Interaction and coevolution of plants and arthropods during the Palaeozoic and Mesozoic

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SUMMARY

Fossil evidence of terrestrial vascular plant life and terrestrial arthropods exists from the Silurian. Fossil evidence suggests progressive interaction between the two groups through the later Palaeozoic and Mesozoic. In this paper we present data, particularly from plant fossils, concerning several interactions: feeding, shelter, transport and reproduction. Evidence of arthropod feeding includes eaten leaves, borings in plant tissues, wound reaction and leaf mining as well as gut contents and coprolites from the arthropods themselves. We trace the changes in leaf eating behaviour from continuous marginal feeding, common in the Palaeozoic and early Mesozoic to the more abundant interrupted-marginal and non-marginal feeding behaviour on Cretaceous angiosperm leaves. This change may reflect the evolution of chemical defence strategies by the plants but may also reflect the evolution of different mouthpart design in new insect groups. Leaf mines and leaf galls, although known from the Upper Carboniferous, only

Phil. Trans. R. Soc. Lond. B (1992) **335,** 129–165
Printed in Great Britain

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become common in the Cretaceous, coinciding with the evolution of several new insect groups and plants. Wood boring is recorded, for the first time, from the Lower Carboniferous and becomes common from the Upper Carboniferous. Data from coprolites suggest that spore feeding preceded leaf feeding. Experiments using pteridophytes and living arthropods indicate that some spores remain viable after passing through the gut and hence this feeding habit may have also been advantageous to some early plants for propagule transport. We conclude that there is much evidence in the fossil record suggesting plant–arthropod interaction, but many more observations are required before detailed interpretations concerning coevolution can be made.

1. INTRODUCTION

An analysis of modern terrestrial ecosystems indicates that there is a wide range of complex interactions between arthropods, especially insects, and plants (Edwards & Wratten 1980) (figure 1). Whereas some appear to be the product of coevolution, the nature of other interactions is less clear. Gilbert (1979) has calculated that the number of interactions between arthropods and plants exceeds the total number of the species concerned. Much of the data relating to such interactions has been collected from extant organisms, and data on past interactions is both scarce and scattered.

The fossil history of insects has been widely discussed (e.g. Carpenter 1969; Wootton 1981, 1988; Whalley 1986; Shear & Kukalova-Peck 1990). We know many of the interactions between Recent arthropods and plants and can recognize the types of damage made by different organisms (see Gillanders 1908; Berryman 1986). The evolution of many detailed interactions has been explored (e.g. with ferns (Gerson 1979; Cooper-Driver 1978, 1985) conifers (Edmunds & Alstad 1978), angiosperms (Gilbert 1979)). Gilbert (1979) states 'it is thus reasonable to think that the parallel diversification of both angiosperms and phytophagous insects is largely the product of their interaction'. However, all these studies take little account of the fossil record. For those not familiar with the fossil record of terrestrial arthropods and plants we provide a brief summary as Appendix 1.

Brues (1946) states that 'Perhaps not a single plant exists which does not afford a delicious food to some insect'. However Lawton (1978), indicates that 'communities of phytophagous insects which are found on particular species of plants are not random assemblages, chewing away independently of one another, rather they have a structure which can be unravelled by a consideration of time and space'. Any group of insects that becomes adapted to plants in general has a wide range of potential foods, for in most terrestrial ecosystems, the biomass of the plant material greatly exceeds that available to predators (Southwood 1984). This continued feeding through time has been the main causal mechanism for the evolution of plant protection such as chemical and physical defences, including thick cuticle and glandular hairs (Southwood 1984). The fossil record is, however, often difficult to understand in this regard. We can interpret feeding habits of fossil insects from a consideration of their anatomy and especially mouthparts (see, for example, Sharov (1966, 1973); Wootton (1981); Labandeira (1986); Shear & Kukalova-Peck (1990)) but much of our evidence must be from damage to plants. Southwood (1973) points out that many arthropods feed on dead plant material and Sharov (1966) considered that the first insects fed on rotting plant material. As Hamilton (1978) points out, a dying tree opens a wide variety of habitats for colonization by insects. It is also clear that feeding on living plant tissues has a long fossil history, as many plants have developed specialized reactions to attack (Van Emden & Way 1973). The recognition of feeding on living tissue necessarily requires the observation of wound reaction tissue or necrotic margins around the site of plant damage.

It has been estimated that half of all known species of insects are more or less dependent on plant hosts (Kogan 1976) and we have no reason to suppose that this was not the case in the past. Evidence of leaf feeding is perhaps one of the most obvious areas of plant–arthropod interactions that can be observed in the fossil record. Southwood (1973) indicates, however, that leaves are only marginally adequate nutritionally and further indicates that pollen (and spore) feeding may have preceded leaf feeding, a hypothesis that can be tested using fossil material. The additional aspect which needs consideration is that insects are also transporters of plant propagules and in return plants are providers of food reward (Gilbert 1979). As Southwood (1985) points out 'plants are not simply a food source, nor are they merely islands but responding evolving entities'. An examination of the fossil record, should therefore provide valuable data for the current considerations of plant–arthropod interactions (Strong *et al.* 1984).

We have, however, considerable potential bias in the fossil record. Not only may damaged plants decay more rapidly and hence may not be fossilized, but it is likely that those specimens of damaged plants that do fossilize may not be collected. Recognition may also prove problematical as, for example, missing leaf damage in narrow leaves. Preservation state may also influence the type of interaction to be recorded, for example wood boring is usually only recognized in permineralized plants.

It is clear that plant–arthropod interactions can be categorized as feeding, shelter, transport and reproduction (see Southwood 1973). Rather than presenting the fossil evidence for these interactions in a simple time sequence, we offer it under the categories of

Figure 1. Some interactions of plants and arthropods, for which evidence has been found in the fossil record.

interactions. We have discussed elsewhere aspects of the nature of the fossil record and methods of study (Scott & Paterson 1984, Scott *et al.* 1985, Chaloner *et al.* 1991) and concentrate here on the fossil evidence itself and its interpretation. By far the largest area of interaction is that of arthropods feeding on plants. The quality of such data is very variable, but they come from plants as well as from the arthropods themselves. The evidence from the plant fossils includes eaten leaves, borings in plant tissues and wound reaction, and leaf mining. Evidence from the arthropods includes anatomical studies, particularly mouthparts, evidence of gut contents and from coprolites (faecal pellets).

2. FEEDING

There is a range of evidence of plant feeding by arthropods from the Devonian onwards. The major evidence of this interaction includes eaten leaves, borings and leaf mines. Occasionally wounding has been detected in anatomically preserved plants, which has been attributed to the action of arthropod feeding. In the case of living plants a wound reaction may result from this kind of feeding behaviour.

(*a*) *Wounding*

In the Lower Devonian Rhynie chert from Aberdeenshire, Scotland some *Rhynia* stems exhibit wounds and wound reactions (Kevan *et al.* 1975). In these cases it has been suggested that these were caused by arthropods sucking sap. Other authors question if these wounds were caused biologically or by a physical process (Rolfe 1985*a*).

The Rhynie chert is of major interest as it comprises not only early anatomically preserved plants but also several arthropod groups. The plants compromise several different types of Psilopsida including *Rhynia gwynne-vaughnii* Kidston & Lang, along with the possible 'cooksonioid' *Aglaophyton (Rhynia) major* (Kidston & Lang) Edwards, and *Asteroxylon mackieii* Kidston & Lang, the earliest recorded protolycophyte of the Northern Hemisphere (Chaloner & MacDonald 1980).

Within the plant assemblage there was also a number of terrestrial arthropods. The exceptional preservation of the chert has revealed the earliest hexapod in the form the collembolan, *Rhyniella praecursor* Hirst & Maulik (Whalley & Jarzembowski 1981), and the earliest arachnid, *Palaeocteniza crassipes* Hirst, (Aranae), and various species of mite (*Protacarus crani* Hirst (Acari)) Trigonotarbids *Palaeocharinoides hornei* Hirst, *Palaeocharinus scourfieldi* Hirst, *P. rhyniensis* Hirst, *P. calmani* Hirst and *P. kidstoni* Hirst. Other possible chelicerates include the fragmentary *Heterocrania rhyniensis* and the jaws of the arthropod *Rhyniognatha hirstii* Tillyard.

Several interactions between these arthropods and the plants may have occurred, and during their early investigations into this unique Devonian ecosystem

Kidston & Lang (1921*a*) noted the presence of lesions in a number of *Rhynia* axes. They later suggested these lesions to be a reaction to some prolonged external stimulus such as the volcanic conditions that accompanied the supply of siliceous water which eventually formed the chert (Kidston & Lang 1921*b*). A number of possible causes and interpretations have since been suggested, these include intumescences due to excess moisture (Butler & Jones 1949), as galls (Jeppson *et al.* 1975; Conway-Morris 1981), as a result of nematode action (Wallace 1973). Probably the majority of workers now consider them to be due to an external biological agent such as one of the coexisting arthropods (Kevan *et al.* 1975; Rolfe 1980, 1985*a*; Scott *et al.* 1985). The pathological features of these lesions include necrosis around the cavities and punctures, accompanied by hypertrophy of the surrounding cells and often the formation, by gummosis, of an opaque plug. Most significantly, the cells adjoining the lesion have divided and expanded into this gap as a typical 'wound reaction'. All these reactions could only have occurred while the plant was still alive. Some wounds still retain their thin epidermis which covered the wound and are very similar to the pocket galls produced by living eriophid mites (Rolfe 1985*a*). Others show the wound to be deep holes extending to the central vascular tissue perhaps caused by an animal probing to feed from the sap (Raven 1983). Kevan *et al.* (1975) classified these lesions into three groups: (i) areas of disturbed tissue, in which some cells show abnormal enlargement associated with in-filling of intercellular spaces with opaque organic material; this suggests a traumatic response by the plant to physical injury; (ii) 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; the plugs appear to be produced by the plant, but fungal origin cannot be ruled out; (iii) extensive injury; very difficult to attribute to any cause other than by an organism.

Kevan *et al.* (1975) suggested that these could have been caused by either the acarine mite, *Protacarus crani*, or by the collembolan, *Rhyniella praecursor* or the trigonotarbid. Crowson (1970, 1985) has suggested that both *Protacarus* and *Rhyniella* are later contaminants of the chert. He bases most of this theory on their advanced features and on the discovery of contaminant Recent thysanopteran insect nymphs which must have crawled into a crevice in the chert. Whalley & Jarzembowski (1981), however, have shown that the silica chert around the specimens is homogenous and represents a single phase of mineral growth, the possibility of a later contamination of these insects being impossible.

Recent studies on *Rhyniella* have revealed the presence of perhaps three species (Greenslade 1988) most belonging to the family Isotomidae (Greenslade & Whalley 1986). This is a primitive group of saprophagous litter-feeding collembolans, not phytophagous as suggested by the *Rhynia* damage. Of the other collembolan species, some have elongated claws, a character suggesting a semiaquatic environment, in keeping with the idea that the chert is a silicified peat bog (Rolfe 1980).

The collembolans were therefore unlikely to have been the possible cause of the wounds and the mites were most probably carnivorous. However, there is no unequivocal proof that these organisms behaved as their Recent relatives do and so they cannot be ruled out completely as possible candidates. Thus, all the possible options of how these lesions were formed and by what should be kept open until less equivocal data is available.

Wounding has also been recorded in other Lower Devonian plants. Banks (1981) reported plants with wound reaction tissue in the periderm of *Psilophyton dawsonii* from the Emsian of Canada. Another species of *Psilophyton*, *P. coniculum*, also from the Emsian of Canada has been described with several wounds (Trant & Gensel 1985). These authors have observed wound periderm, abundant in some axes. The wounds appear to be capped by necrosed cells. Beneath this tissue is a layer of what they believe may be phellem cells and below which may be phelloderm cells. This type of wound reaction was similar in both species of *Psilophyton* (Banks 1981; Trant & Gensel 1985), but there is no evidence in either case of the cause of the wounding.

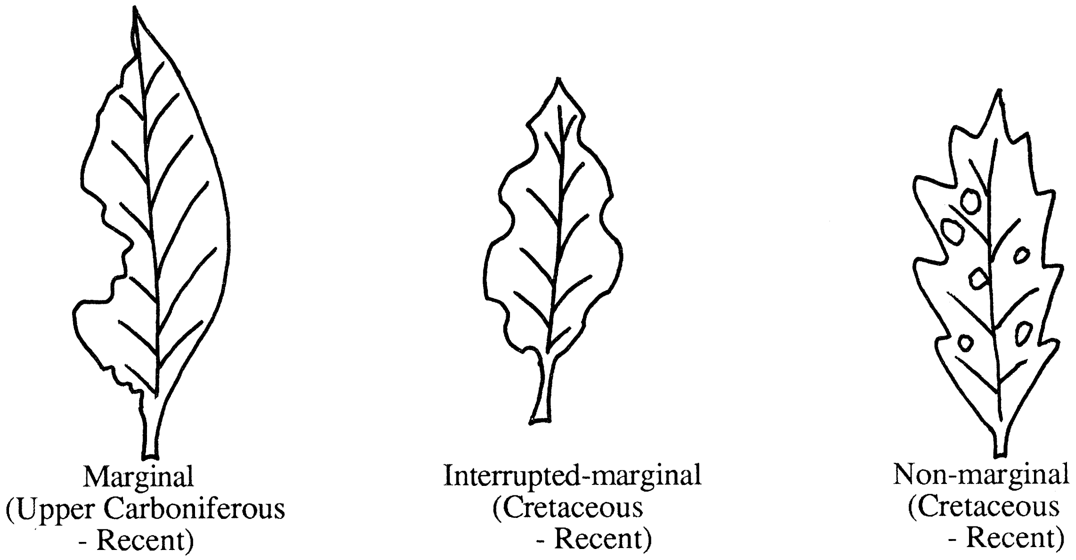
Wounds have also been extensively recorded from Upper Carboniferous coal-ball plants. These include *Calamites* (Seward 1898; Stopes 1907), *Myeloxylon* (Holden 1910) and Lepidodendroid axes (Wilkinson 1930). More recently Scott and Taylor (1983) have illustrated a section of a fern (*Etapteris*) petiole showing a possible puncture wound (figure 12). Lesnikowska (1990) has recently described wound tissue in large *Psaronius* petioles. These wounded petioles have also been illustrated by Stidd (1971).

