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Fossil evidence for plant–arthropod interactions in the Palaeozoic and Mesozoic

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SUMMARY

Some of the earliest Devonian fossils of vascular plants show lesions that may be attributed to plant feeding activity by animals. This is the beginning of a more or less continuous fossil record of plant–animal interactions which extends from the Devonian to the present day. An important feature of pre-Cretaceous material is the evidence from coprolites and gut-contents of spore eating by arthropods. Experiments with living arthropods, of groups represented in the Palaeozoic, show that viable spores can survive passage through the gut in significant numbers. Spore eating could clearly have had a dispersal role of value to the plant, as well as its evident benefit as a source of nutrition for the animal involved. Evidence of wood boring and leaf eating extends from the late Carboniferous onwards. It appears that 'continuous marginal' leaf-feeding preceded 'interrupted marginal' feeding, and that this was in turn followed by 'non-marginal' leaf feeding. The latter first appeared in Cretaceous angiosperms. Some diversity of leaf miners and leaf galls are also represented in Cretaceous angiosperm leaf fossils.

1. INTRODUCTION

The wide range of plant–insect interactions in modern ecosystems has received a great deal of attention from biologists, not least because many of them have enormous economic significance. This is particularly so in the case of insect predation of crops of all kinds, both in the field and storage, and also in the insect pollination of angiosperms, with the commercial activities associated with fruit growing and honey production. In this review we consider some of the fossil evidence of how, and more particularly when, these relationships first appeared. Even dealing with living relationships, available for experimental study, details of the degree of mutuality of the relation are often open to debate. In fossil material, the exact nature of the relationship is inevitably less secure, and the point at which we can claim evidence of coevolution is blurred. We are confined to those few cases where there is tangible physical evidence in either the plant or animal remains, of the kinds of interaction for which we can see living analogues.

In the following review, we consider the evidence in a time sequence, starting with the earliest appearance of land-adapted arthropods and plants and their relationships in the terrestrial ecosystem. We concentrate on the earlier phase of this story, as the angiosperm–insect relationship in the context of biotic pollination (with a solely Cretaceous–Tertiary record) is dealt with in another contribution to this symposium (Crepet *et al.*). However, we deal briefly with the fossil evidence of other aspects of angiosperm–insect interaction, in the form of leaf feeding, leaf miners and gall formation.

2. PRE-DEVONIAN PLANT–ANIMAL INTERACTIONS

Plant fossils showing the characteristic features associated with terrestrial adaptation (stomata, a cuticle, xylem and wind-dispersed spores) do not appear until late in Silurian time. Certain of these attributes appear earlier in the Silurian and even late Ordovician, in the form of isolated spores and tissue fragments, but such evidence leaves open the real nature of the plants that produced them (Gray 1985; Edwards & Burgess 1990; Chaloner 1988). Plants attributed to the genus *Cooksonia* occur from latest Silurian rocks in Wales and the Welsh Border, and were probably inhabiting fluviatile areas close to a shoreline, or on tidal flats (Edwards *et al.* 1986). These were simple undifferentiated vascular plants with sporangia borne as swellings at the ends of the dichotomizing axes. Similar plants, but lacking secure evidence of vascular tissue and the other terrestrial adaptations cited above, occur in rocks as old as the mid-Silurian, and are sometimes referred to as 'rhyniophytoid' plants, by analogy with the securely tracheophyte genus *Rhynia* of the Early Devonian (Edwards & Feehan 1980). Rather more complex vascular plants, with clear stem–leaf (microphyll) differentiation are reported from the mid-Silurian of Australia, but their age relations with fossils from the northern continents remains controversial (Chaloner 1988; Edwards & Burgess 1990; Hueber 1983).

The earliest record of a diverse assemblage of terrestrial arthropods comes from latest Silurian (Pridolian) rocks from the Welsh Border (Jeram *et al.* 1990; Rolfe 1990), and includes two centipedes and a

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trigonotarbid arachnid. Although by analogy with their nearest living relatives these are likely to have been zoophagous forms, it is significant that they occur in association with fossils of the land plant *Cooksonia*. The shelter and humid environment produced by a sward of even quite small terrestrial plants, which were also offering a source of primary productivity, must have been one of the earliest and most critical interactions between plants and arthropods, making possible the land migration of the latter group.

Before looking at the subsequent course of this interaction, it must be acknowledged that there are various records of putative terrestrial life pre-dating this late Silurian plant–arthropod association. Rolfe (1985*a*) interprets the late Silurian record of myriapods as representing the earliest occurrence of what were probably detritivores. Much earlier, we have record of fossil droppings (coprolites) from the Precambrian (Robbins *et al.* 1985) but these are inevitably of uncertain origin, and possibly are not even from a terrestrial animal. Mid-Silurian coprolites containing fungal material are described by Sherwood-Pike & Gray (1985), and these they attribute to fungivorous arthropods. However, it is possible in this case that the fungal material might have grown within the droppings, rather than having been the foodstuff for the arthropods. Even so, they are one of the earliest records of coprolites probably attributable to arthropods in a terrestrial setting.

Equally controversial are the burrows in a fossil soil profile from the Ordovician of Pennsylvania, described by Retallack & Feakes (1987). If they truly represent burrows made by sizeable organisms within a soil profile, as Retallack & Feakes suggest (they are from 3–16 mm in diameter and up to half a metre in depth), then we must assume that there was some form of primary production occurring in the terrestrial ecosystem of which they were a part. To that extent they represent evidence for at least an energy-flow interaction between elements of land-adapted fauna and some terrestrial autotrophs. The latter might have been simple algae living on a moist soil surface, but the size of the borings makes the subsistence of the organisms forming them seem improbable on a diet of soil microfauna and microalgae. However, the possibility exists that the burrows or borings in this Ordovician section pre-date the weathering of the soil profile which identifies its subaerial origin. Alternatively, they might represent the work of aquatic organisms which burrowed during occasional incursions of water over the soil surface, in the overbank deposit in which they occur (Wright 1990).

3. DEVONIAN EVIDENCE OF PLANT–ARTHROPOD INTERACTIONS

The Rhynie Chert of early Devonian (Siegenian–Emsian) age from Aberdeenshire represents a peat-bog ecosystem that was repeatedly inundated by hot volcanic fluids that fixed the plant and animal tissue, and subsequently infiltrated it with near-transparent silica (Kidston & Lang 1921). This remarkable preservation of a wetland ecosystem gives us a picture of the participants in a Devonian food web involving algae, tracheophytes and several other enigmatic, probably land-adapted, plants together with a number of different types of arthropod, some aquatic, some evidently terrestrial. The arthropods include an aquatic crustacean, the earliest record of a hexapod in the form of a collembolan, *Rhyniella praecursor* Hirst and Maulik, mites, including *Protacarus crani* Hirst and the largest of all the Rhynie arthropods, the trigonotarbid arachnid *Palaeocharinus scourfieldi* Hirst. This has book-lungs, as a clear adaptation to terrestrial existence (Jeram *et al.* 1990). It is a reasonable first working hypothesis, based on their nearest living counterparts, that the mites and collembolan were litter feeders, and that the arachnid was zoophagous, and preyed on the smaller arthropods (and presumably any other soft-bodied fauna available to it, of which no fossil remains may have survived). This very conjectural sketch of a food web carries the implication of the underlying terrestrial primary productivity by the plants, upon which this community must have been dependent.

There are two pieces of more tangible evidence which point to plant–animal relations in this early terrestrial ecosystem. Some of the axes in the Rhynie Chert show various types of lesions. These were noted by the first authors to describe the Rhynie plants, Kidston & Lang (1921), and they attributed them to physical injury caused by the circumstances of the (volcanic-based) fossilization process. However, some features of these lesions make this seem improbable. Notch-like lesions extend inwards to the vascular tissue, and specifically to the phloem-like tissue surrounding the xylem. The lesions are filled with a dark plug of ?exudate. Most significantly, the cells abutting on the break in the tissue have expanded into the gap, and have undergone division after the injury occurred. The exudation and the wound response of cell division are typical reactions of a living plant to injury. Patently the lesions were made while the plant was alive, and the plant survived the injury (Kevan *et al.* 1975). It is at least possible that the injury was caused deliberately to gain access to sap exudation as a means of feeding. However, Rolfe (1985*a*) queries the biological cause for these lesions. Of the known arthropods in the fauna, Kevan *et al.* (1975) suggest *Protacarus* and *Rhyniella* as possible causal organisms. In view of the size of the lesions, it must be acknowledged that the much larger trigonoitarbids would have been better equipped to make such injuries. Other biological causal agents – nematodes for example, which might leave no other tangible trace of their presence – are certainly possible, and cannot be discounted (Conway-Morris 1981; Wallace 1973). The possibility of a sap-feeding relation involving the arthropods is probably about as far as this evidence can take us at present.

