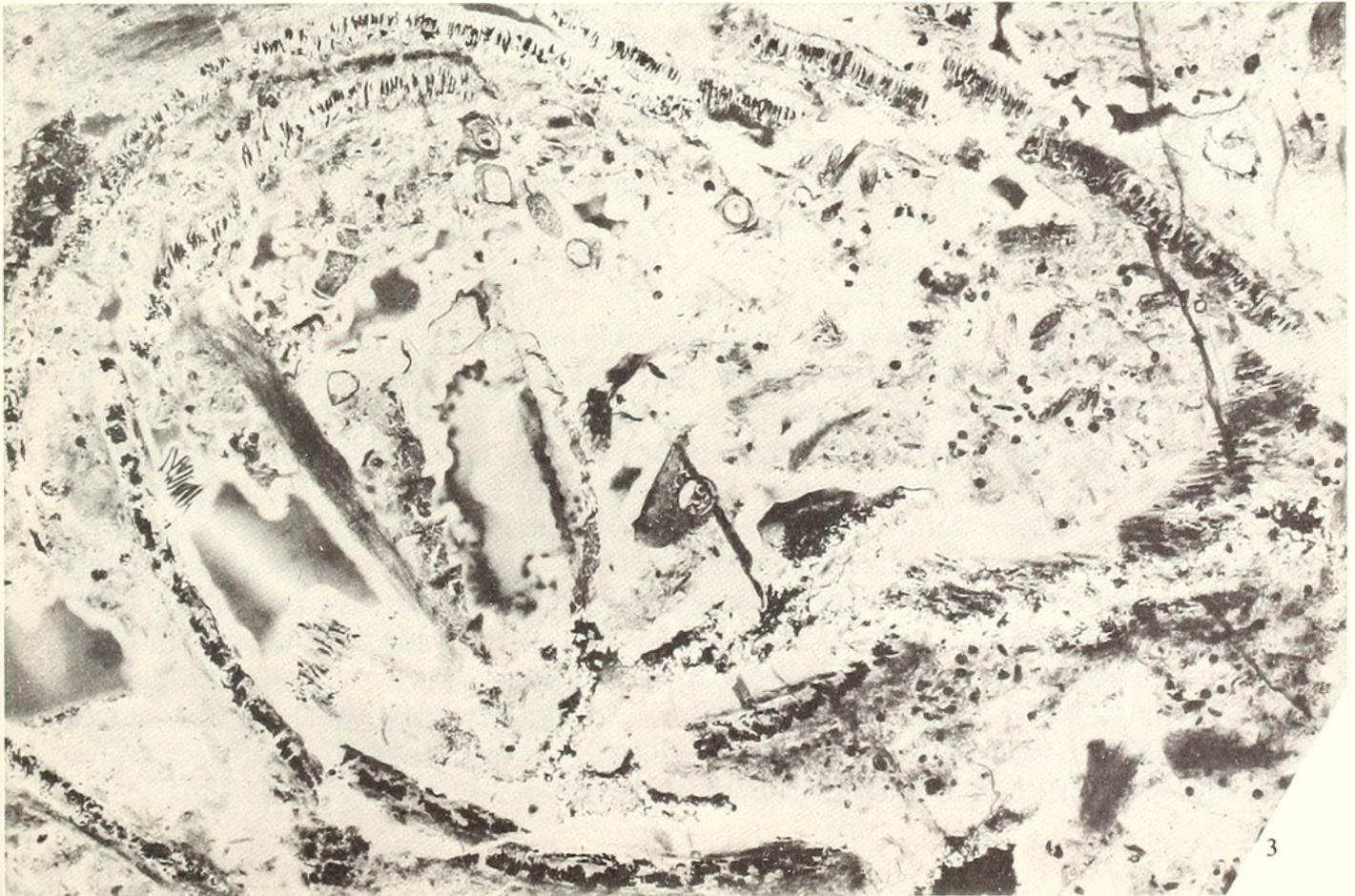
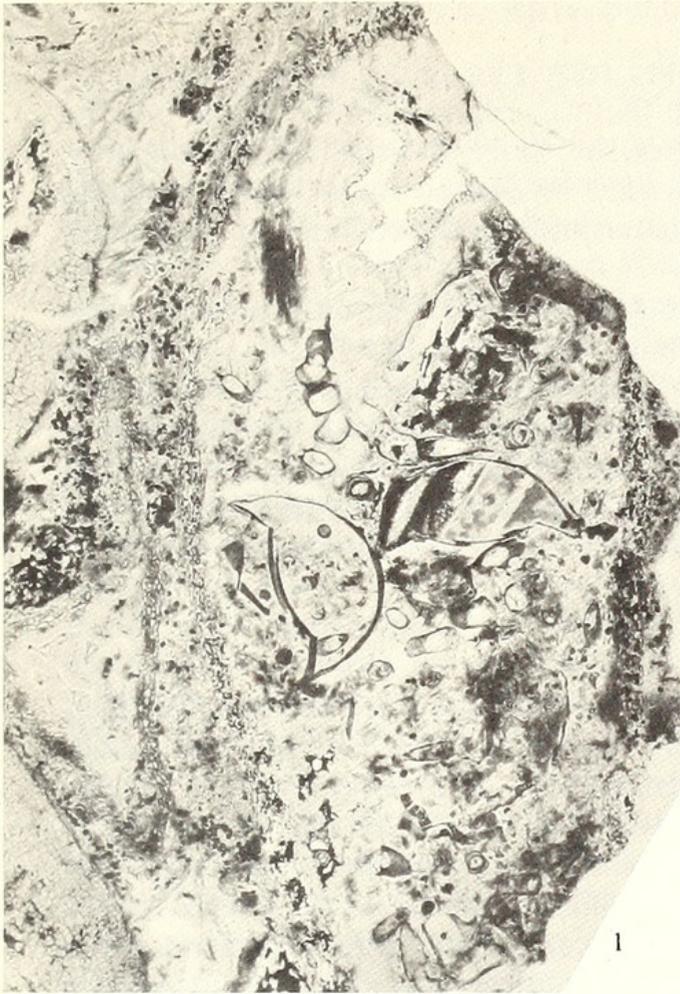
Megaspores (i.e. those over $200\ \mu\text{m}$, Chaloner 1967) start appearing in the Emsian, and by the upper Devonian there are clearly defined occurrences of mega- and microspores (text-fig. 4d). By the Carboniferous insects were already diverse and Hughes and Smart (1967) and Smart and Hughes (1973) suggest some relationships arthropods may have had in evolution of protected ovules, and pollen and spore dispersal. Faegri and van der Pijl (1970) hint at and document the importance of insects in pollinating of modern Cycadales and Gnetales respectively (see also Leppik 1960).