Wounded tissues have not been widely reported in post-Carboniferous – pre-Tertiary plants but almost certainly this reflects lack of study rather than lack of presence.

The discovery of Jarzembowski (1989) of a new fossil aphid (a group which generally feed on angiosperms) from the early Cretaceous, has led the author to postulate that it could be the earliest representative of an ancient gymnosperm-feeding lineage (before the evolution of angiosperms). However, we have no plant fossil evidence for this interesting suggestion. Recognition of puncture wounds caused by aphids may be easiest in permineralized material but also small punctures in leaf cuticle may be the result of such activity. Minute holes in conifer cuticle have been described by Watson (1977) from the Lower Cretaceous, but she did not attribute such damage to aphids.

(*b*) *Leaf feeding*

An examination of any modern living tree leaf litter will reveal a proportion of leaves that have been partly eaten either while still alive by, for example, caterpillars or other insects, or else after death by arthropods such as millepedes or other detritivors. Elton (1973) has demonstrated for tropical forest



Marginal (Upper Carboniferous - Recent)

Interrupted-marginal (Cretaceous - Recent)

Non-marginal (Cretaceous - Recent)

Figure 2. The main types of leaf feeding.

ecosystems that up to 5% of living leaf biomass may be consumed on the tree by arthropod herbivores. Partially eaten leaves have the possibility of being preserved. Eating may be 'marginal' or 'non-marginal', i.e. within a leaf (e.g. Edwards & Wratten 1983) (figure 2). Inter-tissue feeding, such as leaf mines, will be dealt with later. Eating a leaf will induce a wound reaction within the living plant tissues immediately surrounding the site of damage. This 'wound response' includes a localized hypertrophy of the cells either by increasing in size or in number. Cells may differentiate before dividing one or more times (Juniper & Jeffree 1984). This results in the production of a thickened ridge or callus of wound periderm of 6–10 layers of cells, which seals off the damaged area. In addition, the outermost layers of cells surrounding the wound may die due to the physical damage and a characteristic browning occurs where cell compartmentation breaks down (Edwards & Wratten 1983). Both this necrotic layer and the formation of a callus may be preserved in a fossil and can be used to distinguish between damage caused when the leaf was alive, or after leaf abscission, during diagenesis or collecting. Edwards & Wratten (1985) have also shown how the production of toxic chemicals in tissues surrounding the wounds may discourage further feeding. Various types of marginal feeding marks may therefore occur, including sporadic, regular and continuous forms, as well as non-marginal leaf feeding (figure 2).

Southwood (1973), however, concludes . . . ' that the foliage of seed plants is, even for those taxa that have evolved to live on it, only marginally adequate nutritionally: one or more vital constituents may be close to the minimal levels'.

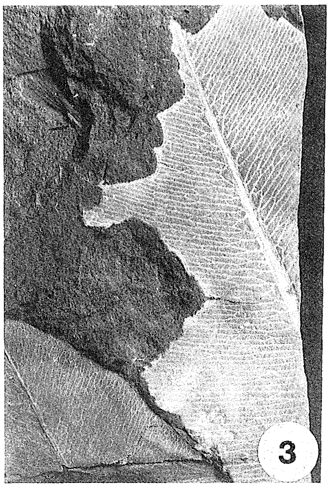
Certain identification of fossil material as representing arthropod damage is difficult. We are concerned about the identification of land snail damage (see for example Khan & Harborne (1990)), as these animals have a fossil record from the late Palaeozoic (Solen & Yochelson 1979). We are currently investigating damage by modern land snails but already note the more indiscriminate feeding patterns. It may be that the damage made by scrapping radulae of snails may be separable from the biting marks of arthropods. Fungal infection may also produce a necrotic zone. In this case it might be possible to search for fungal material but this does not rule out later infection. We are continuing to collect modern material affected in this way for comparison but our studies are at an early stage. In addition, there may be problems in the preservational state of the fossil. It is important that physical breaking either pre- or post-depositionally is not confused with evidence of feeding traces. Likewise, not all fossil specimens have an extensive leaf lamina and certain identification of feeding in some leaf types may be difficult. As with collections of modern plants, fossil collections tend to contain 'good specimens' and damaged leaves may not be present because of non-collection rather than because of a real absence (Condon & Whalen 1983).

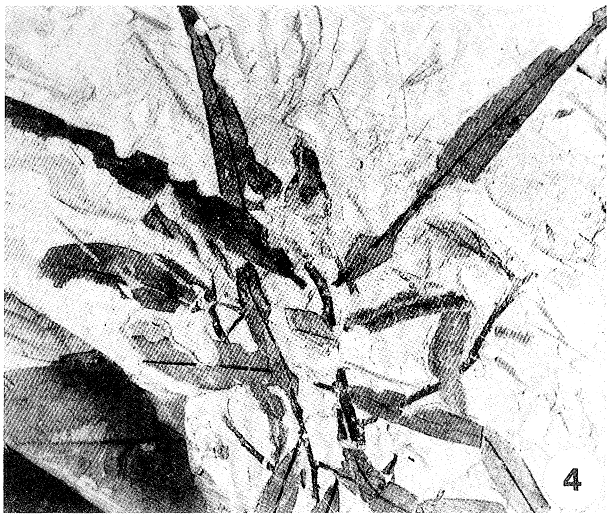
Edward & Wratten (1985) consider the difference between wound repair and defence. They also show negative evidence between different types of leaf damage, such that leaves with edge damage have far fewer internal holes and there is a negative correlation between edge damage and leaf mining.

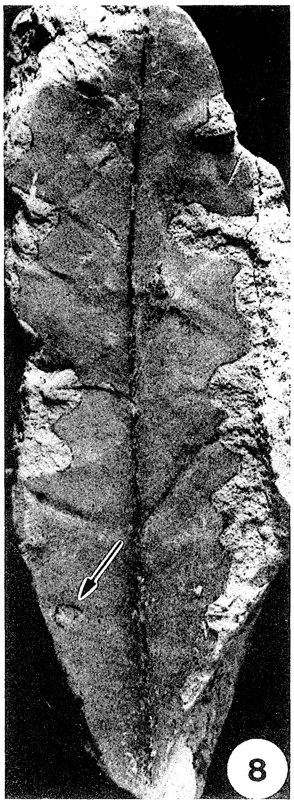
Leaf-eating traces have been assigned by some authors to ichnogenera such as *Phagophytichnus* (Van Amerom 1966). However, a comprehensive review of feeding types is urgently needed and the extensive use of ichnospecies may be unwarranted at this stage.

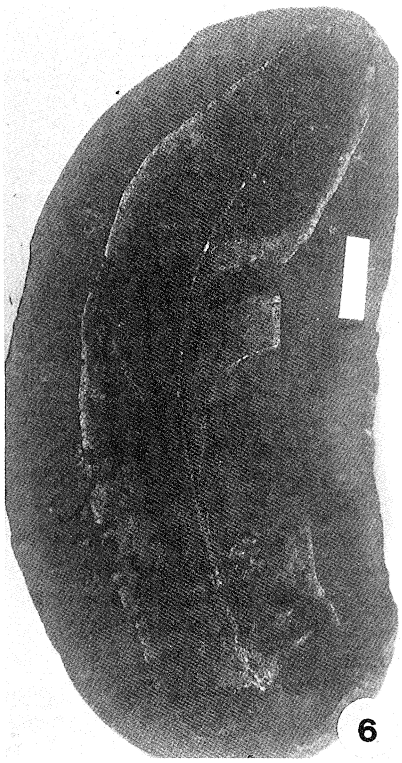
Fossil evidence

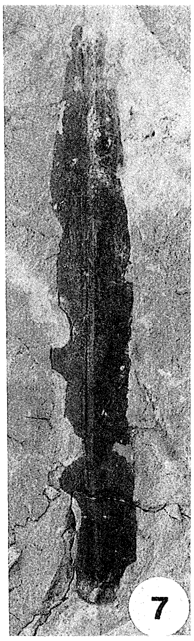
There have been no published reports to our knowledge of pre-Upper Carboniferous eaten leaves. There are three possibilities for this. Leaf feeding is an advanced characteristic for arthropods, there being less digestible food content in a leaf as opposed to a spore or seed (Southwood 1973). Secondly, leaves with a large lamina did not appear until the mid-late











Figures 3–9. Examples of leaf feeding.

Figure 3. *Glossopteris* leaf with continuous marginal feeding traces, Permian, Australia. Scott Colln. Magn. × 1.

Figure 4. Lanceolate leaves showing various forms of marginal feeding types from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago, PP11050. Magn. $\times\frac{1}{2}$.

Figure 5. Detail of figure 4 showing feeding traces with thickened callus tissue. Magn. × 4.

Figure 6. Pteridosperm pinnule, *Neuropteris scheuchzeri* showing marginal feeding damage, Upper Carboniferous, Mazon Creek, Illinois, U.S.A. Field Museum of Natural History, Chicago. PP24268. Magn. × 1.

Figure 7. Continuous marginal feeding trace on cycad leaf, Middle Jurassic, Yorkshire. Scott Colln. Magn. $\times\frac{3}{4}$.

Figure 8. Marginal and rare internal (arrow) feeding traces on angiosperm leaf from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. PP11525. Magn. $\times 1\frac{1}{2}$.

Figure 9. Bud feeding on angiosperm leaf: the animal fed on this leaf while it was still in bud. Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. PP6519. Magn. × 2.

Devonian and only became diverse and widespread in the Carboniferous. Identification of leaf feeding may be uncertain as observation of damage by eating on plants where there is only a small lamina is more difficult. Thirdly, specimens have yet to be found or recognized, and our problem may be lack of study rather than real absence. We have made extensive studies on both Lower and Upper Carboniferous plant compression in museums and from our own collections (see Appendix 2). Eaten leaves are relatively rare in the Upper Carboniferous but we have yet to find any convincing material from the Lower Carboniferous. Despite this, we still have open minds as to the reasons for their absence before the Westphalian.

Relatively few Upper Carboniferous examples have been published. Most of these are from gymnospermous leaves, with a large lamina. Nibbled or chewed examples of the pteridosperm leaf *Neuropteris* have been illustrated by several authors (e.g. Van Amerom 1966; Van Amerom & Boersma 1971; Scott & Taylor 1983) (figure 6). More rarely have eaten *Cordaites* leaves been illustrated (Muller 1982). In a quantitative study of Mazon Creek foliage Scott & Taylor (1983) found only 4% of leaves to have been eaten, all belonging to *Neuropteris scheuchzeri*: all traces show marginal feeding, often continuous, and no examples of non-marginal feeding (i.e. holes within the leaf lamina) have yet been reported.

We have no good knowledge of the kind of arthropods which may have been responsible for eating the leaves. It was suggested by Scott & Taylor (1983) that the most obvious candidates were members of the Orthoptera (grasshoppers and crickets) which are extensive foliage feeders today (Uvarov 1966) and are known from the Upper Carboniferous (Wootton 1981; Shear & Kukalova-Peck 1990)).

Permian data are limited to studies on *Glossopteris* from the southern continents. Plumstead (1963) illustrated several leaf specimens showing marginal-eating from material from South Africa (figure 11b). We have also collected similar material from Australia which we illustrate here (figure 3). *Glossopteris* is a broad spathulate leaf with an entire margin so that the identification of feeding marks is less problematic than with other leaf types. There has been no comprehensive study of Permian leaves for such evidence of eating.

Few Triassic specimens showing evidence of leaf eating have been described. Kelber & Geyer (1989) described several specimens of *Taeniopteris angustifolia* with damaged margins (figure 11c). These are all of the continuous marginal feeding type.