The suggestion of a different relation in the Rhynie biota exists in the occurrence of trigonotarbids inside empty *Rhynia* sporangia (Rolfe 1980, 1985*a*; Kevan *et al.* 1975). The sporangial walls of *Rhynia* are of a distinctive 'prismatic' character, so that it is very clear in Rolfe's Rhynie material that the trigonotarbids were within a sporangial cavity. Their presence in that particular location may of course have been quite

Table 1. *Results of simple feeding experiments on the viability of bracken spores after being eaten by three types of terrestrial arthropod*

(The first line of figures are from the results given by Chaloner (1976); a similar feeding protocol was used for the results given here, but the grass used as feed in the earlier experiments was here replaced by bran. For each of the three arthropod types, their bran was dusted with spores of *Pteridium aquilinum*, the arthropods then separated from their food and the droppings collected for 24 h. The droppings were then dispersed in a small volume of water, plated out on mineral agar and, after a week, all spores observed were scored as having germinated or not, and this expressed as a percent viability (last column). A control germination rate was also scored on spores plated out directly (first column).

The much lower germination rate seen in the current *Locusta* feeding is presumably due at least in part to the different degree of mastication involved in eating spores associated with bran rather than the grass used in the earlier experiments.)

arthropod	% viable in control	ungerminated	germinated	% viable in droppings
Locusta migratoria (Chaloner 1976)	67	—	—	47
Locusta migratoria	74	101	7	6
Spirobolus sp. (giant African millipede)	74	63	5	7
Periplaneta americana (cockroach)	74	100	0	0

fortuitous, as he concedes. However, they might have entered the empty sporangia as a means of obtaining shade or shelter from desiccation. A further possibility is that they might have eaten the contents of the sporangium before occupying it. The biological significance of such spore eating is considered further below in a Carboniferous context, where the evidence for arthropod spore eating is very much stronger.

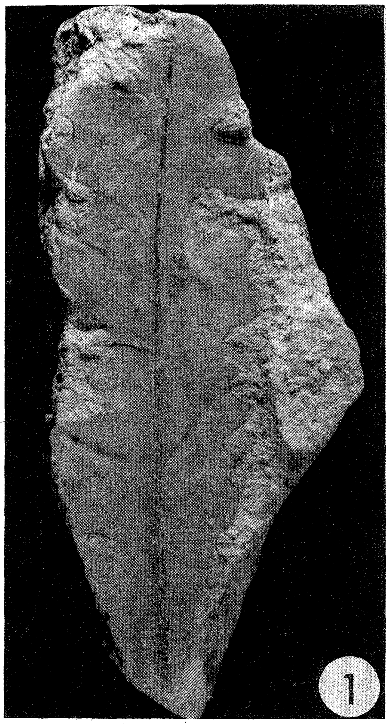
In addition to the evidence from the Rhynie occurrence, Banks (1981) has published illustrations of the leafless early Devonian plant *Psilophyton* from the Lower Devonian of Gaspe showing injuries consistent with stem feeding, either by arthropods or some other organism. Here, the wound reaction is more clearly defined than in the *Rhynia* axes, with a periderm-like response of cell division over quite a wide zone beneath a region of superficial damage. As with the Rhynie material we can only speculate on a biological causal agent, largely because it is so hard to picture any purely physical cause for the injury that Banks reports.

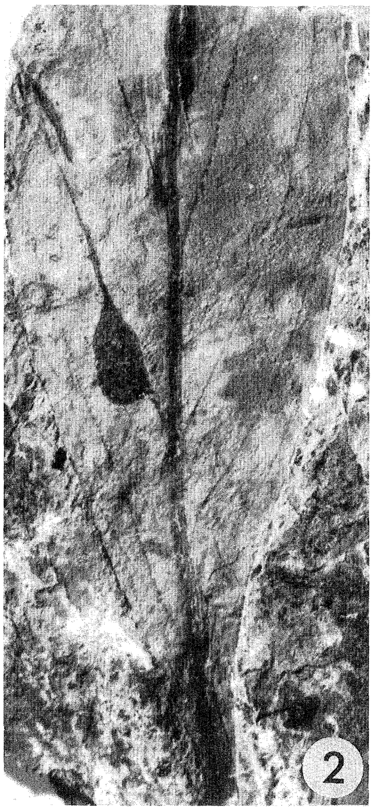
4. CARBONIFEROUS EVIDENCE FOR PLANT–ARTHROPOD INTERACTIONS

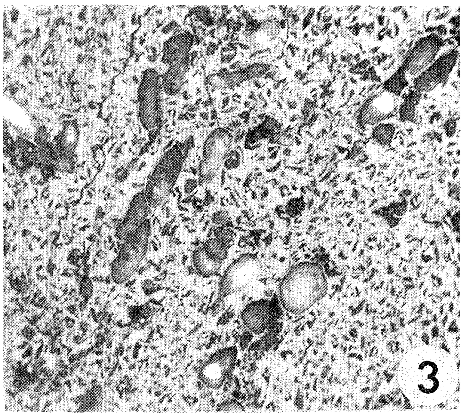
The exploitation of Northern Hemisphere Carboniferous coals has brought a great deal of fossil-bearing rock of that age to the attention of scientists over the last century and a half. For this reason alone it is not surprising that our record of plant–arthropod interactions within the Carboniferous is more diverse and better documented than from the Devonian. But even allowing for this, it is clear that an expansion of terrestrial life within the Carboniferous gave scope for a wider range of interactions. For within this period we have record of arthropod gut contents including plant material, of fossil droppings (coprolites) containing abundant spore exines, together with evidence of wood boring and, by the late Carboniferous, some evidence of leaf eating. There is also sound documentation of a steady increase in the size of plant propagules (megaspores and seeds) which represent an exploitable plant product of high nutritive value, coupled with evidence of a wider range of land-adapted arthropods including winged insects. Carboniferous evidence for plant animal interactions have been extensively reviewed (Hughes & Smart 1967; Rolfe 1985*b*; Scott & Taylor 1983), and we comment on a limited number of instances to illustrate the range of evidence available.

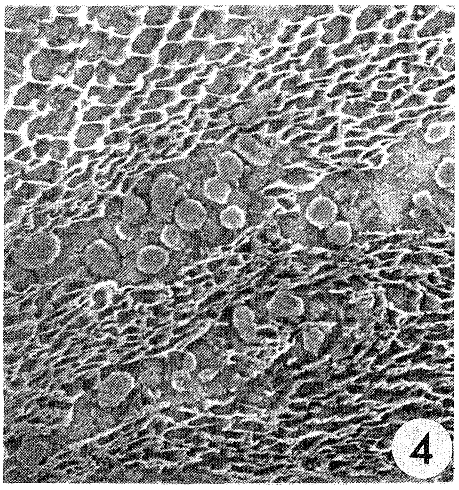
The most convincing record of plant eating by arthropods must of course be the presence of plant remains in their gut contents. Rolfe & Ingham (1967) have illustrated fragmentary xylem, probably of a lycopod, in the gut of the large arthropod, *Arthropleura*, from the late Carboniferous. Scott has prepared fossil spore exines, probably also of lycopod origin, from the gut contents of the winged Carboniferous insect *Eucaenus* from the famous Mazon Creek locality in Illinois (Scott & Taylor 1983). These occurrences are important as they are the most convincing evidence possible for phytophagy, and yet it must also be borne in mind that spore exines and lignified cells of xylem represent two of the most indestructible forms of plant tissue. Their survival through the process of digestion, and subsequent fossilization, would favour their occurrence in any remaining gut contents, even if their ingestion had been quite fortuitous, or formed only a minor dietary component. Even a carnivorous animal living in contemporary grassland in early summer, as a herbivore predator, might well consume quite a lot of grass pollen, either first or second-hand. The presence of a small quantity of grass pollen in the gut of any animal would be a frail basis for deducing that pollen eating was a significant part of the dietary pattern!

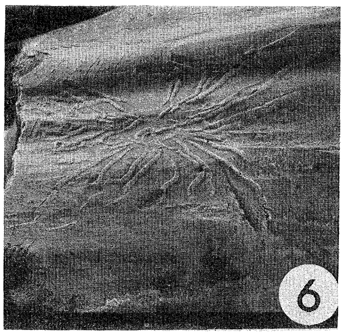
This gentle caution can surely be set aside in the case of the late Carboniferous droppings described by Scott (1977) consisting largely of fossil spore exines (figures 8 and 9). The attribution of any such coprolites to any given source animal is inevitably problematical, but as Scott has argued, there is a strong probability that these droppings are of terrestrial arthropod origin. Although the spore content is diverse, it is so pervasive in these droppings that the

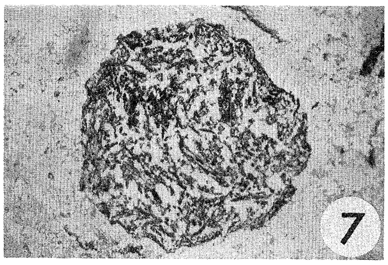


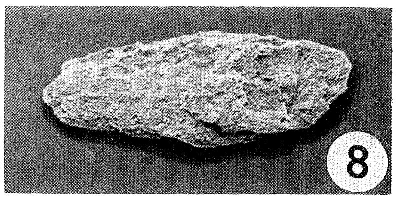


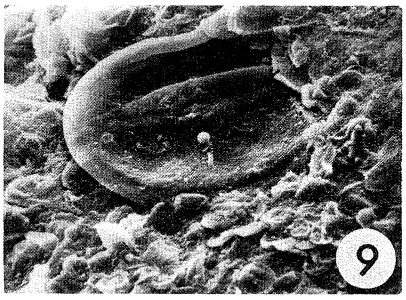


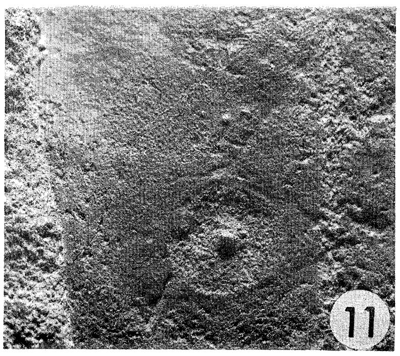


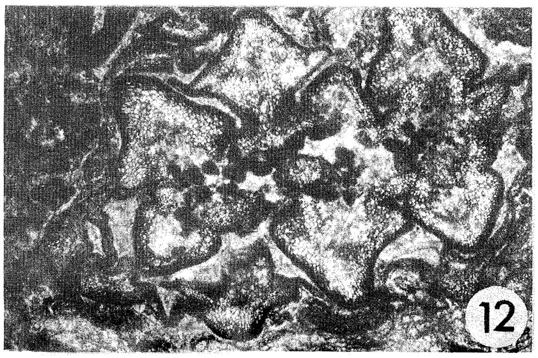












Figures 1–12. For description see opposite.

organism producing them was a spore eater seems inescapable. None the less, as noted above, it is also possible that an arthropod was feeding on some other organism which was itself spore eating, or that it was taking in a high proportion of spores through feeding on spore-rich litter.