Thus it seems that some relationship between the evolution of insects and heterospory might be postulated for some groups of plants even in the Devonian. Indeed, if arthropods visited the sporangia (either microsporangia, megasporangia, or clusters of both, as in *Archaeopteris*) to feed on spores or secretions, then spore dispersal

EXPLANATION OF PLATE 56

Figs. 1-3. Fragments of trigonotarbid arachnids within cavities of plants in thin sections of Rhynie chert. 1, 2, arachnids within stem fragments, cf. *Rhynia* sp. Note chalcedonic 'spirit-level infill' of arachnid in fig. 1, 1×11 ; 2×16 . 3, arachnids inside empty sporangium of *Rhynia major* Kidston and Lang. Note fragments of characteristic prismatic sporangium wall structure at the top centre, and top right, $\times 19$. All slides in the Kidston Collection, Hunterian Museum, Glasgow University. 1, slide no. 2497; 2, no. 2488; 3, no. 2446.

Plate by Dr. W. D. Ian Rolfe.



would be encouraged. Any adaptation by the spores to make them attractive to arthropods, to adhere to them, or to enable them to retain viability while passing through the gut, would increase the efficacy of the spore-dispersal process. Heavy, large spores with hooks or other processes could be carried by arthropods on the ground further than by air currents, which are naturally reduced close to the ground and in forest.

As the degree of heterospory progressed through later Devonian time, the number of megaspores per sporangium decreased, and the size of individual megaspores increased. They must have accordingly come to represent an increasingly worthwhile prize of food reserve for attacking insects. The selective advantage of enclosure of the megaspore within an ovule, achieved at the end of the Devonian, may have been protection from insect attack, much as it is postulated that the Cretaceous enclosure of the ovule in an ovary was primarily protection from pollinating-cum-attacking insects (Grant 1950).