In Jurassic material our information is also limited. Scott & Paterson (1984) illustrate a Jurassic cycad-like leaf showing marginal feeding (figures 7 and 11d) but here again the paucity of observed insect damage is probably due to lack of search. However, it may be significant that Stephenson (1991) in examining Jurassic plants in the Natural History Museum, London, only identified three specimens showing clear evidence of leaf eating out of several thousand examined. Hill (1987), however, described a specimen of the fern *Angiopteris blackii* Van Koninenburgh-Van Cittert from the Middle Jurassic of Yorkshire which had pinnules with internal rings of presumed necrosis, 5 mm in diameter. Similar holes have also been described from *A. antiqua* from the Chinese Triassic (Hsu *et al.* 1974). Hill (1987) is uncertain whether these holes were the result of insect or fungal attack and Hill also mentions *Ctenis* with dead areas. Watson (1977) describing Lower Cretaceous conifers noted small holes within *Pseudofrenelopsis varians* from the

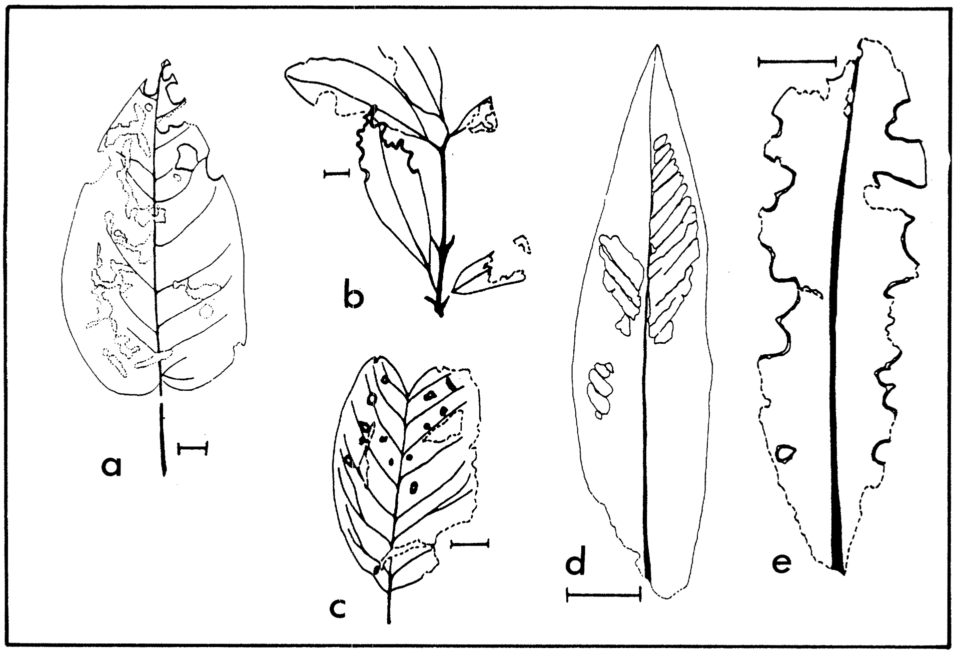


Figure 10. Types of feeding on Cretaceous leaves (scale 1 cm). a. Angiosperm leaf with internal feeding. Cenomanian, Cretaceous of Vyserovice, Czechoslovakia. National Museum of Czechoslovakia. F853. b. Angiosperm leaf with marginal feeding traces. Cenomanian, Cretaceous of Vyserovice, Czechoslovakia. National Museum of Czechoslovakia. F930. c. Angiosperm leaf with non-marginal feeding. Cenomanian, Cretaceous of Vyserovice, Czechoslovakia. National Museum of Czechoslovakia. F866. d. non-marginal feeding in angiosperm leaf. Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. PP10490. e. Marginal and rare non-marginal feeding traces on angiosperm leaf from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. PP11525.

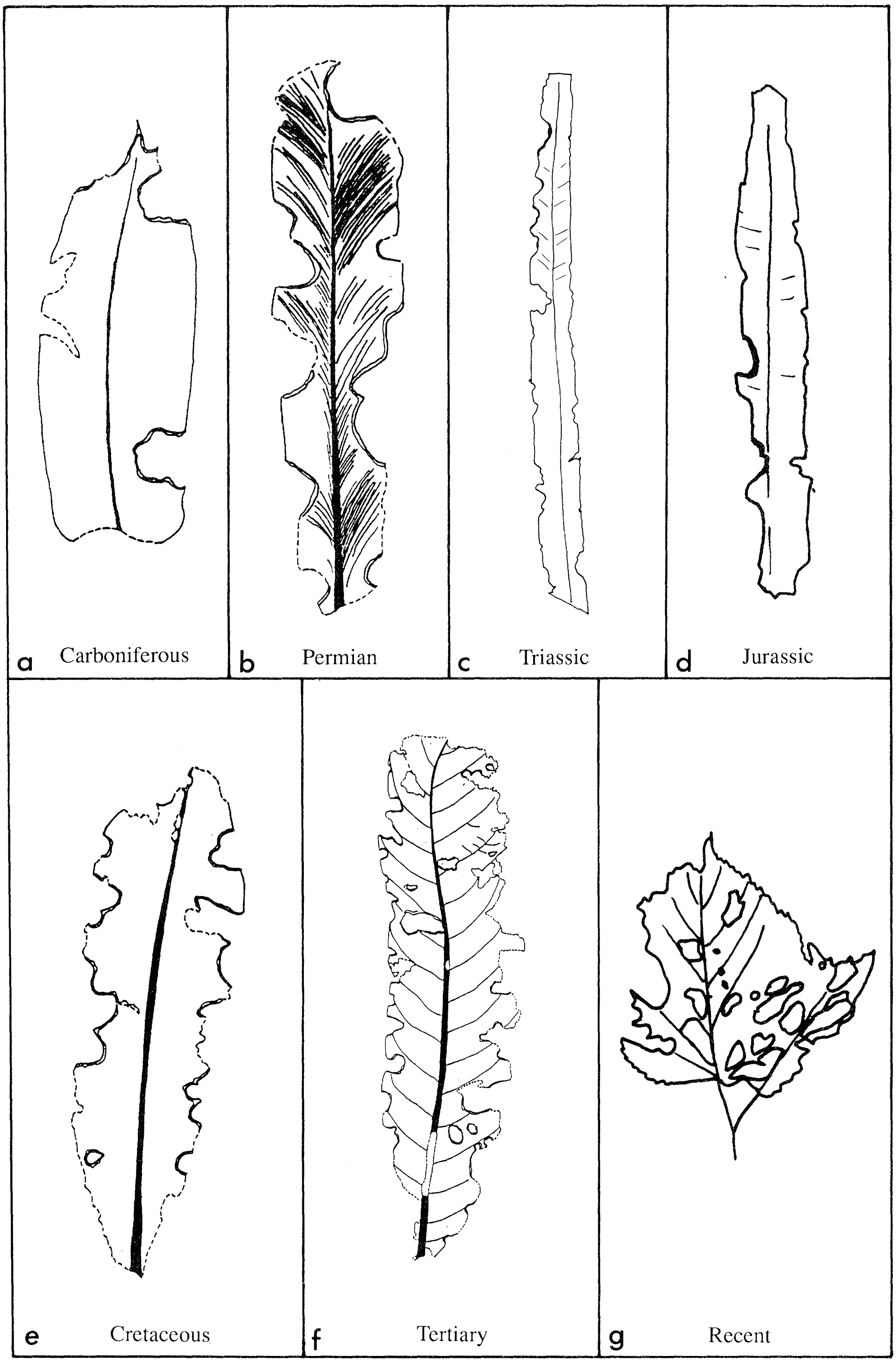


Figure 11. The geological record of leaf feeding types. a. Pteridosperm pinnule, *Neuropteris scheuchzeri* showing marginal feeding damage, Upper Carboniferous, Mazon Creek, Illinois, U.S.A. Field Museum of National History, Chicago. PP4299. Magn. × $\frac{3}{4}$. b. *Glossopteris* leaf with continuous marginal feeding traces, Permian, South Africa (after Plumstead 1963). Magn. × 1. c. Marginal feeding trace on *Taeniopteris angustifolia*, Triassic of Germany (after Kelber & Geyer 1989). Magn. × $\frac{1}{2}$. d. Continuous marginal feeding trace on cycad leaf, Middle Jurassic, Yorkshire. Magn. × $\frac{3}{4}$. e. Marginal and rare non-marginal feeding traces on angiosperm leaf from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. PP11525. Magn. × $1\frac{1}{2}$. f. Angiosperm leaf with non-marginal and interrupted marginal feeding traces from the Claibourne Formation, Middle Eocene, Tennessee, U.S.A. Field Museum of Natural History, Chicago. PP8066. Magn. × 1. g. Foliage of a lime (*Tilia* sp.) tree eaten by larvae of the Winter Moth (after Gillanders 1908). Magn. × $\frac{3}{4}$.

U.S.A. which appeared to have been made while the plant was still living, as they were surrounded by callus tissue. Watson (1977) concluded that 'quite likely they were made by the proboscis or ovipositor of an insect, either to suck at the juicy tissue below or to lay eggs in it.'

In the Cretaceous, evidence becomes more abundant, particularly in the mid-Cretaceous with the evolution of Angiosperms. We have examined extensive leaf collections in North America and have identified numerous examples of marginal leaf eating (Stephenson 1991) and we illustrate some specimens here (figures 5, 8, 9, 10 and 11e). Significantly, we have yet to see any non-marginal feeding in the early Cretaceous. In discussing leaf feeding strategy, Edwards & Wratten (1980) observed that non-marginal leaf feeding was a more difficult activity for insects, requiring specialized mouth parts. It would seem consistent, therefore, to find the earliest leaves to show only marginal feeding, and non-marginal feeding to be more advanced, and hence a later or derived character. In addition Edwards & Wratten (1980) also observed that some taxa have specific modes of feeding, e.g. Orthoptera (which are known from the Upper Carboniferous) bite holes in the edges of leaves, and Coleoptera (known from the Permian) also feed on the edges. Curculionidae (a coleopteran group known from the Jurassic) are known to scoop out the edge of leaves at intervals, whereas Lepidoptera (possibly known from the Triassic and Jurassic but common from the Cretaceous) have a wide range of biting strategies including non-marginal biting (figure 10). Some of the pattern of leaf feeding is, however, caused by a defensive response by the plant, so that wound induced responses in the plant cause the insect to move so as to avoid local accumulation of chemical defences (Edwards & Wratten 1983, 1984).

In contrast, leaf feeding occurs widely in the Tertiary (Scott & Paterson 1984, J. Stephenson & A. C. Scott, unpublished data) and examples include continuous marginal feeding, interrupted marginal feeding and non-marginal feeding of various types. The overall impression, therefore, is (i) an increase in the amount of leaf feeding from the Devonian to Tertiary and (ii) an increase in complexity of feeding habit from a marginal, to interrupted marginal to non-marginal feeding strategies (figure 11).

Modern observations

Over the past ten years there have been several important contributions to our understanding of leaf eating by insects and other arthropod groups. Edwards & Wratten (1980, 1983) have examined the pattern of leaf feeding by insects on angiospermous leaves. They identify a number of specific types from marginal to non-marginal feeding. Non-marginal leaf feeding is apparently more difficult for insects, requiring specific anatomical modifications (Edwards & Wratten 1980).

These authors have also investigated the chemical response of the plants to leaf feeding. In some cases toxins are produced at the site of biting so that animals may adopt an interrupted biting strategy. In this context Cooper-Driver (1978) notes that the main fern-eating arthropods are all members of ancient orders. It has been suggested that these plant chemical defences only evolved in response to eating, and that those organisms already feeding were able, through time, to adapt to these chemical defences, whereas insect groups coming anew to leaf eating were not so adapted.

It is clear that there is a difficulty in fossil specimens in identifying damage to leaves caused by some biological agent as opposed to physical damage. Stephenson (1991) undertook a series of experiments with modern trees under controlled conditions to investigate this problem. He concluded that physical damage occurs as rips, tears or holes. Whereas rips and tears are easily identified as physical damage, holes are harder to distinguish from non-marginal herbivore feeding. However physical damage of this kind is rare, and the size and pattern of feeding holes makes it possible to distinguish them from those caused by wind, rain or hail damage.

Brown & Lawton (1991) have speculated that the shape of leaves may have been influenced by the activity of herbivorous insects. This interesting idea opens up new considerations in interpreting the fossil record of leaf shape.

Conclusions

Although the fossil evidence is at present sparse, some general conclusions can be reached. The common occurrence of leaf-feeding by arthropods does not occur until the late Carboniferous. Further, there is a major increase in biologically damaged leaves in the later Cretaceous and into the Tertiary especially. All Palaeozoic and early Mesozoic leaf-feeding appears to be marginal, firstly mainly continuous marginal feeding, followed by interrupted marginal feeding. Extensive non-marginal leaf feeding occurs firstly in the Cretaceous and in abundance only in the Tertiary. These observations lend support to the idea that marginal feeding arose earlier, and to this extent can be said to be more primitive than non-marginal feeding (figure 11). There is also an increase in data from fossil angiosperm leaves which may be real but may also be because it is easier to recognize bite marks on broad leaves than the narrower leaves of other groups. It must be significant that such increase in feeding on leaves by arthropods is on angiosperm leaves thus explaining their pre-Cretaceous rarity. Much more study is undoubtedly needed to confirm these initial conclusions.

Several authors (e.g. Strong *et al.* 1984; Shear & Kukalova-Peck 1990) have commented on the lack of evidence of herbivory (as opposed to detritovory) in the Palaeozoic. We further note that the pre-Cretaceous evidence for leaf-feeding (herbivory) is sparse. Martin (1991), however, discusses the problem of the digestion of living plant tissues and the need for a gut microflora to break down cellulose, and notes that few (if any) insects produce the enzyme cellulase. Perhaps we should not be asking why do we see so little evidence of pre-Cretaceous leaf-feeding, but why do we see any at all?

(*c*) *Trichomes*

The role of trichomes in plants has been widely discussed (e.g. Edwards & Wratten 1980), especially as an anti-predation strategy. Scott & Taylor (1983) noted and illustrated the common occurrence of trichomes on Upper Carboniferous plants, and considered both defensive and attraction roles for these features. Recently Cleal & Shute (1991) have illustrated the pteridosperm *Neuropteris heterophylla* Brongniart with trichomes, together apparently with an *in situ* exudate. These authors are uncertain of the role of these features. They considered a defensive role but, influenced by the comments of Beerbower *et al.* (1987) who briefly state that herbivory was not a significant feeding mode of Carboniferous arthropods, believed that these trichomes may have had a secretory (non-defensive) function. We do not link the observations of Beerbower *et al.* (1987) and Cleal & Shute (1991) in the same way. Although it is clear that we have relatively few examples of eaten leaves from the Upper Carboniferous it is noteworthy that the majority are of *Neuropteris*. We believe that in addition these trichomes could have had a defensive function and also note that other leaves such as *N. scheuchzeri* are also hairy. However, we have some specimens of this species showing feeding marks (Scott & Taylor 1983). The matter of trichome development in fossil plants and its interpretation as an arthropod defence mechanism clearly needs further study.