With this proviso about the start of the spore-eating food-chain, it is worth noting that the nutritional value (and especially the protein content) of pollen is comparable to that of seeds, (which are generally speaking the most rewarding of plant tissues in the modern flora), and spores of pteridophytic plants are probably of similar composition (Scott *et al.* 1985). It is significant that Southwood (1973), on the basis of comparative studies of living insects (and without reference to the fossil record) wrote that 'the evolutionary path of the phytophagous insect has not been an easy one; pollen feeding often seems to represent "the first step" and feeding on foliage "full success". One might add that spore eating was the first step, which led not only to pollen eating as the seed plants evolved, but that this particular plant–animal interaction was in turn the pathway into biotic pollination in the flowering plants.

The probable significance of spore eating as a lead into insect pollination makes it appropriate to reflect on how far this relationship might be as mutually advantageous to the spore-bearing plant and its spore predator, as is biotic pollination to both flowering plant and vector. As Chaloner (1976) and Scott *et al.* (1985) have suggested, spores able to survive passage of the gut would then be deposited in the moist and sheltered environment of the insect's faecal pellet, after having been transported away from the parent plant (perhaps some considerable distance, in the case of a flying insect). Unlike the randomly deposited wind-dispersed spore, a spore transported in this way would presumably end up in an environment at least acceptable to the insect. In that the insect 'predator' would thus have assisted in the survival and spread of its own food source plant, the relationship would obviously be mutually advantageous.

Chaloner (1976) did some simple experiments on the survival rate of *Pteridium* spores fed to locusts. (The insect order Orthoptera, to which the locusts belong, is known from the Carboniferous onwards.) He showed that passage through the locust gut only reduced spore viability by about 50%. We have repeated these experiments, using millipedes and cockroaches, in addition to locusts (see table 1). The choice of these arthropods was influenced by the occurrence of the Class Diplopoda, and the insect Order Blattodea (to which these two groups respectively belong) also being amongst the fossil forms known from the Carboniferous (Scott *et al.* in preparation). Although the cockroach spore feeding gave no viable spores in the droppings, the spore survival rate in the millipede gut was actually higher than that in the locust. The feeding protocol and the procedure for collecting the droppings, uncontaminated by the spore-dusted food, were essentially the same as those that Chaloner had used, and the fern spores had a higher initial viability than in his material. Even so, the new locust results gave a much lower survival rate than in the earlier experiments. It is not clear just why these later feeding experiments produced a higher mortality in the fern spores eaten by

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Figure 1. Partially eaten angiosperm leaf showing marginal and rare non-marginal feeding (notably, *ca.* 2 cm up leaf near left-hand margin) from the Ripley Formation (Maastrichtian, Cretaceous), U.S.A. (PP11525, Field Museum of Natural History, Chicago, U.S.A.) (× $1\frac{1}{2}$.)

Figure 2. Trumpet type leaf mine in angiosperm leaf. The mine originates near the margin then proceeds along a secondary vein until it forms a relatively large blotch-like pupation chamber which is full of frass. There is a central exit pore. Dakota Formation (Cenomanian, Cretaceous). (Indiana University Collection, IU15703-2529, U.S.A. Courtesy of D. Dilcher.) (× 2.)

Figure 3. Possible arthropod borings in gymnospermous wood preserved as fusain, late Lower Carboniferous, East Kirkton, Scotland. (Scott Collection.) (× 100.)

Figure 4. Gymnospermous wood with borings filled with frass from the Upper Carboniferous of the U.S.A. (Botany Department, Ohio State University, Columbus Ohio, U.S.A.) (Scanning electron micrograph × 60.)

Figure 5. Partially eaten leaf of *Glossopteris* from the Permian of Australia, showing continuous marginal feeding traces. (Scott Collection.) (× 1.)

Figure 6. Traces of a bark-burrowing beetle on a gymnosperm log from the Lower Cretaceous of southern England. (v7535, Natural History Museum, London, U.K.) (× $\frac{1}{2}$.)

Figure 7. Cross section of coprolite containing plant material from the Kingswood Limestone, Lower Carboniferous of Pettycur, Fife, Scotland. (Scott Collection.) (× 10.)

Figure 8. Coprolite containing plant material, from the Upper Carboniferous of Yorkshire. (FSC2063, Hunterian Museum, Glasgow, U.K.) (Scanning electron micrograph × 15.)

Figure 9. Detail of Upper Carboniferous coprolite from Yorkshire showing contents of spores and pollen. (FSC 2068, Hunterian Museum, Glasgow, U.K.) (Scanning electron micrograph × 250.)

Figure 10. Sandstone cast of seed (*Trigonocarpus*) with plug representing hole in original seed coat. Upper Carboniferous. (Geology collections, unregistered, National Museum of Scotland, U.K.) (× $1\frac{1}{2}$.)

Figure 11. Angiosperm leaf with spot gall with central exit hole, from the Dakota Formation (Cenomanian, Cretaceous), U.S.A. (UP348, Field Museum of Natural History, Chicago, U.S.A.) (× 2.)

Figure 12. Small coprolites (possibly of mite) in lycopod axis, from the Lower Carboniferous Pettycur Limestone, Pettycur, Fife, Scotland. (Gordon Collection No. 176, Natural History Museum, London, U.K.) (× 15.)

locusts, but the point of real significance is that spores, in what ever proportion, can survive passage through the gut of two such voracious plant eaters as the locust and the millipede.

If, for every hundred spores eaten, five are deposited well away from the parent source, in a moist humus-rich environment, presumably in a habitat suitable for both plant and spore-eater, then the exercise may be seen as well worth the cost of the 95 spores lost to the plant. In angiosperm biotic pollination, a pollen production of a thousand grains per ovule produced must be rated as being at the efficient end of the range (Faegri & Van der Pijl 1971). It seems that spore eating, coupled with ensuing dispersal (which might yield successful gametophytes, rather than the viable seed of a successful pollination) would be a worthwhile process to the spore-bearing plant. These simple experiments at least give some support to the suggestion that spore eating would have been of mutual benefit to both plant and spore eater. This is of course simply a special case of the process long-recognized as endozoochory, in which seed dispersal is effected by many fruit-eating animals. In that case it is the seeds, which are often specially adapted to survive passage through the processes of eating and digestion, which are dispersed when they are voided, still in a viable state, by the animal.

Coprolites formed of plant debris, other than those containing spores, have been described from the early Carboniferous of Scotland and France (Scott 1977; Scott *et al.* 1985; Rex & Galtier 1986; figures 7 and 12). The latter authors recognize four different types of coprolites, which they regard as evidence for some diversity in the phytophagous fauna, some of these occurring within plant tissue, and others dispersed within the matrix.

There is other evidence from within the Carboniferous of arthropods eating plant propagules (spores, seeds) without any element of a mutual benefit. The megaspores of some of the tree-sized lycopods of the Carboniferous evidently represented a nutritional source worth tapping, and megaspores have been reported showing a neat borehole through which feeding presumably had occurred, much as in modern insect damage to seeds (Scott & Taylor 1983). Seeds of Carboniferous age showing (presumed) arthropod borings have been reported by several authors. We illustrate an internal cast (i.e. a sediment infill of the stony integument) of the Carboniferous seed *Trigonocarpus* (figure 10). The boring appears as a sediment plug, protruding from the cast, as matrix filled both seed cavity and the bored hole through the integument. It is not clear from the nature of the hole in either megaspore wall or seed integument whether it was made to facilitate access for feeding, or whether it represents emergence of a mature or maturing insect or other arthropod, after egg-laying within the plant propagule. In the two instances cited, the former case seems more likely for the megaspore, on the basis of the relatively large size of the hole, whereas the seed boring could be plausibly explained on either basis.