Arborescence and arthropods

The evolution of trees has been partly attributed to the upward struggle for light. Although the appearance of fossils of winged insects in the Carboniferous is substantially later than the appearance of trees (e.g. *Lepidodendraceae*, *Cyclostigmataceae*, and *Archaeopteris*) in the late Devonian (text-fig. 4l), perhaps spore-feeding arthropods had some role in stimulating the elevation of sporangia out of their reach. Desiccation is a problem to soft-bodied insects, and the long ascent to terminal sporangia would subject them to harsh conditions, quite unlike the more stable and humid conditions of the forest floor. The protection of height must have been short-lived as insects took to the air, and acquired waterproof cuticles and closing spiracles (cf. Hocking 1957; Hughes and Smart 1967). Indeed, it is conceivable that in some plants stem and spore structures subsequently correlate in regard to spore dispersal by arthropods (see p. 404). The purpose of this short paragraph is not to suggest that the struggle for light was not important in the development of trees, but that other benefits could also have accrued from that habit.

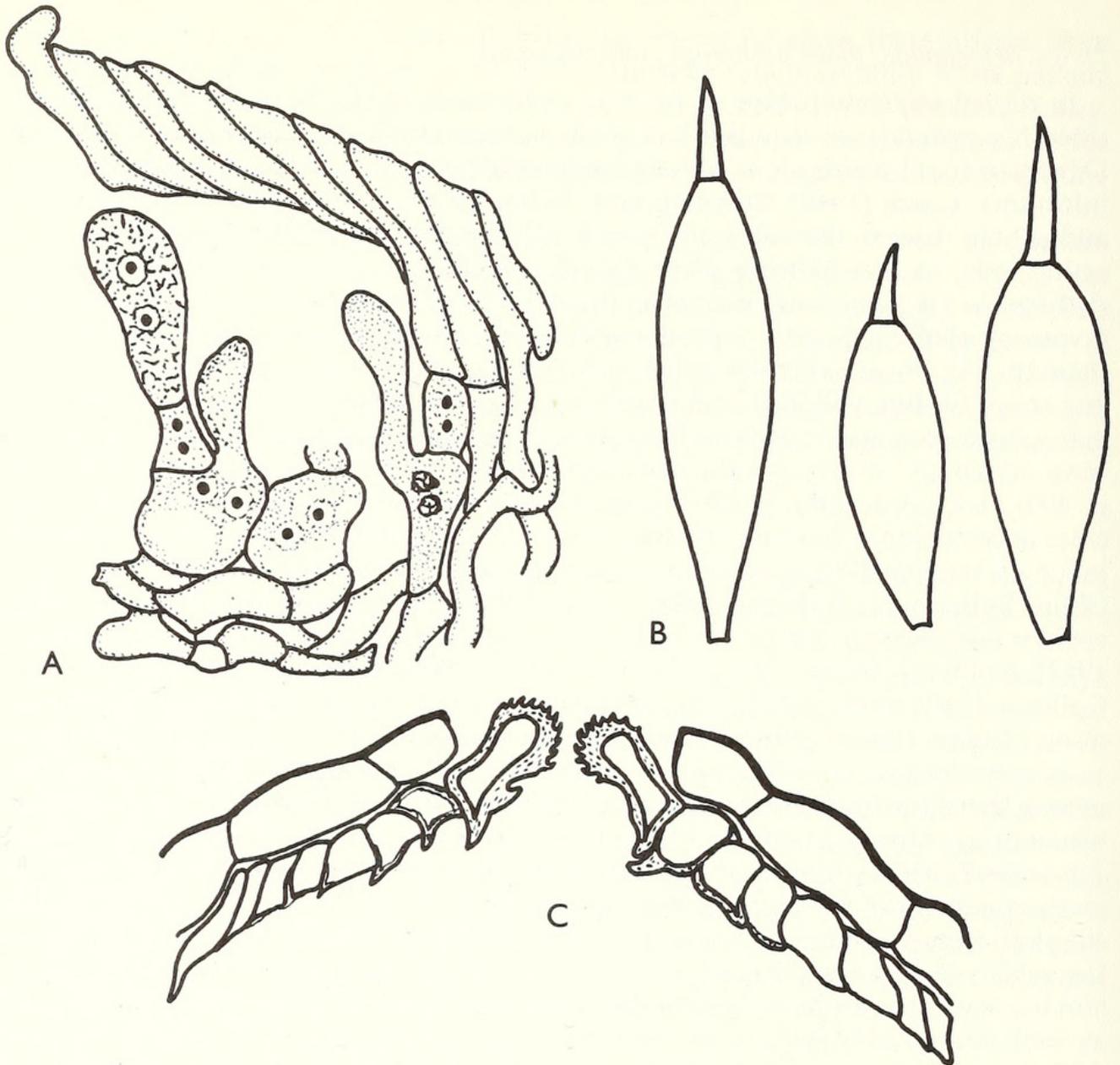
FUNGI

Our understanding of the early fungi is still extremely fragmentary, and is strongly dependent on host relationships of some of the more primitive parasitic genera. The remains of Devonian land plants contain abundant fungal mycelium (Pl. 54, figs. 5 and 6; text-fig. 4q) but these seem to have been nearly all phycomycetes or ascomycete-like fungi: some appear to have been associated with living tissue, notably of *Asteroxylon* (Kidston and Lang 1921b; Martin 1968). By the upper Carboniferous we have well-authenticated records of Ascomycetes (e.g. *Protoascon*, Batra, Segal and Baxter 1964) and Basidiomycetes (*Palaeancistrus*, Dennis 1970) (text-fig. 4t). Growth as internal parasites must have been the main, if not only, method by which fungi were able to leave wholly aquatic habitats and start a subaerial existence (Savile 1968). By growing within host tissues and fruiting on the surface (text-fig. 4q) (at first in a saturated atmosphere only) fungi were subjected to selection for mutations favouring protection from desiccation.

Fungi, arthropods, plant pathology, and dispersal

In regard to relationships of fungi to arthropods in the Devonian, there is considerable circumstantial indication of their importance. As discussed above, some Devonian fossil plants show lesions attributable to animal wounds and subsequent infections. Leach (1940), Stakman and Harrar (1957), Carter (1962), Ingold (1971) and others discuss the roles of animals, illustrating the particular importance of arthropods, in transmitting plant diseases, including viral, bacterial, and fungal pathogens. Of particular interest is the conclusion of Kevan (1965) that animals favouring plant pathogens as food would be more likely to spread them than control them (p. 45). Presumably