(*d*) *Borings*

Unless an insect has some form of wood-digesting gut symbiont, wood feeding (xylophagy) will only occur after the tissues have become bio-degraded to some degree (Martin 1991). The majority of recorded specimens showing borings in lignified tissue are not accompanied by any form of wound reaction, suggesting that the tissues were dead when invaded by the insects (see, for example, Hollick (1906); Walker (1938); Brues (1936); Chican & Taylor (1982); Scott & Taylor (1983)). Only rarely have some Carboniferous ferns been shown to have produced wound response tissue (de Witt West 1962; Lesnikowska 1990).

Most borings in wood or stem tissues contain coprolites (see Rothwell & Scott 1983; Cichan & Taylor 1982) (e.g. figure 20) but identification of holes not containing coprolites as arthropod borings may be problematic (e.g. figure 21) because of potential preservation causes, such as certain types of mineralization (e.g. growth of spherulitic calcite or silica) or even fungal degradation (see, for example, Creber & Ash (1990)).

In Tertiary wood, boring is quite common (see Brues 1936) and has been attributed to the activity of coleoptera and termites. In addition, some modern box mites also produce significant galleries with infilling of frass (Luxton 1972). Some millepedes are also known to bore into wood (Miller 1974). We know of no published record of wood boring before the Upper Carboniferous. We have, however, begun a search for the older bored wood and have found some fusain (fossil charcoal, being studied by Tim Jones in our laboratory) from the late Lower Carboniferous of East Kirkton, Scotland (Rolfe *et al.* 1990) with what appear to be small borings or galleries (figure 21). No evidence of frass (coprolites) have been found which would confirm this record. Small plant stems in which small areas are filled with coprolites are, however, common from the late Lower Carboniferous of the Midland Valley of Scotland (figure 26). The rarity or absence of late Devonian and Carboniferous bored wood, we believe, is probably due to a failure of palaeobotanists either to recognize or record such damage rather than its real absence, but it may be significant that the earliest beetle, one of the main wood boring groups, does not appear until the

Figure 12. Partial transverse section of fern (*Etapteris*) petiole showing possible puncture wound (arrow) and wound reaction tissue. Upper Carboniferous, Ohio. Ohio State University, CB73531 (1) Top. Magn. × 20.

Figures 13–15. Sections through permineralized tree-fern stems of *Psaronius magnificus* from the Upper Carboniferous of Ohio. University of Ohio.

Figure 13. Transverse section showing meristeles with ground tissue replaced by coprolites (e.g. at arrow). (P-008). Magn. × 2.

Figure 14. Transverse section showing well-preserved ground tissue, meristele at left. (P-006). Magn. × 7.

Figure 15. Transverse section showing ground tissue replaced by coprolites (e.g. at arrow) meristele at left. (P-008). Magn. × 7.

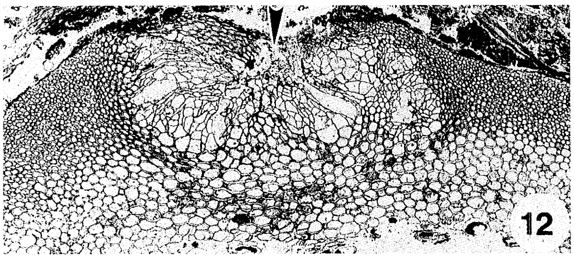
Figures 16 and 17. Sandstone cast of seed *Trigonocarpus*, with plug representing hole in original seed coat. Upper Carboniferous. National Museums of Scotland. Unregistered specimen. Magn. × $1\frac{1}{2}$ & × 2.

Figure 18. Bark-burrowing traces of a beetle on a gymnosperm log from the Lower Cretaceous of Southern England. Natural History Museum, London. v. 7535. Magn. × $\frac{1}{2}$.

Figure 19. Scanning Electron Micrograph of boring in *Setosisporites praetextus* megaspore from the Westphalian B, Upper Carboniferous, Thorpe, Yorkshire, Scott Colln., showing detail of boring (Magn. × 125) and whole megaspore inset (Magn. × 32).

Figure 20. Scanning Electron Micrograph of *Premnoxylon* wood containing frass from the Lower Middle Pennsylvanian, Upper Carboniferous, Ohio. Ohio State University. Magn. × 350.

Figure 21. Possible arthropod borings in gymnospermous wood preserved as fusain. A polished surface photographed in reflected light under oil. Late Lower Carboniferous, East Kirkton, Scotland. Scott Colln. Magn. × 100.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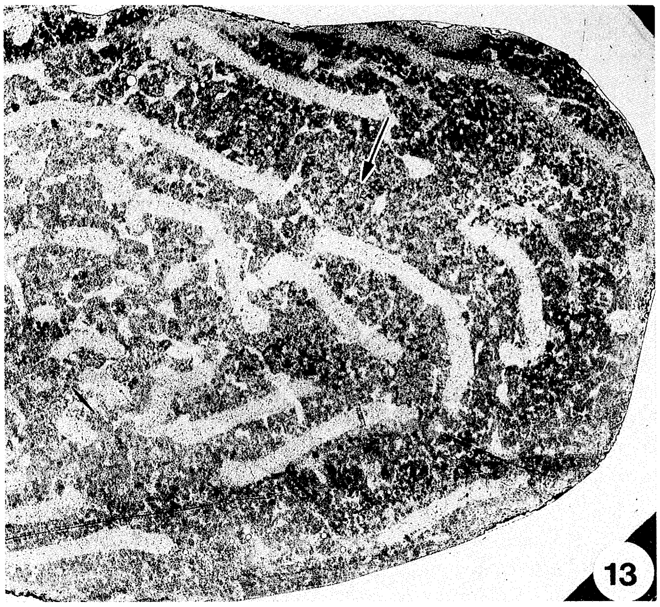
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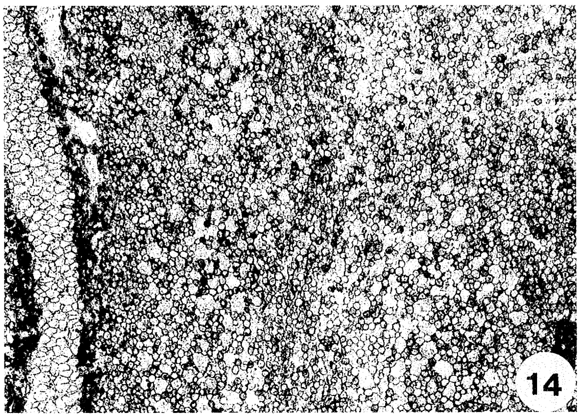
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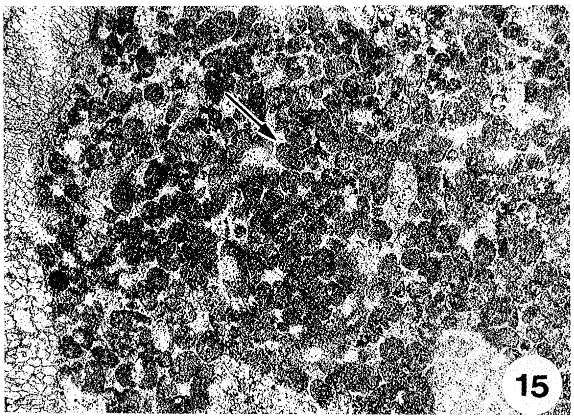
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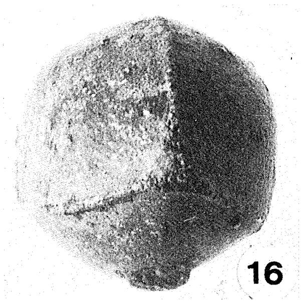
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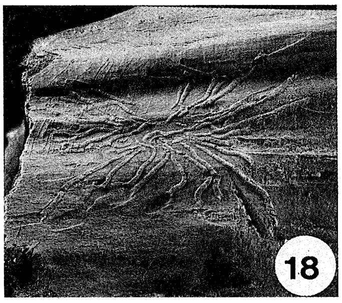
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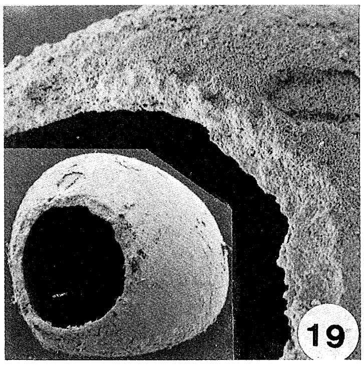
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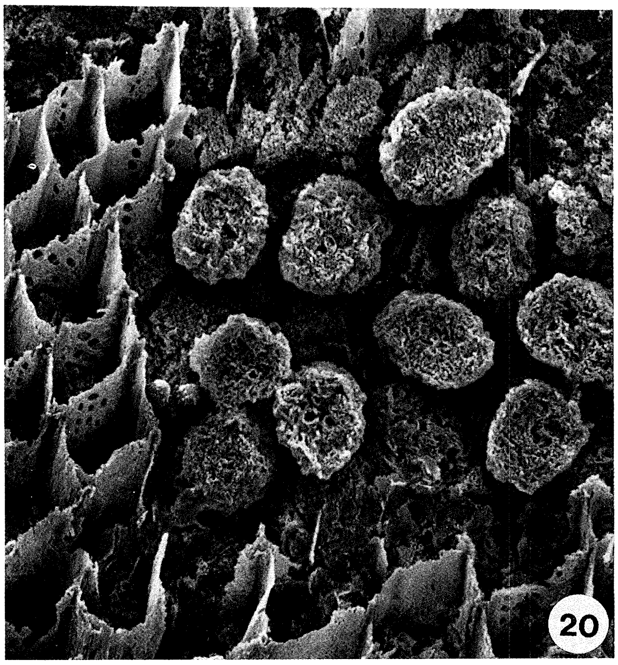
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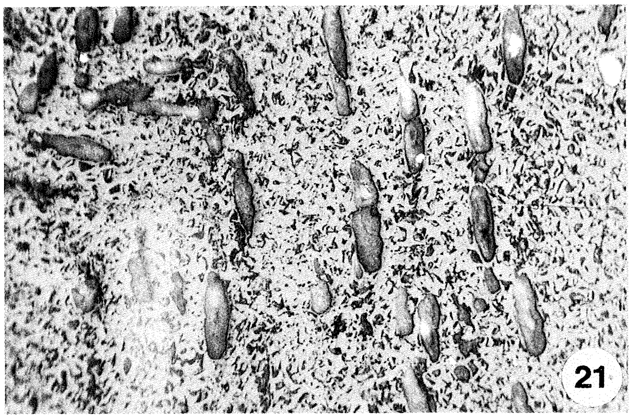
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Figures 12–21. For description see opposite.

Permian. Crowson (1975) has considered that a wood boring habit is likely for the earliest beetle. Pre-Permian wood boring could be by orabatid mites which are common wood borers today (Jacot 1939) and are known from the Middle Devonian (Norton *et al.* 1988).

In the Upper Carboniferous, however, there is extensive evidence of boring in wood or other lignified tissues, mainly from anatomically preserved tropical Euramerican coal ball plants. Galleries with coprolites have been described by numerous authors and include gymnospermous wood where the holes and coprolites (?) within them may be of the correct size to have been made by orabatid mites (Cichan & Taylor 1982; Scott & Taylor 1983) (figure 20). Several examples have been described from fern stems and petioles. Rothwell & Scott (1983) illustrate stems of the tree fern *Psaronius* where ground tissue has been replaced by coprolites (figures 13–15). In addition, Lesnikowska (1990) has illustrated *Psaronius* petioles which show not only cavities filled with coprolites but also wound tissue, indicating that the plant was still living when the feeding was taking place.

In addition to bored lignified tissue, seeds and megaspores with borings have also been reported (Scott & Taylor 1983) (figures 16, 17 and 19) but our material is very limited. Wooton (1976) considered that palaeodictyopteran nymphs, as well as adults, fed on vegetation above the ground. Sharov (1973) described several late Carboniferous cordaite seeds (*Samaropsis*) with puncture holes (about 30% of the collection bore traces of damage). The holes were restricted to one side of the seed and measured 0.5–1.1 mm in diameter. These Sharov (1973) observed, were the same diameter as the beaks of palaeodictyopterans which were found at the same locality. From the detailed structure of the holes Sharov (1973) also concluded that they were not made by gnawing through the seeds, but by piercing. The close interrelationships between the Palaeodictyoptera and the seed plant groups of the cordaites and pteridosperms was emphasized by Sharov (1973) who believed that their extinction in the Lower Permian coincided because these insects could not adapt to feeding on other gymnosperms, particularly because of the resins in the plants and their effects on insect beaks. This hypothesis must be regarded with some caution. Sharov (1973) believed that two other insect groups: Megasectoptera and Archodonata with short beaks sucked on leaves and young shoots and hence are found in the Upper Permian.

Scott & Taylor (1983) have described megaspores with holes (figure 19) but these appeared to have been chewed. Other megaspores with holes have also been illustrated by Djikstra and Pierart (1957, their figure 28) which appear to be similar to puncture holes. We know of no evidence for such boring in the Mesozoic. One of us (A.C.S.) has recently been shown possible Cretaceous fruits with borings similar to those of bruchid beetles from the Upper Cretaceous of Argentina (J. F. Genise, personal communication, September 1991).