The evidence from the Carboniferous spore-rich coprolites certainly pre-dates any abundant evidence of leaf eating, although leaves with bite holes are known from the late Carboniferous. However, the number of records is absurdly low, in relation to the number of fossil leaves of Carboniferous age in museums, and reported in the literature. Scott & Taylor (1983) in a survey of a well-worked late Carboniferous flora from North America reported only 4% of one of the commonest leaf species present showing evidence of leaf feeding. It must be accepted that the apparent rarity of Carboniferous leaves showing feeding damage may be a result of such 'imperfect' fossil specimens being deliberately – or perhaps even subconsciously – ignored by collectors. But even acknowledging this possible collecting bias, Southwood's suggestion quoted above is certainly consistent with the evidence of spore eating preceding any extensive evidence of leaf feeding within the Carboniferous.

It has become the practice of palaeobiologists working on a wide range of 'trace fossils' (ichnofossils, such as partially eaten leaves or footprints, in which the causal animal leaves no actual fossil remains of itself), to apply formal binomial names to the traces. These so-called ichnotaxa are nomenclaturally somewhat curious. We have, for example, the genus *Phagophytichnus* (see, for example, Van Amerom (1966)), which is applied to the trace fossil comprising bite marks along the edges of leaves, from Palaeozoic to Tertiary in age (see figures 1 and 5). The name relates of course to the somewhat elusive concept of the unknown animal that did the biting. The nomenclatural type-specimen of such a 'trace fossil' is the plant fossil showing the bites, or perhaps more exactly, the missing parts of the plant fossil, resulting from the biting. None the less, these ichnofossil names form a useful language to record the evidence of the important process of leaf feeding.

We have well-documented evidence of marginal leaf feeding from the late Carboniferous with *Phagophytichnus* bites on the leaves of the seed-fern *Neuropteris* (Van Amerom 1966; Scott & Taylor 1983). Such evidence of marginal leaf feeding has been recorded more frequently in the Permian (figure 5), and is considered below.

Our earliest record of wood boring also comes from within the Carboniferous (fig. 3), even though sizeable stems with extensive secondary xylem occur from the mid-Devonian onwards. The wood-boring habit has, of course, the dual role for the borer in combining 'feeding' with 'protection' from predators, within the bulk of the plant tissue. However, unless it has some form of cellulose-digesting microflora in its gut, the bulk of wood consumed by a boring insect is unusable nutritionally. The mites and collembolans of the early Devonian were presumably detritivores, consuming plant material already partially degraded by microbial activity (fungal, bacterial) in the soil litter. We have at least some well-documented evidence of fungal activity within the tissue of the Rhynie plants (Kidston & Lang 1921) even though later authors have favoured a symbiotic basis for their role rather than a saprophytic one. It seems an obvious progression from this relationship of arthropod–soil-microflora–litter-feeding, to one of arthropod–gut-microflora–plant-feeding.

This would represent the evolution from a casual relationship of arthropod and cellulose-degrading microorganisms to one of mutual advantage between the arthropod and its gut microflora.

The first evidence of any considerable wood-boring activity is none the less in late Carboniferous gymnosperm wood, with 'galleries' containing coprolites of the boring organisms described by several authors (figure 4). Orabatid mites are favoured as likely borers (Cichan & Taylor 1982; Scott & Taylor 1983). Several examples of insect boring within fern tissue have also been reported (Rothwell & Scott 1983; Lesnikowska 1990). The latter is important in showing a wound response associated with the boring, indicating that the plant was alive when the feeding took place. There are a number of records of wood boring (and even bark burrowing, figure 6) in Mesozoic gymnosperm material, with a wider range of possible causal organisms, and these are reviewed in Scott *et al.* (in preparation).

Leaf mining is a further type of insect attack on plants which combines 'feeding' with 'protection' (fig. 2). The majority of modern leaf miners are found in angiosperm leaves, where the causal insect lays its eggs upon or within the leaf and the larva then feeds on the mesophyll, leaving a trail within the leaf that is recognizable in the fossil state. The earliest record of leaf mining is in late Carboniferous specimens of the seed-fern genus *Neuropteris* (Muller 1982), which show blotches and linear markings. These and somewhat younger leaf mines described by the same author are said to show similarity to those produced by modern lepidopteran miners, but fossil insect remains of that group do not appear until the Cretaceous.

5. POST-CARBONIFEROUS PLANT–INSECT INTERACTIONS

All the types of tangible evidence of plant–arthropod interactions reported above are known in post-Carboniferous material. In the Permian we have further evidence of leaf eating with *Phagophytichnus*-type marginal feeding from the Southern Hemisphere gymnosperm *Glossopteris* (Plumstead 1963; Stephenson & Scott 1991) (figure 5). Mesozoic records of leaf eating are fairly sparse, but they increase in number and diversity of feeding strategies as the angiosperms come to dominate the terrestrial flora towards the close of the Cretaceous. In the early angiosperms we see a more extensive record of 'continuous marginal' and 'interrupted marginal' leaf feeding, and eventually the appearance of 'non-marginal' feeding: the taking of isolated patches of tissue within the body of a leaf (Stephenson, unpublished data) (figure 1). The latter is evidently a more difficult feeding process for insects, and significantly, we have no record of it earlier than the Cretaceous.

Inevitably the fossil record gives little indication of what was probably the most prevalent interaction between plants and animals, namely the 'chemical warfare' involved in the plant kingdom seeking respite from the plant eater. This, more than any other interaction short of biotic pollination, must have been in the nature of a coevolutionary response as the production of antifeedant or toxic defence substances by the plant was countered by some physiological modification of the plant-feeding animal. The seemingly trivial differences of leaf feeding strategy probably reflect aspects of this complexity of the plant–animal and herbivore–predator biochemical relation, in ways only hinted at in the simple observation of damaged fossil leaves. Edwards & Wratten (1980, 1983) give a helpful review of the significance of various feeding patterns. The production of antifeedant substances in immediate response to leaf damage is doubtless connected with discontinuity of marginal feeding, and probably also to 'internal' feeding. We illustrate an example of a Cretaceous leaf showing one of the earliest records of such 'internal' feeding damage in an angiosperm (figure 1). Avoiding the advertisement to predators offered by extensive and conspicuous leaf feeding is clearly also a factor governing feeding behaviour, but of this we can have no direct evidence from fossil leaves showing feeding damage.

One of the most elaborate and biochemically finely-tuned interplays of the plant–animal relation is that of plant galls induced by a parasite. This response of plant tissue, in abnormal growth caused by substances produced by the invading parasite, may give the animal both protection against predators, and an enhanced food supply for a developing larva. Our earliest record of plant gall formation is in the Permian report of Potonié (1893) of leaf galls on the pteridosperm *Odontopteris* (see also Conway-Morris (1981)). This isolated Palaeozoic occurrence is followed by a scattered record of Mesozoic galls (Scott *et al.*, in preparation). With the rise of the angiosperms from the mid-Cretaceous, a wide range of leaf galls gives increasing evidence of this type of insect activity. Stephenson has explored mid-Cretaceous angiosperm leaf floras for evidence of gall formation, and recognizes 26 leaf specimens with galls, which fall into eight distinct categories. An example of one of these is illustrated in figure 11. The range of forms is consistent with those formed by present-day Acari, Hemiptera, Diptera and Hymenoptera. It is a little surprising that none are clearly attributable to the Lepidoptera, as this group has a fossil record from the Cretaceous, and is likely to have been involved in insect–angiosperm coevolution in the role of vectors of biotic pollination.

Leaf mining has a record that runs from the Carboniferous, as reported above, through records in Permian and Mesozoic gymnosperm leaves (see Scott *et al.*, in preparation). Angiosperm diversification – and perhaps, in particular, the soft leaf texture of their deciduous forms – seems to have given added scope to this strategy. One of us (J. S.), in a study of Cretaceous angiosperm leaves has found 50 occurrences, representing 18 different types of leaf mine patterns. In some cases the mines are so well preserved that they trace the growth of the expanding larva from the site of entry to the pupation chamber, where the insect finally vacates the leaf (figure 2; see Hering 1951).

Spore feeding also has a Mesozoic record in the form of spore-containing coprolites. Harris (1957) gives one of the earliest reports of small coprolites containing the pollen of the gymnosperm *Caytonia* from the Middle Jurassic. In terms of plant–animal coevolution, this direct evidence of some small animal engaged in pollen feeding is inevitably to be seen in the context of the biotic pollination that characterizes some of the primitive (and earliest) angiosperms. The role of pollen feeding as the lead into repeated flower-visiting, and hence into a mutually advantageous flower–vector relationship has been amply expounded on the basis of observation of living plants (Faegri & Van der Pijl 1971), and is discussed elsewhere in this symposium (Friis & Crepet).

We thank Deborah Parsons and Geoffrey Prior for their help with the modern arthropod experiments, and Kevin de Souza for photographic help. J.S. gratefully acknowledges the receipt of a NERC research studentship.

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Discussion

E. A. Jarzembowski (*Booth Museum of Natural History, Brighton, U.K.*). Please could the authors consider providing criteria to distinguish insect or other arthropod feeding marks on fossil leaves as Crane & Jarzembowski (1990) have attempted for leaf mines. This is to distinguish them from the vagaries of geological preservation and damage from other physical or biotic causes. Necrotic tissue provides evidence of damage during the life of a plant but, like fungal attack, may help obscure important evidence, for example the jagged edge left on a leaf by a mandibulate insect.

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Crane, P. R. & Jarzembowski, E. A. 1990 Insect leaf mines from the Palaeocene of southern England. *J. Nat. Hist.* **14**, 629–636.