this conclusion could be extended to the thesis that almost any spore feeding will lead to a scattering of spores helpful to the parent plant. In many cases such zootic dispersal has resulted in adaptive modifications. This is seen most strikingly in insect-pollinated angiosperms, in some fungi (Ingold 1971 and p. 409) and, apparently, in Devonian vascular plants. A variety of animals whose close ancestors may have made up part of the Devonian fauna have been implicated in fungus transmission: e.g. nematode worms (Solov'eva 1965; Jensen 1967), molluscs (slugs, Pulmonata) (Johnson 1920; Talbot 1952), worms (unspecified, Talbot 1952; enchytraeid, Kevan 1965), isopods (woodlice) (Talbot 1952), chilopods (Talbot 1952), diplopods (Kevan 1965), Protura (Kevan 1965), Collembola (Theobald 1910; Collinge 1910; Talbot 1952; Hinson *in* Burges 1958; Stainer and Kevan 1973) and mites (Talbot 1952; Griffiths, Hodson and Christenson 1959; Mignolet 1971).

In considering the evolution of fungi and likely events during the Devonian, among fern parasites there is a revealing series. On *Osmunda* is found *Mixia osmundae*, which bridges the gap between Phycomycetes and the primitive ascomycetous genus *Taphrina*. *Taphrina* occurs on ten genera of polypodiaceous ferns, as well as on various predominantly woody and ancient dicotyledons; and in structure it is among the simplest of unequivocal Ascomycetes (Savile 1955, 1968). *Uredinopsis*, the largest of the genera of fern rusts, has telia that are little more than rounded-up mycelial cells and has several conspicuous resemblances to *Taphrina*; its species occur on *Osmunda* as well as many Polypodiaceae. However, *Uredinopsis*, and its companion genera *Milesia* and *Hyalopsora*, have the full life cycle, with pycnia and aecia on *Abies* and uredinia and telia on ferns. Thus a substantial evolutionary period must have been interposed between the extant genera and the first *Taphrina*-like fern rust. Savile (1955) has suggested that this early development occurred on marattiaceous ferns in the Carboniferous, but it may possibly have started in the Devonian. Uredinia of all three rust genera are small and produce a limited number of spores, but all have a simple peridium with an irregular central opening through which spores are thrust at maturity (text-fig. 4r). This peridium (text-fig. 3A) is composed of relatively thin-walled cells and could effectively protect unshed spores and sporogenous cells only against small animals without powerful jaws. The spores are borne on short pedicels and converge toward the central opening under the shallow peridium. In *Uredinopsis*, each spore bears a slender apical spine (text-figs. 3B, 4s), which plainly must serve to repel small animals attempting to penetrate the ostiole. In the related but more advanced genus *Pucciniastrum*, generally on woody dicotyledons, the peridium is more firmly constructed and the ostiole is ringed by specialized cells bearing upwardly