The record of wood boring in Permian material is very poor, with no published illustration. Beetles first appear in the Permian (Wooton 1981). Larval stages of some beetles are able to digest cellulose (Wallwork 1970) and hence beetles are amongst the most successful of modern wood borers. It is surprising that we have no records from the Permian which is almost certainly due to a lack of reporting rather than a real absence. A single Triassic record is represented by one specimen described by Walker (1938) from the Triassic Petrified Forest National Monument in Arizona. He considered these galleries to have been formed by insects.

Jurassic examples are also scarce. Zhou & Zhang (1989) described galleries and coprolites in secondary wood of the conifer *Protocupressinoxylon* sp. from the Middle Jurassic of China. These authors also identify some possible wound reaction in this material and also believe that beetles were the most likely causal organisms. One of us (A.C.S.) has recently been shown bored Jurassic wood from Argentina which has yet to be described (J. F. Genise, personal communication, September 1991).

Similar material has also been recorded from the Cretaceous (Hollick 1906; Seward 1923, 1924; Scott & Paterson 1984). Again, these are predominantly of galleries with small (less than 100 μm) faecal pellets. In the case of the material illustrated by Scott & Paterson (1984) it is interesting to note that it was from a tree fern, *Tempskya*, rather than gymnosperm wood.

Wood boring is the habit of several groups of beetles, notably the Buprestidae, Lyctidae, Anobiidae, Bostrychidae, Scolytidae, Ipidae and Cerambycolidae. Various beetle trails have been noted on the surface of Mesozoic wood specimens (Brongniart 1876; Lovendal 1898, Walker 1938; Blair 1943; Jarzembowski 1990; Chaloner *et al.* 1991*b*). Most of these borings have been attributed to the work of extinct members of the Coleopteran family Scolytidae which is interesting since fossil insect specimens of this group do not occur earlier than the Tertiary (Zherikhin 1980). The borings are very characteristic (figure 18) and it is surprising that more material has not been described. The most important example described in detail comes from the Lower Cretaceous Wealden deposits from Southern England but the detailed description and interpretation of the borings has been disputed (Blair 1943; Jarzembowski 1990; Chaloner *et al.* 1991*b*) with the pupal chambers only being recognized following the work of Stephenson (1991). Stephenson concludes that the chambers may not have been produced by a scolytid beetle but by a weevil similar to *Pissodes*. A new extensive collection of borings in Upper Cretaceous permineralized woods from Argentina is currently being studied by J. F. Genise and will give much important new data on the timing of some interactions.

It is clear that although we have a few examples of bored wood from the Palaeozoic and Mesozoic much more data are required to elucidate the early phases in the evolution of this mode of life.

(*e*) *Leaf-mines*

A highly specialized form of plant feeding with the additional bonus of shelter (in terms of protection from an unfavourable environment and from predators) is to tunnel into leaves, producing 'leaf-mines'. Leaf-mines are produced by insects which hatch from eggs within the leaf tissue and in the course of their development pass through larval, pupal and adult stages. Insect leaf mines are linear tunnels or blotch-like excavations produced by certain specialized larvae feeding within the mesophyll or epidermis of a leaf. The mesophyll feeders eat the palisade layer or the spongy mesophyll or both, leaving the epidermis and cuticle complete. The epidermal feeders leave the cuticle and outer walls of the epidermal layers intact. The mines are, therefore, completely enclosed by the plant tissue and are protected from the external environment (Hering 1951).

Most modern leaf-mines are found in angiospermous leaves. Some, however, have been recognized in other plant groups (Hering 1951). The leaf-mining habit is only known to have evolved in four extant orders of insects: the Coleoptera, Diptera, Hymenoptera and Lepidoptera, where the leaf-mining larvae belong to the more primitive groups of these orders (Hering 1951).

The adults corresponding to leaf-mining larvae are generally small with one of their main activities being to find a suitable plant host in which to lay their eggs and provide food for the next generation (Crane & Jarzembowski 1980). In most cases the eggs are either deposited upon the surface of the leaf or inserted into it. The larva excavates the tunnel or mine by means of either chewing mouthparts capable of devouring whole cells or by the use of a cell-shearing apparatus which usually accompanies the sap-feeding habit. The insect passes through a series of larval stages (instars) each of which may signify a change in the feeding habit which is often recognizable in irregularities in the appearance of the completed mine (Needham *et al.* 1928).

Once the pupal stage is reached there is a quiescent phase. The pupa may remain within the mine (often in a blotch-like excavation termed the 'pupation chamber') or may produce an external shelter or cocoon. During the pupal phase the insect undergoes metamorphosis which leads to a fully winged adult.

Unfortunately most insect larvae are soft-bodied and are not readily fossilized. The evolution of mining larvae from surface feeding larvae is, therefore, difficult to document in the fossil record, even when fragments of the discarded chitinous skin at the end of each instar are preserved within the fossil mine (as in Rozefelds 1988). Although the Coleoptera have been recorded from the Permian, the earliest families containing leaf-mining members, such as the Nitidulidae, Cerambycidae and Curculionidae, are known from the Jurassic while the other families of that Order have a Tertiary origin. Whereas the Diptera are known from the Triassic all the extant leaf mining families are known only from the Tertiary. The same may be said for the Hymenoptera. The Mesozoic Lepidoptera are known most commonly from the Cretaceous but a few records exist for the Jurassic and possibly for the Triassic (Whalley 1986) and apart from the Incurvariidae all the leaf-mining families have a record from the Tertiary or have no fossil record (35 families). The number of pre-Tertiary insect groups containing leaf-miners would appear, therefore to be very limited, perhaps explaining the paucity of the pre-Tertiary and certainly pre-Cretaceous fossil record of leaf-mines.

Muller (1982) records the earliest leaf-mines in material from the Upper Carboniferous (Westphalian D). They consist of both blotch-like and linear-like mines of the ichnogenus *Cuniculonomus* Strauss on the pteridosperms *Neuropteris britannica* Gutbier and *Neuropteris subauriculata* Sterzel but we are uncertain of their validity. Muller (1982) also records the presence of similar mines in the later Carboniferous (Stephanian C) and Lower Permian specimens attributed to *Odontopteris* and notes their close similarities to Recent lepidopteran mines. The earliest evidence of lepidopteran adult insects does not occur until the Triassic (Whalley 1986) and any reference of these pre-Cretaceous mines to lepidopteran forms seems doubtful. H. Potonié (1893; R. Potonié 1921) described the presence of linear mines in the leaflets of Lower Permian *Callipteris conferta* Sternberg. Muller (1982) has named these *Asteronomus (?) maendriformis*. Kerp (1988) has subsequently restudied the plant material, and reassigned it to *Autunia conferta* (Sternberg) Kerp, possibly belonging to the extinct gymnosperm order Peltaspermales (Kerp & Haubold 1988).

Few Mesozoic leaf-mines have been documented. Rozefelds (1985) and Rozefelds and Sobbe (1987) discuss the presence of linear mines in the leaves of the conifer *Heidiphyllum elongatum* (Morris) Retallack from the late Triassic Ipswich coal measures of southeastern Queensland, Australia. In naming them *Triassohyponomus dinmorensis*, Rozefelds & Sobbe (1987) note their very close similarity to a 'mine or burrow of coleopterous larva in the stem of a plant' figured by Tillyard (1922). Kelber & Geyer (1989) also record a doubtful leaf mine from the Triassic of Germany on *Schizoneura paradoxa*.

Leaf mines, which may belong to the Neptieulidae (Lepidoptera) have been reported from seed-fern foliage in the late Jurassic (Grogan & Szadziewski 1988). A later Upper Jurassic–Lower Cretaceous specimen is also figured by Rozefelds (1988) collected from Clack Island, north Queensland, Australia. He suggested that they were repticulid mines found on a single frond of *Pachypteris crassa* (Halle) Townrow (Corystospermales).

Cretaceous examples of leaf-mines are also poorly documented. Fritsch (1882) assigns one specimen from the Cenomanian of Bohemia to *Tinea araliae* Fritsch: Knowlton (1917) figures a 'microlepidopteran' mine from the Frontier formation of southwestern Wyoming. Hagen (1882) and Skalski (1979) only mention the presence of Cretaceous leaf-mines but do not figure or describe them. As is probably the general case the rarity of Cretaceous leaf-mines may represent under-reporting, or lack of search for such evidence. In a study of Cretaceous (mainly Cenomanian) leaves of North America, Stephenson (1991) has found a wide variety of forms. He has observed more than 50 specimens which he can categorize into 18 types. These include small sinuous mines, serpentine mines, linear and blotch

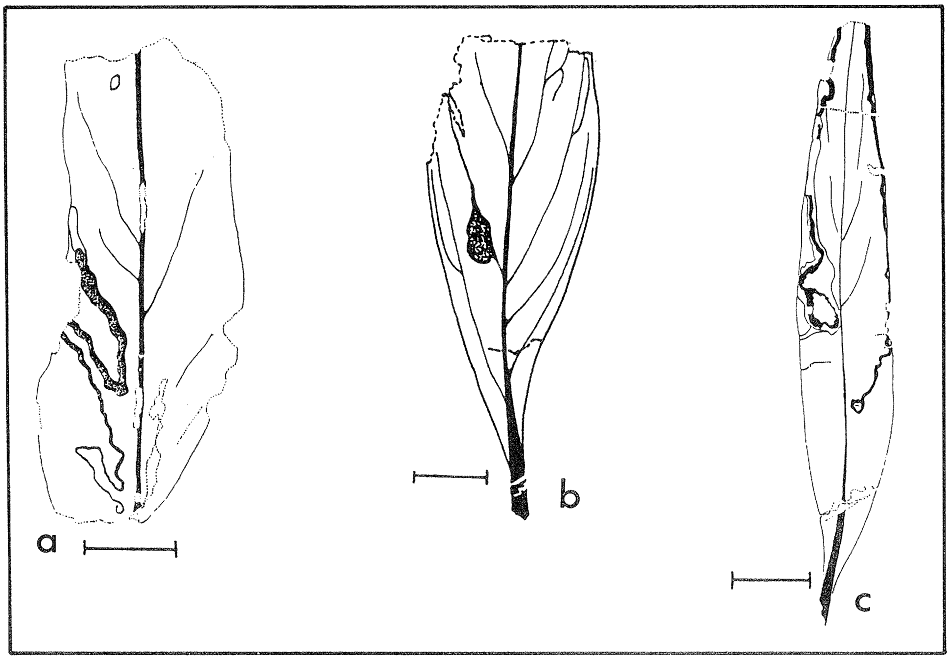

Figure 22. Examples of Cretaceous Leaf Mines (scale 1 cm). a. Sinuous mine in angiospermous leaf. Dakota Formation, Cenomanian, Cretaceous, U.S.A. Indiana University. IU 15703-3856. b. Trumpet-type leaf mine in angiospermous leaf. The mine originates near the margin than proceeds along a secondary vein until it forms a relatively large blotch-like pupation chamber which is full of frass. Central exit pore is visible. Dakota Formation, Cenomanian, Cretaceous, U.S.A. Indiana University. IU 15703-2529. c. Marginal leaf mines in angiospermous leaf. Dakota Formation, Cenomanian, Cretaceous, U.S.A. Indiana University. IU 15709-4818.

mines. We illustrate here a few examples of different mine types (figure 22). All occur in angiosperm leaves but significantly Stephenson (1991) believes that he can recognize forms produced by Lepidoptera (the most abundant forms), Diptera and Coleoptera. Interestingly there does not appear, within these specimens, to be any major host-type specificity shown by the leaf-mining insects. Those members of the lepidopteran family Nepticulidae are particularly well represented. This is surprising considering the relatively short geological history of the Lepidoptera at this time, according to their insect fossil record. The presence of such a variety of lepidopteran mines may be an indication of how rapid the insect radiation was after the advent of angiosperms, or that the Lepidoptera were in existence for a much longer period than is portrayed by the insect fossil record.

An inevitable conclusion of this review is that further investigations, particularly on pre-Cenomanian angiosperm and non-angiosperm leaf material is needed to yield useful data on the evolution of this specialized type of plant–insect interaction.

(*f*) ***Evidence from Arthropods: coprolites***

One piece of tangible evidence for plant-eating by arthropods is that of coprolites, fossil faecal pellets. The study of coprolites, both their shape and size as well as their content, has yielded significant data for the interpretation of plant–animal interactions (see Scott

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Figures 23–30. Coprolites in Carboniferous permineralized peats.

Figures 23 and 24. Coprolites containing spores, originally described as a pteridosperm pollen organ *Heterotheca*, from the Lower Carboniferous Pettycur Limestone, Pettycur, Fife. Natural History Museum, London. Benson Colln, Slide 307–18. Figure 23. Magn. × 64. Figure 24. Detail. Magn. × 160.

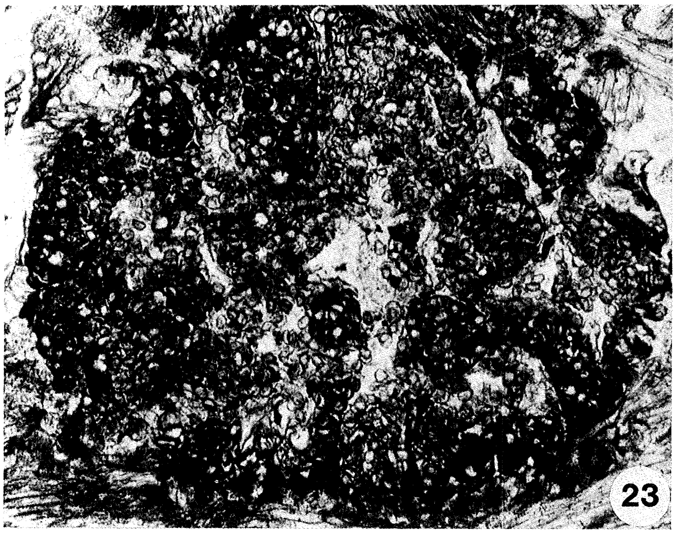
Figure 25. Small coprolites (arrow) within permineralized peat. Pettycur Limestone, Pettycur, Fife, Scotland. Scott Colln. Magn. × 20.