W. G. Chaloner. The best indication we can have that damage to a fossil leaf has occurred while it was alive is the presence of necrotic tissue at the margin of the injury. We discuss this matter in further detail in Scott *et al.* (1991).

E. A. Jarzembowski. *Rhyniella praecursor* (Collembola: Isotomidae) from the Rhynie Chert (Lower Devonian: Pragian), the earliest known insect (hexapod), is now known from the whole anatomy, the previously unknown hindbody having been described by Whalley & Jarzembowski (1981). A new reconstruction of *R. praecursor* is modelled by Jarzembowski (1989, figure 5).

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W. G. Chaloner. We refer to the 1981 record in this paper, and are pleased to learn of the new reconstruction of *Rhyniella*.

E. A. Jarzembowski. An important element of the Upper Carboniferous fauna was the presence of rostrate palaeopterous insects that may have occupied the ecological niche later held by hemipteroid insects (Jarzembowski 1987). Could the pierced *Trigonocarpus* and spores be the feeding traces of these insects as suggested by A. G. Sharov and P. Barnard (Wootton 1981)?

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W. G. Chaloner. Yes, this is possible; see also Shear & Kukalova-Peck (1990).

Reference

Shear, W. A. & Kukalova-Peck, J. 1990 The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Can. J. Zool.* **68**, 1807–1834.

E. A. Jarzembowski. The beetle-bored wood from the English Wealden is of additional interest because it shows two types of borings (Jarzembowski 1990) supporting the view that a stressed tree is liable to attack by more than one vector. Bark beetles, which have been considered responsible for some of these borings belong to the same family as weevils (Crowson 1981) which are now being suggested; could the burrows have been produced by larvae belonging to stem-group Curculionidae?

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W. G. Chaloner. Yes, of course, this too is possible.

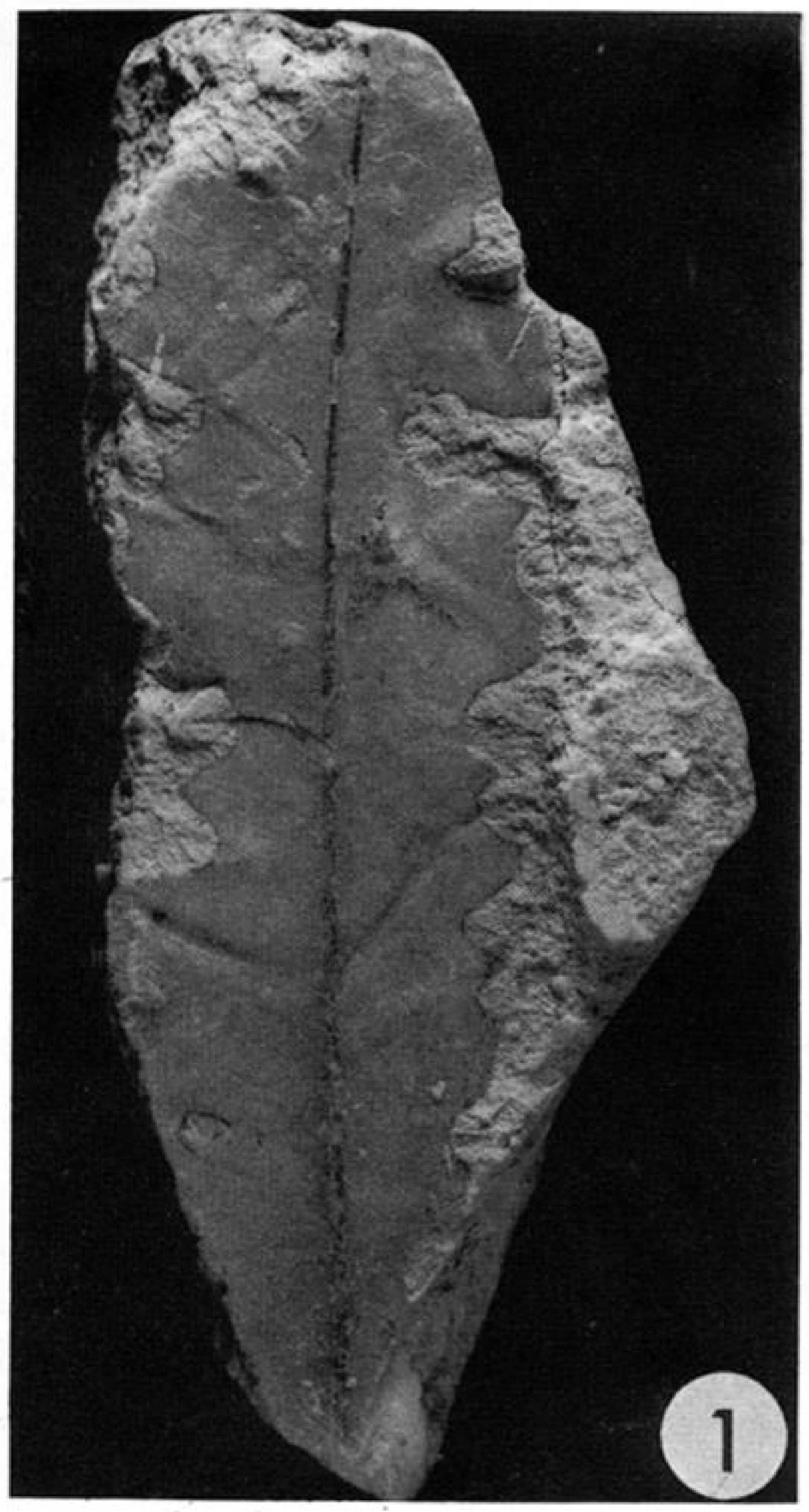
R. McN. Alexander (*Department of Pure and Applied Biology, Univrsity of Leeds, U.K.*). I am interested by the suggestion that spores may be a rewarding food material although a substantial proportion pass through the gut unharmed. Does this imply that digestion of a spore is very much an all-or-nothing matter: that a spore either breaks open and is thoroughly digested, or survives intact and unharmed?

W. G. Chaloner. Yes, it does seem to be a more or less hit-or-miss affair: that is, any particular spore is either ruptured, presumably in mastication, or it is not. In the latter case, it has a chance of surviving and germinating. As a result we see three categories of spores in the droppings: (i) those which germinate (and which we score as such); (ii) those which are ruptured and empty and (iii) those which appear intact, but which have not germinated. This last category may have already been in a non-viable state when they were eaten, or may have been killed during or after eating, but without being ruptured. In any event, we scored these two latter categories together as being non-viable in the droppings. We could (and perhaps should) have disoriminated between these, and scored them separately.

It is a little surprising that quite a significant fraction do pass the gut unharmed. But it seems likely that the proportion is influenced by the nature of the food on which they are fed to the arthropod, and hence presumably to the degree of mastication to which they are subjected. The entire process is obviously susceptible to much more serious experimentation than we have attempted!

M. E. Collinson (*Biosphere Sciences Division, Kings College London, U.K.*). Do the authors have evidence that herbivores change their diet to exploit new groups of plants as they evolved, or do new feeding strategies appear coincident with new plant groups? In particular, in the extensive evidence of herbivore damage present in angiosperm leaf fossils due to newly emerged herbivore groups, do you see diversification of feeding evidence coincidental with diversification of angiosperms? Did anything significant change in the Palaeocene 'between' dinosaur and mammalian herbivore browsers?