TEXT-FIG. 3. A, part of uredinium of *Miliesia marginalis* after Moss (1926). B, urediniospores of *Uredinopsis osmundae*. Apical mucro is 6–18 μm long. C, uredinal peridium of *Pucciniastrum arcticum*, showing strongly modified ostiolar cells, after Moss (1926). (A, C, by permission of the Annals of Botany Company, Virginia Water, Surrey, England.)

pointing spines (text-fig. 3C) (Moss 1926). These ostiolar cells also clearly serve to discourage entrance to the sorus by very small animals, while not interfering with outward movement of mature spores.

The realization that *Rhyniella praecursor* belonged to a spore- and pollen-eating assemblage strongly suggests that these protective devices in early rusts operated against Collembola, and probably also mites, at a time before the appearance of true insects.

Protective devices, often consisting of massive and variously fused paraphyses, are seen in more modern rusts, in which they perhaps evolved as protection against true insects; but it is noteworthy that they have gradually been eliminated in several

lineages. It is suspected that, as improved nutritional balance with the host allowed markedly increased spore production, these far from perfect protective devices were no longer adaptive.

Pycnia of the rusts are analogous to entomophilous flowers, in that they are composed of spermatial cells (pycniospores), receptive hyphae, and a nectary. The nectary attracts insects, which spread pycniospores to compatible receptive hyphae. The small volume of nectar generally makes study of its scent difficult. However, the scent is strong in a few systemic species. It is significant that in the relatively primitive rusts *Melampsorella caryophyllacearum* on *Abies*, and *Chrysomyxa arctostaphyli* on *Picea*, the nectar is weakly carrion-scented; whereas in the much more modern *Aecidium physalidis* on *Physalis*, and *Puccinia punctiformis* on *Cirsium*, the nectar is sweet-scented. These differences probably reflect the times of origin of groups of blossom-visiting insects.