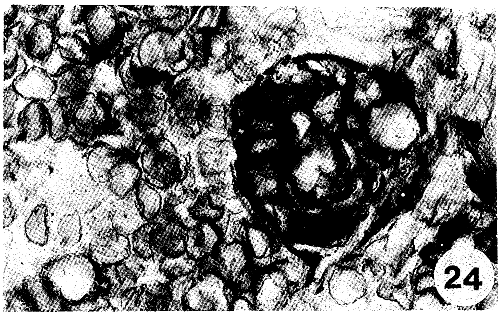
Figure 26. Small coprolites (arrow) (possibly mite) within axis of lycopod (*Paralycopodites*) in permineralized peat, Pettycur Limestone, Pettycur, Fife, Scotland. Gordon Collection 176. Natural History Museum, London. Magn. × 15.

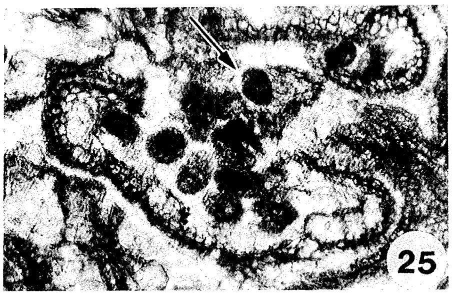
Figure 27. Coprolites of different sizes (arrows) in matrix of coal ball (permineralized peat) from the Pennsylvanian, Upper Carboniferous of Kentucky. Ohio State University. CB6664. Magn. × 16.

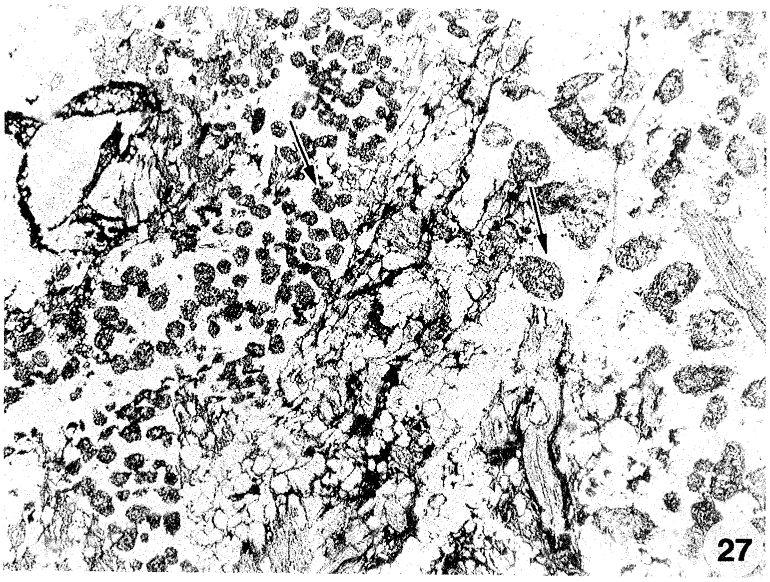
Figures 28–30. Scanning Electron Micrographs of the contents of large coprolites in coal balls from the Pennysylvanian, Upper Carboniferous of Kentucky. Ohio State University. CB 7245.

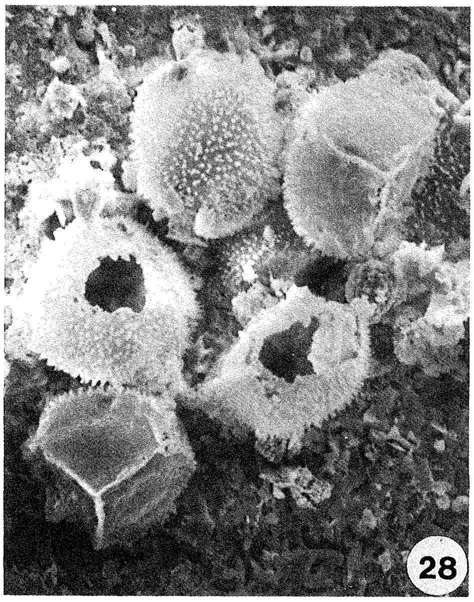
Figure 28. *Lycospora* spores. Magn. × 700. Figure 29. Fern sporangium. Magn. × 150. Figure 30. Tracheids. Magn. × 1000.











Figures 23–30. For description see opposite.

(1977)), Baxendale (1979) and Scott & Taylor (1983 for a more detailed discussion of this topic). Shape and size records may give clues concerning the arthropod or insect group responsible, and the contents of the coprolites will give a lead on what has been eaten. In contrast, other groups such as spiders and snails do not appear to produce coherent faecal material. A survey of modern material is currently under way.

Some types of coprolite are very characteristic, such as those of dung beetles (Retallack 1990) and it is clear that studies of fossil soils yielding coprolites may be significant especially concerning the evolution of detritivores (Retallack 1981; Piearce 1989).

The fossil record of terrestrial coprolites is patchy. Small (less than 100 μm) coprolites containing plant material have been described by Robbins *et al.* (1985) from the Precambrian. The animal responsible for these is uncertain and may not be terrestrial but it emphasizes the point that detailed studies are needed of late Precambrian and early Palaeozoic sediments to search for coprolites as they may be preserved where the animals or macroplants are not.

Retallack & Feakes (1987) in studying putative Ordovician soils indicate that they can identify the activity of terrestrial arthropods but this evidence is equivocal. Sherwood-Pike & Gray (1985) describe fungal aggregates which they attribute to micro-arthropod frass or coprolites. The material is of Ludlovian age (Silurian) from Gotland, Sweden and is significant in that it pre-dates the oldest known terrestrial arthropod faunas. Sherwood-Pike & Gray (1985) use the occurrence of fungi in coprolites to infer fungivory of the arthropods (see also Sherwood-Pike (1990)) but an alternative view is that the original plant tissues in the coprolite were later destroyed by fungal activity. Until recently, our oldest diverse terrestrial micro-arthropod assemblage was from the early Devonian Rhynie chert (Kevan *et al.* 1975) which has led to the hypothesis that early micro-arthropod assemblages may have first appeared in the early Devonian or possibly in the latest Silurian (Rolfe 1980). However, the discovery by Sherwood-Pike & Gray (1985) argues that the terrestrial decomposer niche was already occupied by mid-Silurian times (Rolfe 1985*a*). The discovery of predatory arthropods, including centipedes and arachnids, in sediments of late Silurian (Pridoli) age from Ludlow, Shropshire, England supports the idea of an extensive Silurian evolution and diversification of terrestrial invertebrates (Jeram *et al.* 1990; Rolfe 1990).

Despite our increasing evidence of evolving complex plant–arthropod interactions through the Silurian and Devonian we have as yet no coprolites described from these systems. A few coprolites have been described from the Lower Carboniferous (Visean) of Scotland and France. Scott (1977) illustrated one of a number of large coprolites preserved as compression fossils from the Visean of Scotland, which range in length from 20–26 mm and when found unsquashed are approximately cylinder shaped with prominent ridges (figure 32). The origin of such a coprolite is uncertain but may have been from a large millepede or even an early arthropleurid (see Rolfe 1985*b*). Another form from the Visean of Scotland described by Scott (1977) were also circular in cross section with a diameter of 5 mm and preserved in association with permineralized plants (figures 33 and 34). The plant material is layered internally and comprises stelar and woody elements. These larger coprolites bear a resemblance to forms described by several authors from the later Carboniferous and may be of millepede origin (Scott & Taylor 1983). Scott *et al.* (1985) illustrate a coprolite containing spores of *Dictyotriletes* (fern) and *Knoxisporites* (affi-

Figures 31–46. Isolated Carboniferous and Recent coprolites.

Figure 31. Scanning Electron Micrograph of coprolite containing spores of *Dictyotriletes* (fern) and *Knoxisporites* (affinity uncertain) from the Lower Carboniferous of Loch Humphry Burn, Dumbartonshire, Scotland. Magn. × 180.

Figure 32. Compression of coprolite from the Lower Carboniferous of Loch Humphrey Burn, Dunbartonshire, Scotland. Hunterian Museum Glasgow. Pb2576. Magn. × 2.

Figures 33 and 34. Cross-section of coprolite from the Lower Carboniferous of Glenarbuck, Dunbartonshire, Scotland. Figure 33. Whole coprolite. Magn. × 4. Figure 34. Detail showing plant debris and stelar fragments. Magn. × 30. Hunterian Museum Glasgow. FSC 780.

Figures 35–37. Transverse sections of coprolites in Limestone from the Lower Carboniferous Kingswood Limestone, Fife, Scotland. KIN 289. Figure 35. General transverse section. Magn. × 35. Figure 36. Detail of another coprolite. Magn. × 40. Figure 37. Longitudinal section. Magn. × 27.

Figures 38–43. Scanning Electron Micrographs of coprolites containing megaspores and miospores from floodplain shales, Westphalian B, Middle Coal Measures, Upper Carboniferous, Swillington, Yorkshire. All in the Hunterian Museum Glasgow (FSC).

Figure 38. Coprolite containing megaspore fragments. FSC 2061. Magn. × 40.

Figure 39. Detail of figure 38 with fragment of *Tuberculatisporites* megaspore. Magn. × 150.

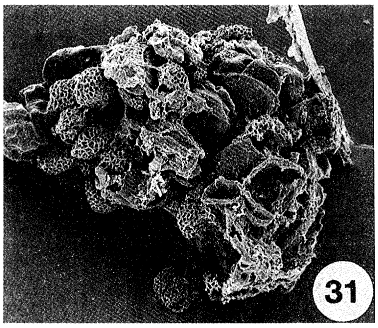
Figure 40. Coprolite containing miospores. FSC 2066. Magn. × 25.

Figure 41. Detail of coprolite with spores including ?*Ahrensisporites*, FSC 2068. Magn. × 500.

Figure 42. Detail of FSC 2067 with microspores and megaspore fragments. Magn. × 250.

Figure 43. Detail of FSC 2063 with microspores including ?*Cristatisporites*. Magn. × 600.

Figures 44–46. Scanning Electron Micrographs of faecal pellets from the Recent millepede *Narceus americanus*. Figure 44. Longitudinal view. Magn. × 15. Figure 45. End view. Magn. × 35. Figure 46. Detail showing tracheids. Magn. × 150.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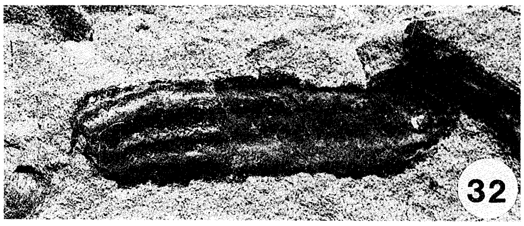
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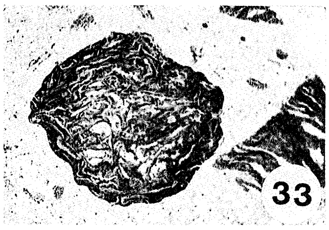
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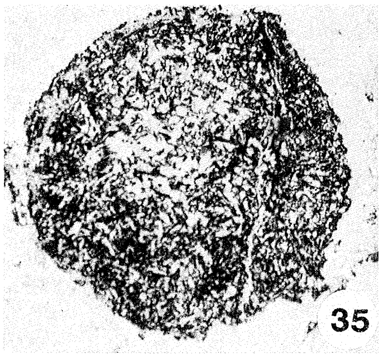
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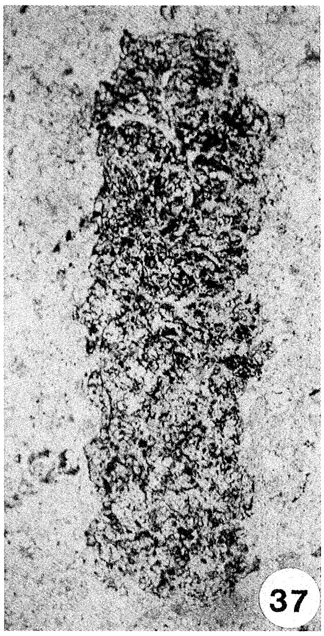
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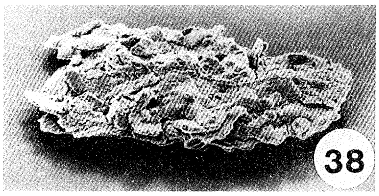
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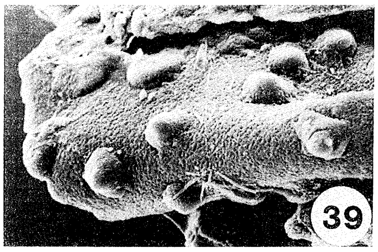
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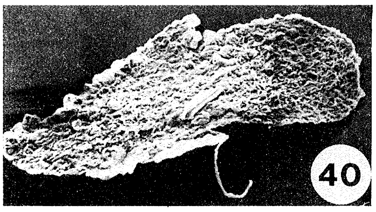
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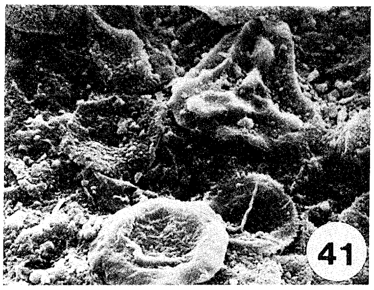
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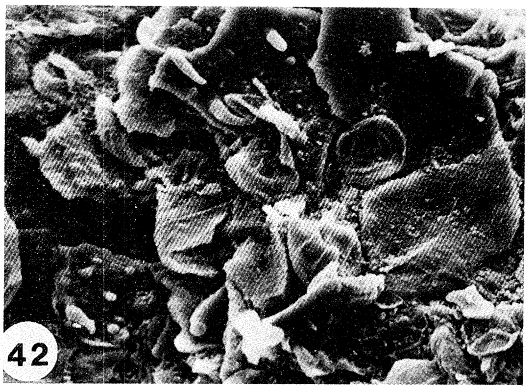
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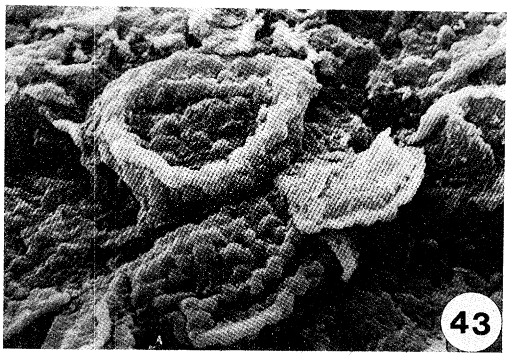
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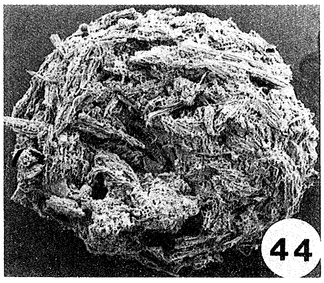
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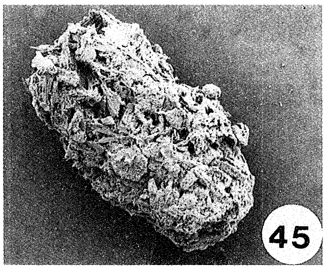
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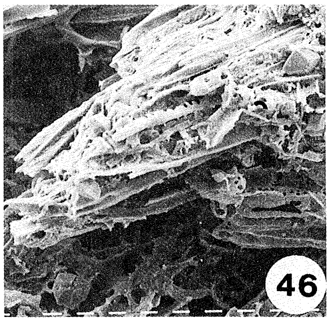
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Figures 31–46. For description see opposite.