W. G. Chaloner. We are pleased to be asked these questions by Dr Collinson, who is probably more competent to offer answers than we are ourselves. We do not have sufficiently tight time control on the first appearance either of leaf-damage types or of the animals known to be involved, to be able to answer these very pertinent questions. If, as Brown & Lawton (this symposium) suggest, the serrations of leaf margins are a defensive adaptation in response to insect marginal feeding, it becomes of particular interest to note the rarity of such non-entire leaves in pre-angiosperm Mesozoic floras, and their near-absence in Palaeozoic leaves.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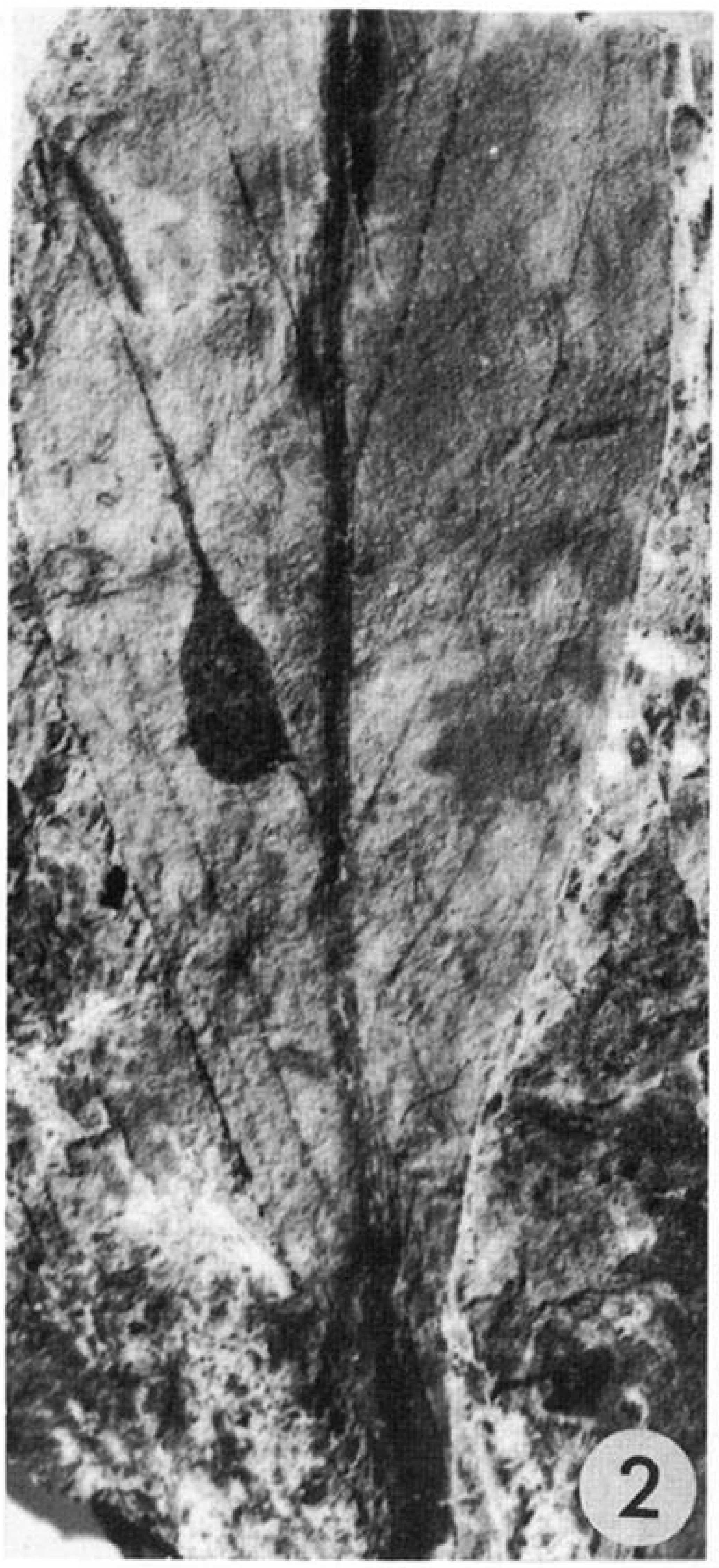
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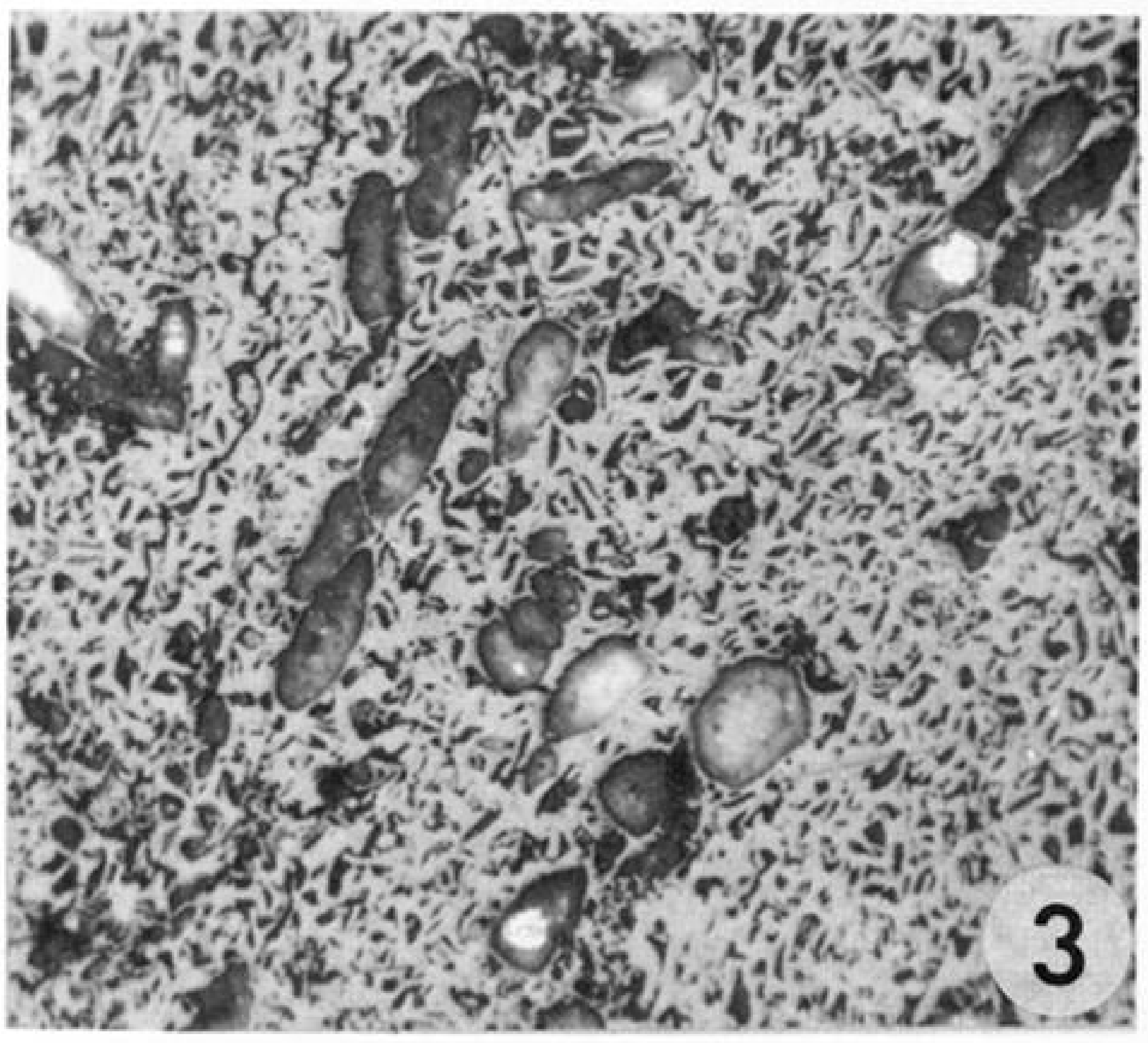
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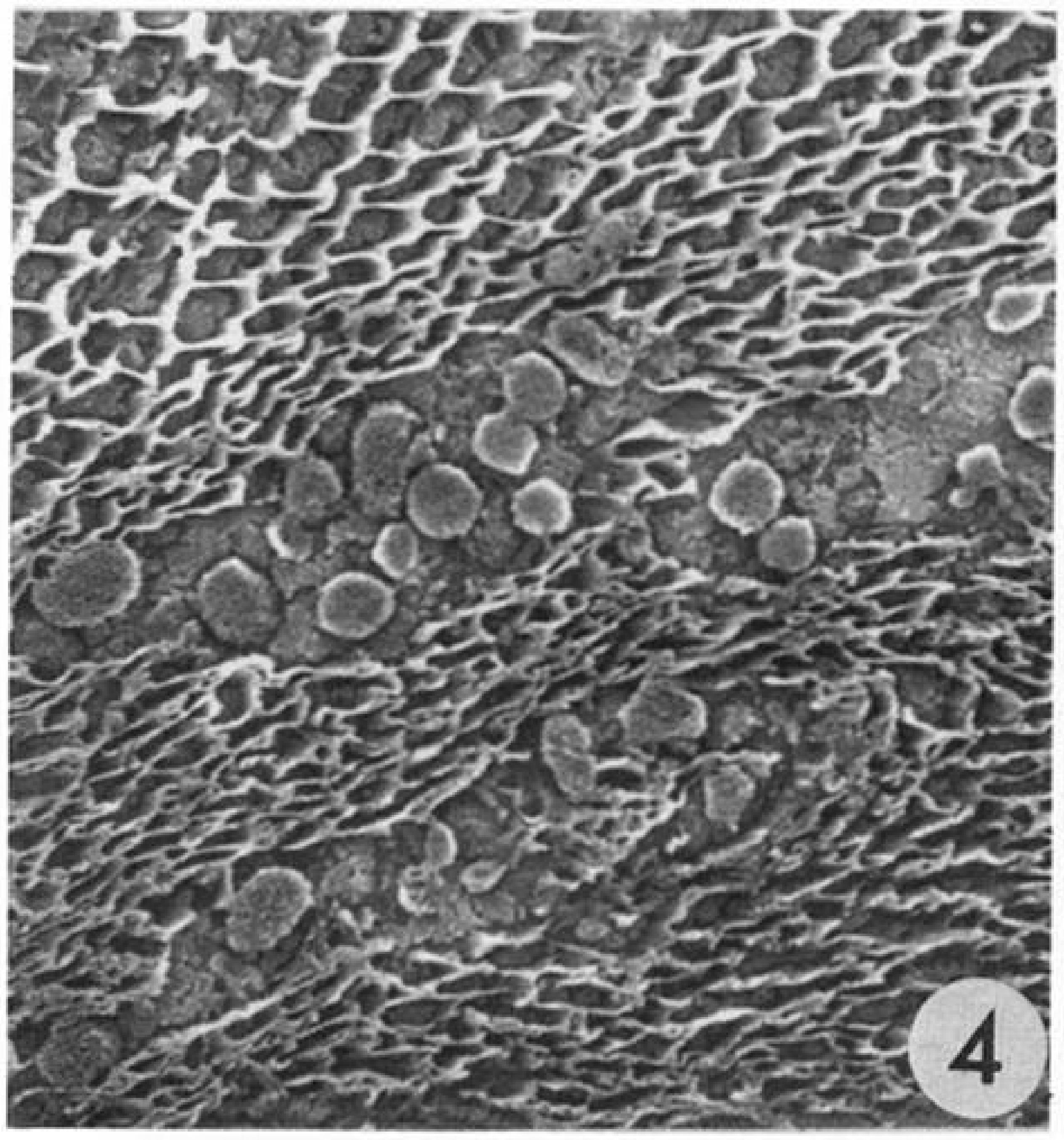
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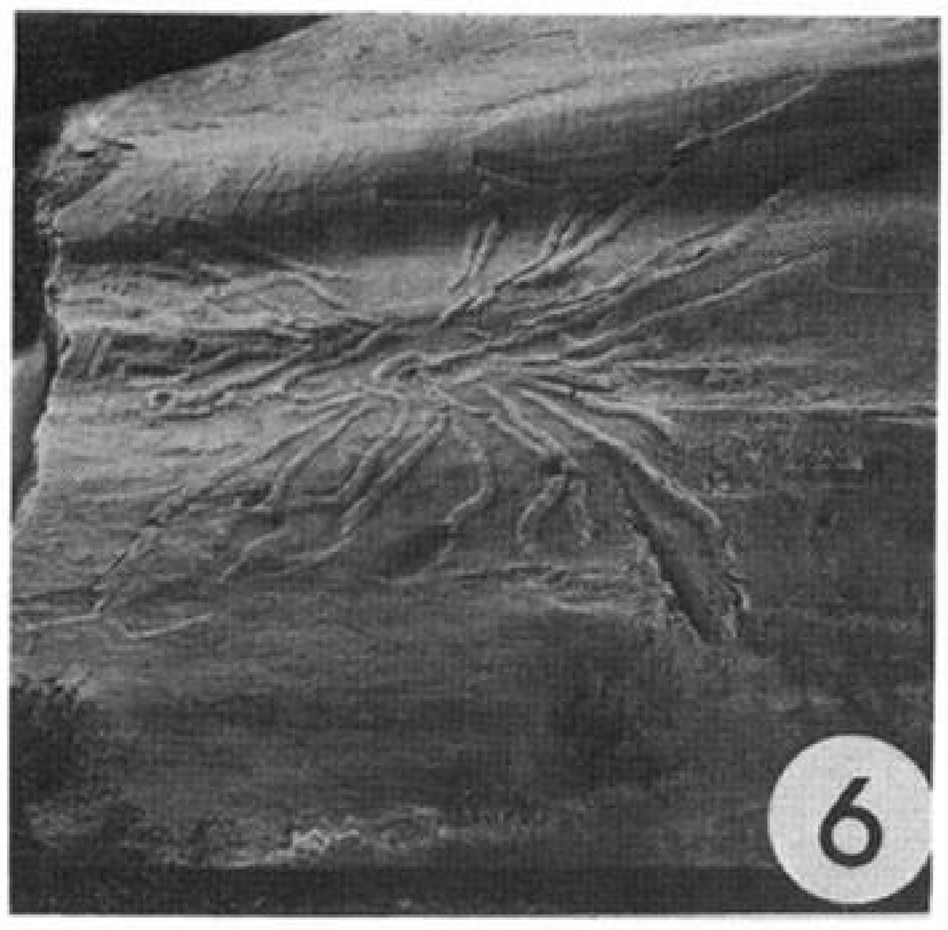