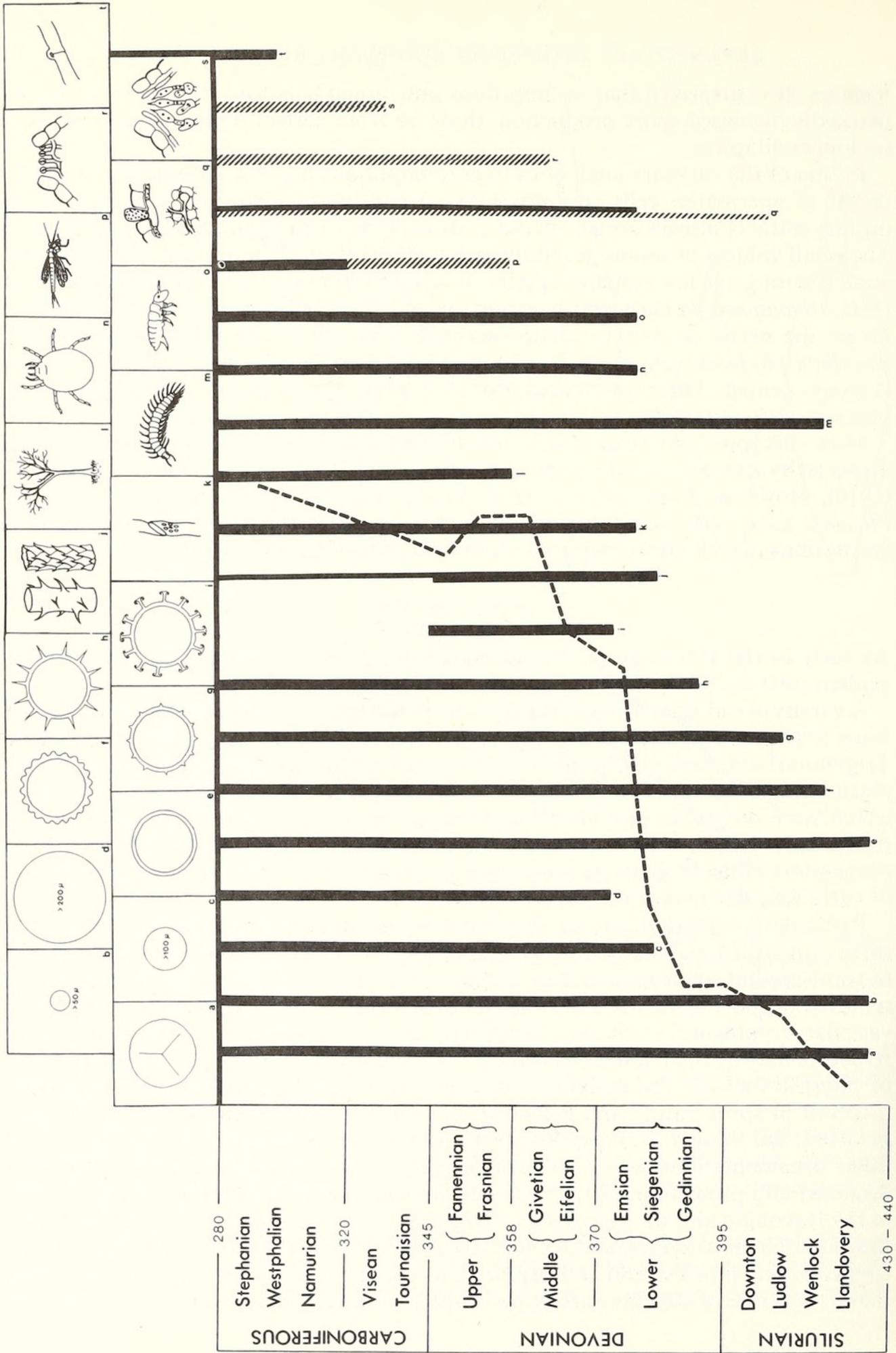
Most rust spores are strongly adapted for dispersal by wind, although some casual dispersal by arthropods must occur as has been suggested for Collembola by Theobald (1910). However, some teliospores of *Nyssopsora* and a few unrelated species of *Puccinia* have very coarse spines, grapnel-hook appendages, or elaborate pedicel decorations, which clearly serve to promote dispersal by arthropods.

CONCLUSIONS

As early as the Devonian co-evolution of arthropods, tracheophytes, and fungi is evident (text-fig. 4).

A variety of soil-inhabiting arthropods are preserved as fossils. Some were predators, some were probably mainly detritus feeders (e.g. myriapods), and others (e.g. mites, Trigonotarbida, and springtails) may have fed extensively on spores, spore protoplasts, and plant sap. Presumably other animals, protozoa, and soft-bodied metazoa, which were not preserved, also flourished in the soil and were an integral part of ecosystems. Mites, trigonotarbids, and springtails, and the hitherto undiscovered progenitors of the true insects could have had considerable influence on the evolution of early vascular plants and their diseases.

Particularly remarkable is the simultaneous increase in complexity of spore structures with arthropod diversity. This is especially interesting considering the likelihood of spore-feeding arthropods acting as spore dispersers; the ensuing adaptation being reflected in spore structure and other modifications, such as are seen in some fungi, vascular cryptogams, and most strikingly in angiosperms. Complexity of spore structure may be related to dispersal by wind and water, to protection from a variety of physical factors, and equally, protection from destruction by those arthropods involved in spore eating and dispersal. Indeed, living arthropods, related to those involved, are known to disperse spores and to eat them. The elaborate spines and other ornamentations seen on Devonian spores seem clearly related to arthropod dispersal and protection, as with modern pollen grains. Heterospory has its origins in the Devonian and we suggest a possible early relation between this and arthropod mediated fertilization. Arborescence precedes the arrival of alate arthropods. It is suggested that the elevation of the sporangia may have been advantageous in reducing the effectiveness of attacking arthropods which were relatively sensitive to desiccation.