nity uncertain) from the late Tournaisian of Scotland (figure 31). The arthropod responsible is unknown.

Rex & Galtier (1986) describe several plant-bearing coprolites from Visean silicified cherts from Central France. These authors identify four types of coprolites which they interpret as indicating that there was a diverse arthropod assemblage associated with the flora. One type was around 1 mm long and 0.5 mm in diameter which incorporated material from *Botryopteris antiqua* (fern) sporangia and was a common element in the assemblage from Esnost. Type 2 was nearly as large, 0.4–1 mm long and 0.2–0.5 mm in diameter which incorporated spores of *Lepidodendron esnostense*. Type 3 coprolites were spherical or ovoid 70–100 μm in diameter and were distributed both in the chert matrix at Roanne, and within plant tissues. Type 4 coprolites were found uniquely at Esnost, associated with the fern *Botryopteris antiqua*. The cortex of the rachis *Botryopteris* showed cavities which may have been caused by arthropod attack and the chert surrounding contained minute coprolites 30 μm long and 10 μm in diameter. The coprolites described from these French deposits are very similar to ones described by Scott & Taylor (1983) from Upper Carboniferous coal balls and hence discussion of their origin will be taken together.

Coprolites from the Lower Carboniferous are more widespread than previously thought. Examination of several thousand peels in our collections from the Tournaisian and Visean deposits of Scotland has indicated that certain forms are particularly abundant. In late Tournaisian sediments cylindrical coprolites, up to 0.5 mm in diameter occur frequently. Late Visean assemblages are, however, more common. Large cylindrical coprolites are relatively abundant in the limestones of Kingswood associated with abundant and diverse plant remains (Scott *et al.* 1986) (figures 35–37). The coprolites are up to 7 mm in diameter but the only preserved associated arthropods are scorpions. A more diverse assemblage of forms are found in the nearby Pettycur limestone. These included pollen-bearing coprolites which were once described as pollen organs (*Heterotheca*) (figures 23 and 24) but a recent reinvestigation has demonstrated their true nature (Rothwell & Scott 1988). These specimens are irregularly subspheroidal–ellipsoidal, ovoid in cross section, 1 mm in diameter and 3.5–4.0 mm long. Rothwell & Scott (1988) consider that their relatively constant size and heterogenous content suggests that they represent the faeces of a single type of animal with a relatively nonspecific diet. Some specimens described, however, comprised almost exclusively spore exines. Interestingly, Meyen (1984) also considered that the putative Permian pollen organ *Thuringia* is also an arthropod coprolite. Other large cylindrical coprolites are also encountered free within the 'peat' facies of the Pettycur limestone (Rex & Scott 1987). In addition small, ovoid, 30 μm coprolites occur rarely within the peat (figures 25 and 26). No damage to the fern rachises *Botryopteris antiqua*, similar to that described from France by Rex & Galtier (1986), has yet been found.

More extensive studies have been undertaken on Upper Carboniferous coprolite assemblages. Scott (1977) described plant-bearing coprolites from clastic sediments from the Westphalian B of Yorkshire. These were generally cylindrical in shape (up to 3 mm × 1 mm), although some had been flattened. Some contained indeterminate plant debris whereas others contained a variety of spores, including megaspore fragments (figures 38–43).

Studying the contents of the coprolites may yield clues to the diet of the animal. Bernays (1991) has shown how particles remain surprisingly intact and identifiable in the gut and faeces of some insects.

In a study of coprolites from North American Upper Carboniferous coal balls, Baxendale (1979) described several types, as seen in section. In his paper, Baxendale described three types of coprolite based on gross morphology and content. His type A were large 4.5 mm × 2.5 mm × 1.9 mm in size with a heterogeneous composition. Type B were 6.5 mm × 3.5 mm × 3.1 mm and type C had an average size of 4.5 mm × 2.5 mm × 1.8 mm with an amorphous content. In a detailed study of coprolites from Lewis Creek Coal balls of Kentucky of early Westphalian age, Scott & Taylor (1983) described a much greater diversity of coprolites which they studied combining light microscopy with SEM observations. They demonstrated a broad size range of forms and noted their occurrence, shape and content. They described three size classes broadly ranging from 1–7 mm in diameter (class 1) to 120 μm–1 mm (class 2) to 30–120 μm (class 3) (figure 27). Some of these forms, particularly class 1 and 2 forms contained abundant spores, and in some cases sporangia of ferns and lycopods (figures 28 and 29) but also one coprolite was identified that consisted of broken fragments of a synangium of the pollen organ *Feraxotheca*. These authors considered that the coprolites were derived from a number of sources. In a consideration of modern arthropod and insect faecal pellets it was considered that the smallest of the Carboniferous forms may have belonged to mites and Collembola. For example faecal pellets of the mite *Tyrophagus* sp are 45 μm × 20 μm (Robaux *et al.* 1977) and Scott & Taylor (1983), illustrate ovoid faecal pellets 150 μm in length from oribatid box mites. Collembolan faecal pellets also range in size from 10–100 μm (Kuhnelt 1976). The larger coprolites may include forms typical of millepedes such as those illustrated by Paulusse & Jeanson (1977) and Scott & Taylor (1983) which are 0.8–1.5 mm long and approximately 0.5 mm in diameter (figures 44–46). Scott (1977) also describes coprolites 6 mm long and 3 mm in diameter from an African millipede 9 cm long. Feacal pellets of insects may also be similar as pointed out by Scott & Taylor (1983). For example Scott (1977) describes faecal pellets from a Recent cockroach, 6–7 cm long which were 3 mm × 1 mm with longitudinal striations. Our major problem is that we do not know what the faecal pellets of extinct insect groups were like but it is clear that by the Upper Carboniferous there was a considerable diversity of coprolites of apparently terrestrial organisms.

Permian and Mesozoic forms are poorly known, almost certainly because of lack of study rather than because of a real absence. Harris (1957) described coprolites containing fragments of *Caytonia* and it may be that arthropods were even involved in the pollination of this unusual gymnosperm thought by some to have been close to the ancestral stock of the angiosperms. The only other coprolites described occur associated with borings as indicated above. Borings in wood filled with frass (coprolites) have been illustrated from the Jurassic (Zhou & Zhang 1989) and Cretaceous (e.g. Scott & Paterson 1984) but there have been no full descriptions. No general picture can emerge until more material becomes available for study.

(*g*) *Evidence from arthropods: gut contents*

One area of direct evidence for arthropod phytophagy is that of gut contents. Unfortunately few fossil arthropod specimens have been studied in this respect but more serious is the fact that of those that have, few fossil specimens yield gut-contents. Most of the material of which we have knowledge is from the Carboniferous.

Arthropleura was a giant 'millepede-like' arthropod 1.8 m long and represents an extinct group within the Myriapoda (Rolfe 1985*b*). Gut contents of this form have yielded lycopod tracheids (Rolfe & Ingham 1967). The general composition of the plant material suggested to Scott (in Rolfe 1985*b*) that the central woody stele of trunks and branches were being eaten rather than the leaves. This led Rolfe (1985*b*) to suggest that the animal not only used hollowed out trunks for shelter but also as a food source.

Gut contents of Upper Carboniferous insects have been described by Scott & Taylor (1983). Three specimens from the Westphalian D Mazon creek assemblages yielded spores in their gut. One specimen yielding spores is a new undescribed genus of a thysoneuron and another is a protoorthopteran. Lycopod spores, *Cappasporites distortus* were found in the gut of an undeterminate protoorthopteran. Shear & Kukalova-Peck (1990) illustrate a specimen of a young nymph of a diaphanopteran from the Upper Carboniferous of Illinois with its gut packed with spores, but these were not identified. These represent the only terrestrial arthropod specimens with gut contents so far described from the Carboniferous.

Few other insects with gut contents have been reported but Krassilov & Rasinitsyn (1982) describe Cretaceous insects with pollen in their guts. However, in this case the pollen is bisaccate: an occurrence of pollen of this type in both living and fossil plants is limited to gymnosperms showing strong adaptation to anemophily (wind pollination). For this reason it seems unlikely that the Russian pollen-eating insects were involved in a biotic pollination process.

It is particularly surprising that none of the cockroaches that make up the bulk of Upper Carboniferous insect collections have yielded gut contents, but many records are from wings rather than whole bodies. It has been suggested that several early insect groups fed on plants (Wigglesworth 1976) including orthopterans and even palaeodictyopteran nymphs (Wootton 1976, 1981) but direct evidence is lacking.

It is clear from a survey of modern insect groups that feed on plants, that many have an extensive fossil record. This is especially true of, for example the Orthoptera (grasshoppers and crickets) (Brues 1946; Uvarov 1966) but we have to rely on indirect evidence of feeding habits rather than direct evidence of gut content for much of the fossil record.

3. SHELTER

Observations on plant–arthropod interactions in modern ecosystems indicate that shelter is an important link (Southwood 1973). Often the animal may shelter from predators rather than just the physical environment but it is also possible that some arthropods use shelter to hide from prey as well. For the most part, direct observations of this interaction in the fossil record is problematical but some specific interactions are complex and involve more than one activity which is then identifiable in fossil material. Leaf-mining, for example, has already been discussed under feeding but equally it may be considered as a protective adaptation, the insect larvae sheltering within the leaf, between the epidermal layers.

In the Lower Devonian Rhynie Chert sporangia have been found which contained specimens of trigonotarbid arachnids (Kevan *et al.* 1975; Rolfe 1985*a*). Kevan *et al.* (1975) suggested that the animals may have been feeding on the spores, a theme expanded by Scott *et al.* (1985). Rolfe (1980, 1985*a*) suggests, however, that the arthropods may have been using the empty sporangia for shelter to conserve body moisture in particular. It is clear, as Rolfe (1985*a*) points out, that the interpretations of these observations are equivocal.

We have already mentioned that *Arthropleura* from the Upper Carboniferous probably fed on lycopod trunks and may have used the hollowed out trunks as a shelter (Rolfe 1985*b*), especially from tetrapod predators. It has even been suggested (Milner in Rolfe 1985*b*) that the amphibian *Eogyrinus* was suitably elongated to seek out *Arthropleura* in this niche.

Some Trichoptera (caddisfly) larvae make cases out of plant material. Although such cases are known from the later Jurassic they become more common and diverse from the early Cretaceous. We have not made any new observations and their geological history has been recently reviewed by Sukatsheva (1982) and Boucot (1990). A step removed from shelter is that of the use of camouflage. A good example of this is mimicry. Several authors have suggested mimicry of arthropods, including insects mimicking plants in the Carboniferous (see Scott & Taylor (1983) for a review)), but few other comparisons have been made elsewhere in the Palaeozoic or Tertiary.

(*a*) *Galls*

According to Meyer (1987) galls are 'all manifestations of growth, whether positive or negative, and of abnormal differentiation induced on a plant by animal or plant parasite'. Galls are a physiological reaction induced in the host plant tissues immediately surrounding the invasive parasite. They can be morphologically classified into two main groups according to Kuster (1911). Organoid galls are characterized by abnormal production of organs, by their modifications of the arrangement of organs or even by their transformation. These are more commonly caused by viruses. Histioid galls are characterized by production of abnormal tissue, either by cellular hypertrophy, by cell proliferation or by the appearance of new differentiations. Within this category cataplasmic galls are amorphous with no tissue differentiation and prosoplasmic galls have a definite size and shape with a marked tissue differentiation.