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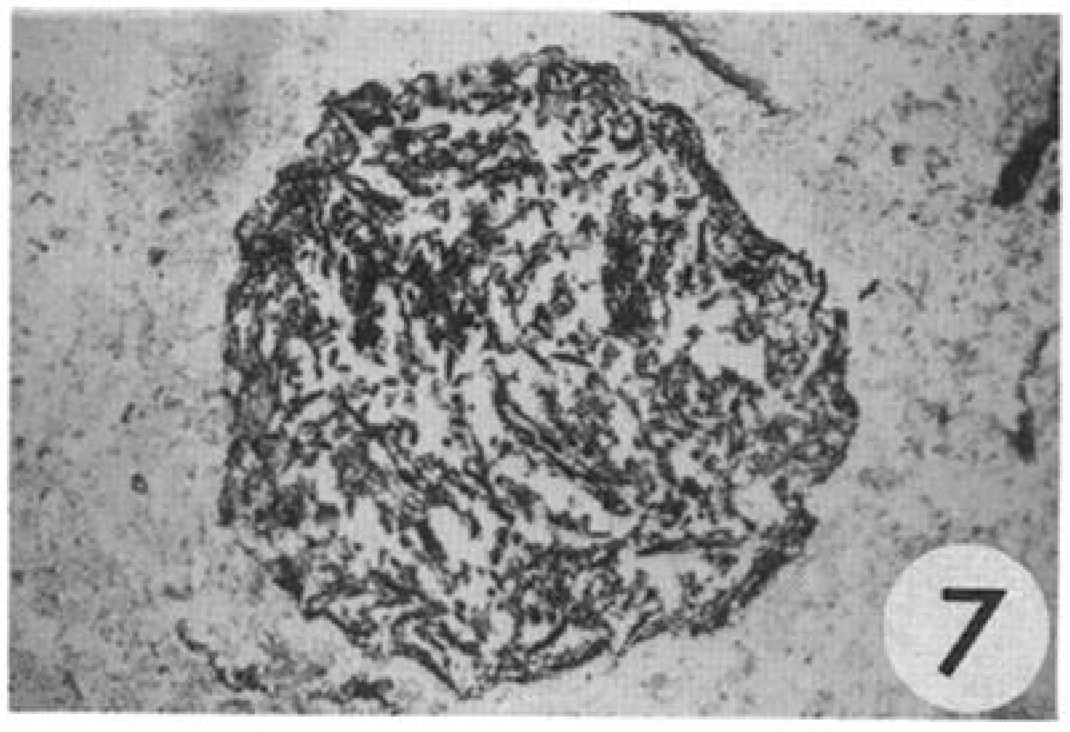
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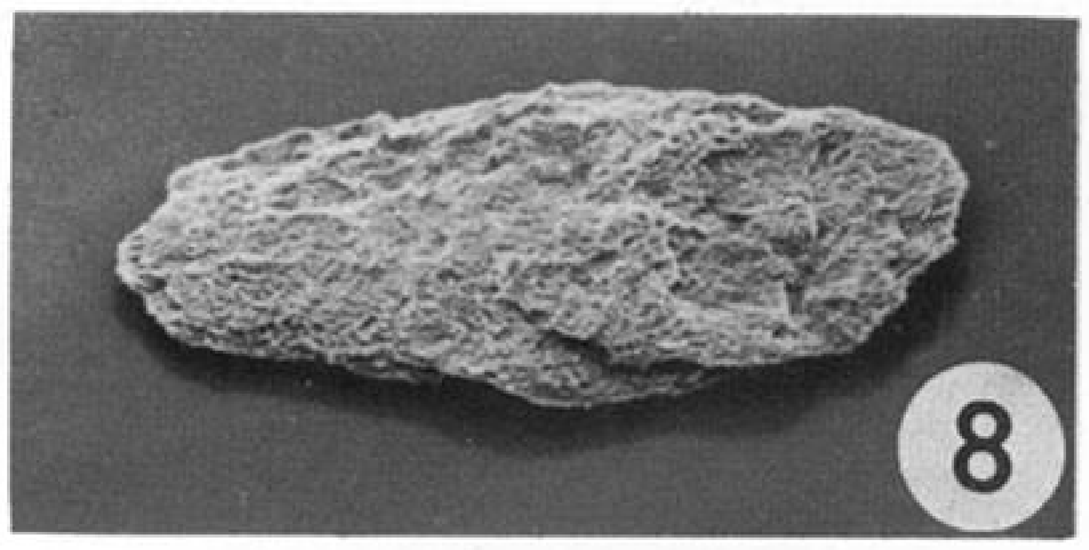
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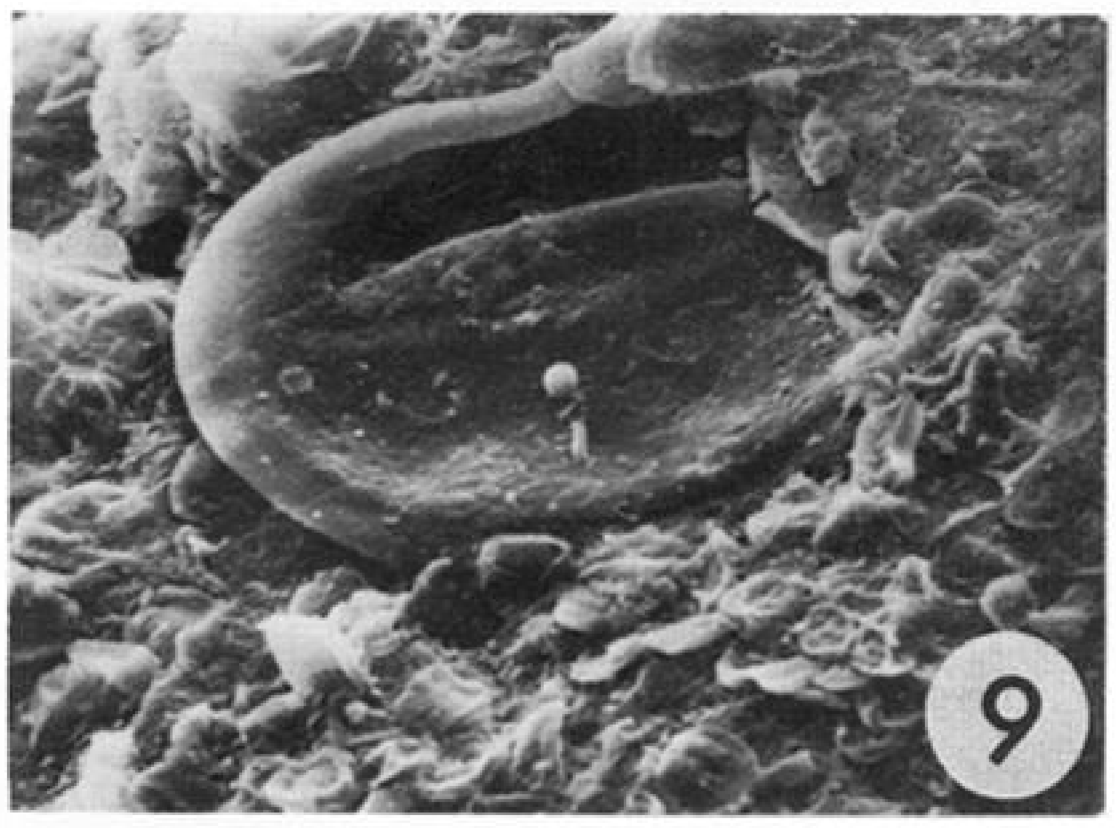
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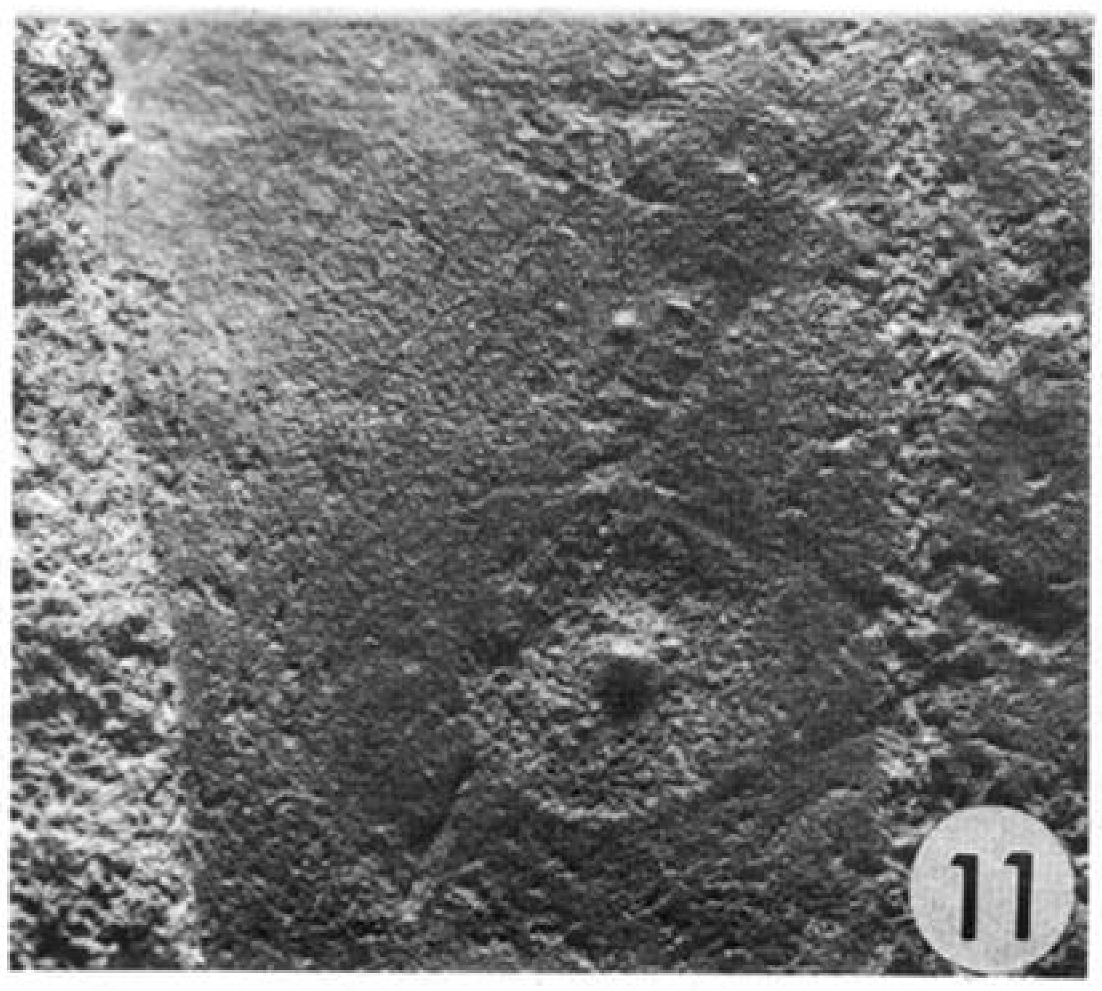
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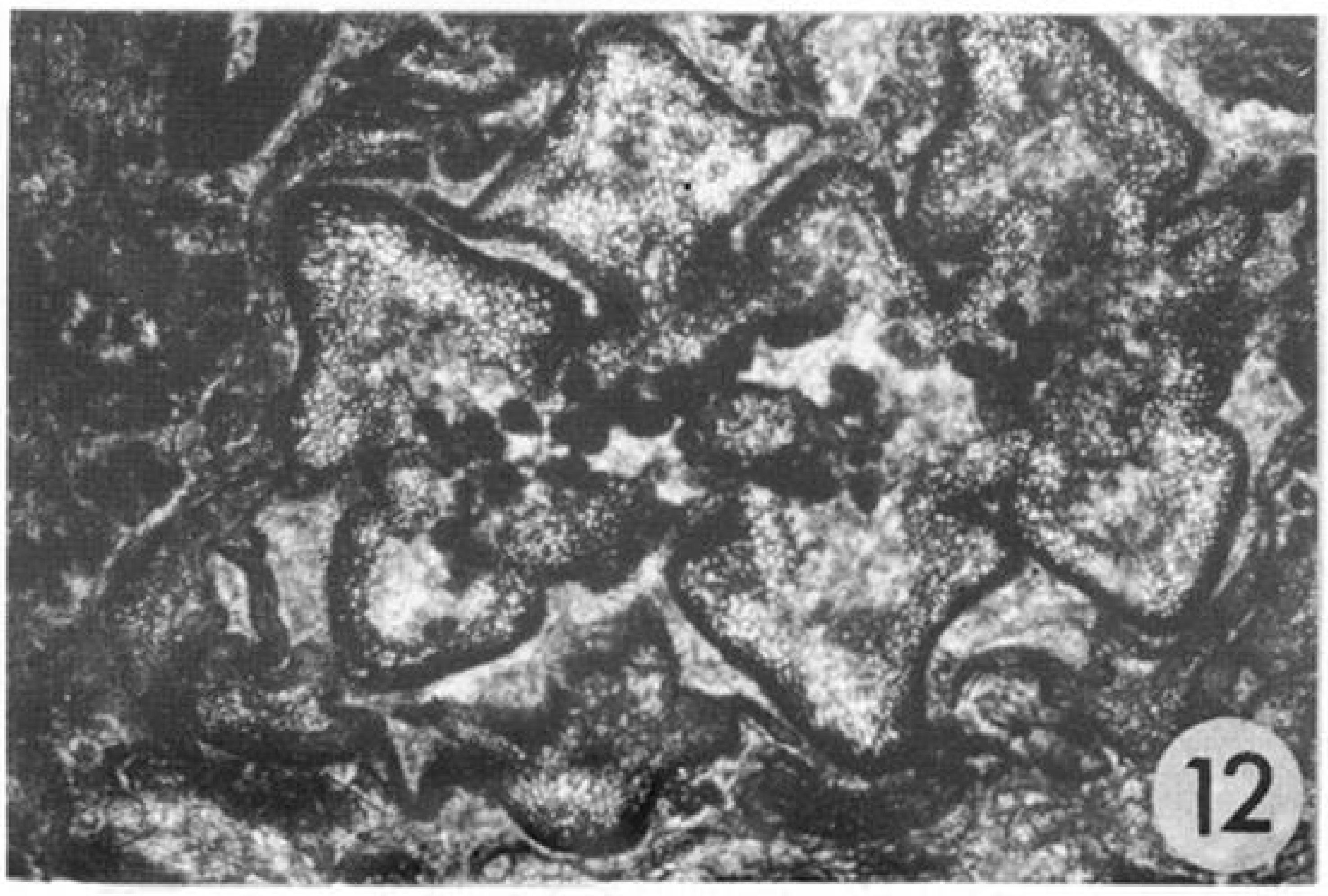
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Figures 1–12. For description see opposite.