Subsequent events indicate relationships between the existence of trees and the development of wings in the true insects.

Fungi appear as parasites of land plants as soon as the terrestrial habit develops. Arthropods, notably insects, mites, and springtails, are known vectors of plants diseases: thus the possibility exists that they had the same roles in the Devonian, or even before. Some primitive fungi show some of the characteristics for arthropod dispersal, and protection from attack by arthropods.

Although we have interpreted some features of early terrestrial plants (e.g. spiny stems, arborescence) as having had possible protective value against arthropod attack, lesions found in fossils of Devonian plants are strongly indicative of damage caused by animals. In some wounds there are clear signs of traumatic responses of living tissue in which cases attacks by mites, springtails, or other animals known from the same habitat seems a more plausible explanation than vulcanism.

Most of the remarks in this paper have concerned the concept of short-distance spore dispersal, and local spreading of propagules. However, the role of arthropods, and especially those capable of becoming aerially planktonic, in long-distance dispersal, not just of themselves, but also of the spores they no doubt carried, could have had great significance to the Devonian ecosystem. Wigglesworth (1973), in discussing origins of insect flight, suggests that the first significance to becoming airborne was to disperse from areas which were becoming unfavourable (drying up), to new favourable areas. This would appear to broadly parallel events leading to the adaptiveness of amphibian progenitors. In the case of arthropods, the likelihood of their carrying spores ready to colonize the potentially favourable destination, could have had considerable significance.

In terms of food sources and an environment less hostile to arthropods than the

TEXT-FIG. 4. The contemporaneous appearance of a variety of phenomena discussed in the text indicative of co-evolutionary processes in and around the Devonian period.

a, simple triradiate sutures; *b*, spore diameters exceed 50 μm ; *c*, spore diameters exceed 100 μm ; *d*, spore diameters exceed 200 μm indicating heterospority; *e*, exine smooth; *f*, exine verrucate; *g*, exine with small conical spines; *h*, exine with long spines; *i*, exine with grapnel-like ornamentation; *j*, stem structures: *left*, spiny stems which disappear entirely before the Carboniferous; *right*, leafy stems; *k*, phloem evident in vascular strand; *l*, arborescence; *m*, Myriapoda; *n*, Acarina; *o*, Collembola; *p*, Pterygota; *q*, first terrestrial fungus: *above*, conjectural phycomycete ancestor with multi-nucleate mycelia and spore sacs sheltering in tissues of early emergent aquatic or terrestrial plant; *below*, branching, aseptate hyphae in host tissue; *r*, first rust uredinial state (conjectural); *s*, first *Uredinopsis*-type uredina (conjectural); *t*, mycelium with clamp connection indicative of Basidiomycetes. *Dashed line*: number of genera of spores (each box width is ten genera, each bar five genera).

It is worth noting that it was towards the end of the Silurian that the oxygen level in the atmosphere began to increase more rapidly than before, and that resulted in greater filtering of short-wave ultra-violet radiation, so reducing these biotically harmful rays near the surface of the earth (Berkner and Marshall 1965). The Devonian was a period of high incidence of geomagnetic reversals (McElhinny 1971) yet shows a relatively low extinction rate (Simpson 1966). This appears to contradict the theories of the direct or indirect causal relation between geomagnetic reversals and extinctions proposed by Crain (1971) and Uffen (1963) respectively. Perhaps the circumstance of the unprecedented opportunity of terrestrialization presenting itself as providing marginal environments and the subsequent catastrophic selection in speciation (Lewis 1962) is enough to have delayed the expected decline in diversity until the end of the Devonian when indeed the occurrence of new genera, at least as exemplified by spores, declines (dashed line).

bare mineral soil, algae, fungi, and bacteria must have been as important to soil-dwelling arthropods as the early vascular plants. The latter presumably appeared only after an extensive non-vascular flora had pioneered dry land. During that time, as today, fungi and bacteria must have been important as pathogens and decomposers and, with detritus feeders, were an integral link in the formation of organic soils and humus. The increase in soils and humus creates additional habitats for soil animals, allowing for evolution of a more diverse, more widespread, and more vagile fauna. This in turn, has its effects on the diversity and development of the flora, and so the process continued.

APPENDIX

The function of many spore structures has received little attention. It is therefore worthwhile making a short aside on the possible significance of structures seen in Devonian spores, which may not be directly related to the subject of this paper.

Of course, not all spore structures need be related directly to dispersal or protection from animals. Double ('cavate') spore walls (e.g. *Geminospora*, Pl. 55, fig. 8) could be effective against animal attack, against dehydration, or have a protective function against infection by pathogens prior to germination. Darkly pigmented areas (the so-called dark areas in Devonian and other fossil spore walls are a post-preservation feature; there is no evidence that they represent pigment) could be effective in protection from the adverse effects of ultraviolet light, as is suggested for darkly pigmented fungal spores which remain exposed for long periods (Rabinovitz-Sereni 1932; Buller 1924, p. 541); or dark pigmentation could be effective in absorbing solar radiation, as hastening the mechanisms of spore discharge as has been demonstrated in *Morchella esculenta* by Falck (1916) (Buller 1934, pp. 166, 300, 321). Pigmentation in spores or rust fungi is markedly correlated with aridity (Savile 1970, 1972) and, indeed, the common brown pigment found in various fungal groups offers extreme impermeability to water and other fluids when in high concentration. Pigmentation has been lost in several lines of rusts that have invaded tropical rain forest from less equable climes (Savile, unpub.). Preventing dehydration is probably the most important of the three functions of fungal spore pigments. Pigmentation in fungal spores tends to correlate with wall thickness too, and in coprophilous fungi, whose spores are usually shot from dung to adjacent herbage where they are eaten, the frequently very dark pigment must protect against digestion in passing through the gut of an animal which may be required by some fungal spores for germination (cf. Johnson 1920; Bekker 1947; Talbot 1952; Ingold 1971). In this way, the process broadly parallels that of seeds which require scarification, naturally often by passage through a gut, to germinate (Ridley 1930; Stebbins 1971).

Thickened radiating ribs (e.g. *Emphanisporites*, Pl. 55, fig. 9) and equatorial thickenings (e.g. *Ambitisporites*, Pl. 55, fig. 2) both seen in late Silurian/early Devonian spores may confer rigidity, equipping the spore to survive some water loss without collapse, or physical stress associated with passage through the gut of an animal.

Minor ornamentation (e.g. *Streelispora*, Pl. 55, fig. 4; *Dictyotriletes*, Pl. 55, fig. 5; *Spinozotriletes*, Pl. 55, fig. 3), seen generally in aerially dispersed spores, serves to hold a thicker than usual boundary layer of air, so increasing the buoyancy of the spores by reducing the density of the airborne unit (Stokes's Law as mentioned in the main text). This is especially true of the small and sparse echinulations of most rust urediniospores. Although Buller (1924, p. 542) attributes this to host-attachment function in some rust fungi, the reverse can be said of spores of two large groups of *Puccinia* in which the urediniospores have two flattened cheeks from which echinulation is missing in a circle of diameter about 8–16 μm , which are related to host attachment. Large, smooth, flat pigmented spores of *Pleospora* and related genera with smooth walls can be seen under the microscope to adhere readily and strongly to foliage.

Air sacs are borne on many present-day conifer pollen, and comparable features are recognizable from the middle Devonian onwards (e.g. *Rhabdosporites*, Pl. 55, fig. 1). In conifers, this feature has been regarded as an adaptation to wind pollination, but researchers have differed in their detailed interpretation of their actual role. The broad wing-like flange seen on some living lycopod spores is another feature recognizable from the middle Devonian (e.g. *Hymenozonotriletes*, Pl. 55, fig. 6). Enhanced aerodynamic properties are

usually invoked as the adaptive significance of such a feature, as with the saccus. But so many wind-pollinated conifers (including some Pinaceae) have non-saccate pollen that the selective advantage in these terms seems to be questionable. Doyle (1945) advanced the suggestion that they were associated with orienting the pollen during flotation through the liquid-filled micropyle of inverted ovules. The subsequent work of McWilliam (1958) has shown that ovules of *Pinus* became fertilized just as effectively if artificially turned upright immediately after pollination. The sacchi may function to protect the large germination area against moisture loss during wind transport—they certainly 'close' across this area when the grain is dry, as Wodehouse (1935) pointed out. The difficulty of attributing function (and hence adaptive *raison d'être*) to pine pollen sacchi well illustrates the general problem of interpreting functionally all spore exine morphology.

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