The gall which is induced by the invading parasite develops not only a protective layer but also develops a water and food connective system to the host plant (Fourcroy & Braun 1967; Maresquelle & Meyer 1965). Variations in gall formation caused by different parasites are numerous but basically the female arthropod lays her eggs within the host plant tissue, often with a high degree of specificity for both plant and site of oviposition. The larva grows feeding from the surrounding plant tissues either directly or from a modified nutritive layer. Pupation may occur either internally or externally, after which the mature adult assails other plant hosts.

Although there is a wide diversity of arthropod groups which produce galls, none of their extant families are known in the Palaeozoic. Of the insects, only some Hemiptera (Homoptera) including the Cercopidae and Membracidae have been found from the Triassic. The Psyllidae are known from the Jurassic, as are the Hemiptera (Heteroptera), Tingidae and the coleopteran families Cerambycidae and Curculionidae. The Hemipteran (Homopteran) Family Aphididae and the Hymenopteran family Cynipidae are known from the Cretaceous but all other families including the lepidopteran and dipteran gall producing families are known only from the Tertiary.

Very little has been published on fossil galls. Whilst in some cases the evidence for a gall is clear (such as the presence of the organic material of a gall, figures 47g and 49), in others where only the potential gall sites are apparent (figure 50) there is the possibility that they represent fungal infection. In these cases, however, the presence of fungal hyphae should help resolve the matter. The earliest and only recorded examples from the Palaeozoic appear on *Odontopteris* leaves from the

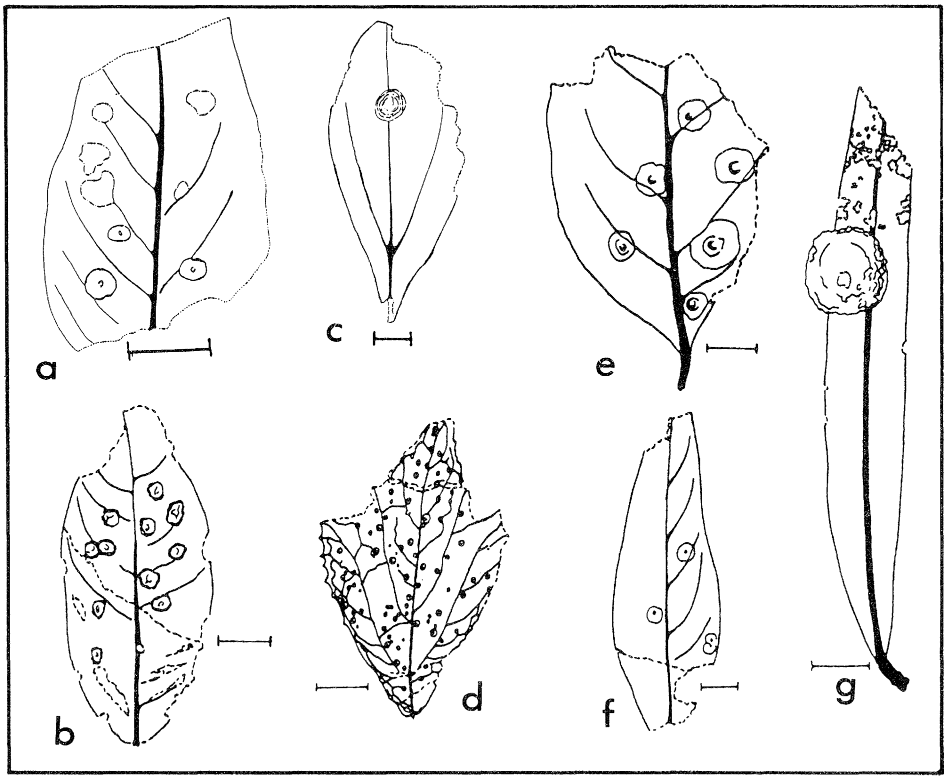
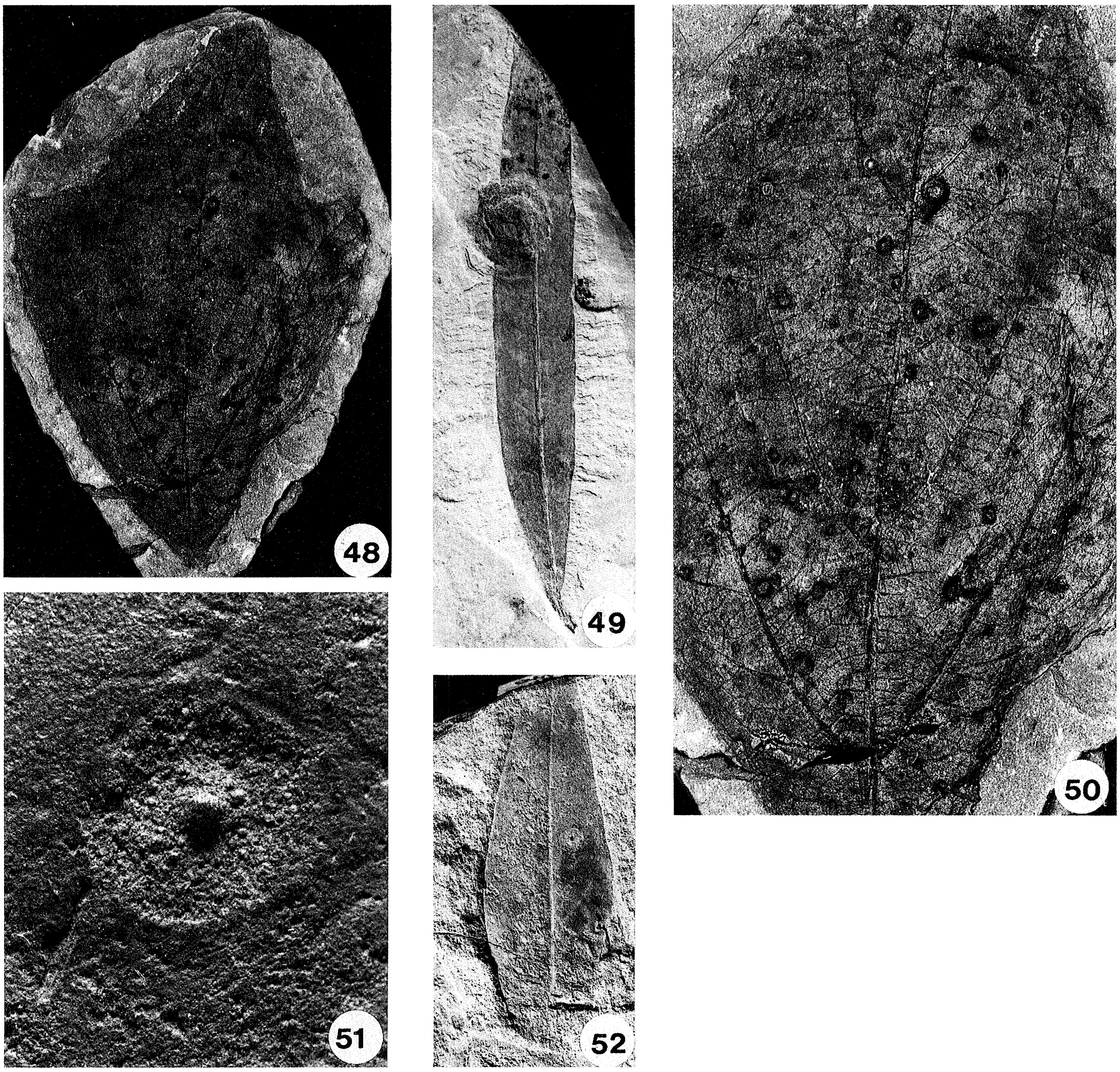


Figure 47. Examples of Cretaceous galls on angiosperm leaves (scale 1 cm). a. Small cone-galls on angiosperm leaf, Tuscaloosa Formation, U.S.A., Turonian, Cretaceous Field Museum of Natural History, Chicago. PP14026. b. Small-medium sized galls on angiosperm leaf from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. PP13553. c. Large galls on angiosperm leaf from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. PP196. d. Angiosperm leaf from the Cenomanian, Cretaceous of Vyserovice, Czechoslovakia with small cone galls, each with a central exit hole. Natural History Museum, London. v53724. e. Medium-large pouch galls on angiosperm leaf, Tuscaloosa Formation, U.S.A., Turonian. Field Museum of Natural History, Chicago. PP13471. f. Angiosperm leaf with spot gall with central exit hole from the Dakota Formation, Cenomanian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. UP 348 g. Angiosperm leaf with large ball gall from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. PP14154.

Permian (Potonié 1893; Conway-Morris 1981). There are very few examples of Mesozoic age. Alvin *et al.* (1967) note the presence of insect galls on an *Anomozamites* leaf from the Middle Jurassic (Bajocian) while Brues (1946) mentions the occurrence of Cretaceous galls but without documentation. Hickey & Doyle (1977) figure a number of possible insect galls from the early Cretaceous and Lesquereux (1892) and later Berry (1923) figure a gall from the mid-Cretaceous Dakota Formation which Lesquereux described as representing an 'oak gall' implying that it was produced by a member of the Cynipidae (Hymenoptera).

In a detailed study of mid-Cretaceous galls, Stephenson (1991) has investigated 26 specimens which he classifies into eight types. The criteria used for classification include size, both diameter and area, shape, position on leaf, nature of the gall wall, nature of the exit pore and a comparison with Recent specimens. A selection of forms from angiosperm leaves are illustrated here from the Cenomanian and Turonian of the U.S.A.



Figures 48–52. Examples of Cretaceous galls.

Figures 48 and 50. Angiosperm leaf from the Cenomanian, Cretaceous, Vyserovice, Czechoslovakia with small cone galls, each with a central exit hole. Magn. $\times \frac{1}{2}$ Natural History Museum, London. v53724. Magn. $\times \frac{1}{2}$. Figure 50. Magn. × 1.

Figure 49. Angiosperm leaf with large ball gall from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago, PP14154. Magn. × 1.

Figures 51 and 52. Angiosperm leaf with spot gall with central exit hole from the Dakota Formation, Cenomanian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. UP 348. Figure 51. Magn. × 6. Figure 52. Magn. $\times \frac{1}{2}$.

and of the Maastrichtian of Czechoslovakia and include those that he categorizes as 'very small generally dispersed forms, small cone galls, small to medium sized galls, medium sized spot galls to large pouch galls and very large galls'. We illustrate several examples here (figures 47–52). A detailed comparison with modern forms led Stephenson to conclude that a variety of gall types were present by the Cretaceous. These were similar to types formed by the Acari (Eriophyidae), Hemiptera: Homoptera (Aphididae or Psyllidae), Diptera (Cecidomyiidae) and Hymenoptera (Cynipidae).

This work indicates that such material may be more common than previously thought but more material is needed before meaningful conclusions can be drawn. The accuracy of comparisons with modern forms must be viewed with caution as the criteria used in their identifications are at best rather crude, their preservation is poor and there is little published on modern leaf galls, especially those which do not have any economic importance. Nevertheless, the 'best match' approach can be viewed with some confidence on a family or ordinal level. Our conclusion is that there was a variety of gall types by the mid Cretaceous. The majority were caused by gall mites although there is some evidence to suggest the work of gall gnats, aphids and perhaps even gall wasps. What is surprising is that no examples were found attributable to the Lepidoptera which are known from the Cretaceous and may indicate that this strategy was not developed by early members of this group. Important late Palaeozoic groups such as the Coleoptera rarely produce leaf galls but attack other parts of their plant hosts such as roots and stems. Plant stems were likely to have been the primitive gall site; galling soft stems must have been a relatively simple beginning for prosoplastic gallers (Shorthouse 1973, 1982, 1986). This is in accord with the Permian origin of the Coleoptera. The variety of galls found in the relatively 'new' angiosperms of the Cenomanian suggests that the coevolution of the gall-producing arthropods and host plants must have occurred over a very long period of time and may be the reason why it is the more ancient groups which have been more successful in developing this life style.

4. TRANSPORT AND REPRODUCTION

Further to Southwood's (1973) classification of the basic interactions as feeding, shelter and transport, Hocking (1975) also distinguished between the transport (dispersal) of propagules, and other forms of assistance in reproduction. Gilbert (1979) later qualified this distinction by suggesting that the transport of pollen and seeds are 'two very different processes that would have to be separated in any evolutionary or ecological model of a real system'.

Although we acknowledge this further classification, both transport and reproduction will be included together, as with the fossil data such distinction is less easy to make. 'Transport' is used here to include any movement of plant, plant part or arthropod brought about by, or aided by, a member of the other group.

(a) Transport of plant propagules by arthropods: entomochory

Few extant plants have mechanical dispersal mechanisms for the dissemination of their seeds. The majority rely upon the wind, water or animals, as their dispersal agents. This is called 'entomochory'. Seeds and spores (and pollen) may be 'dispersed' by arthropods in three different ways: (i) by taking them into their nests where they only eat the oily body (elaisome) attached to certain seeds; (ii) by adhesion of the spores and seeds to the host's body ('epizoochory'); and (iii) by swallowing and depositing them undigested in their excreta ('endozoochory'). Although this latter process may have been important in spore dispersal it has not been reported in living arthropods as a means of seed dispersal. It is important here that we acknowledge that while spore dispersal by these means could contribute to reproductive success of the plant, pollination would only be facilitated by category (ii) process above. Indeed this process, augmented by active pollen gathering in some groups, is the essential element in entomophily.

It has been suggested by Southwood (1973) that spore (pollen) eating was the first step for phytophagous insects. We have already noted the suggestion that spore eating may have existed since the early Devonian, using evidence from the Rhynie chert (Kevan *et al.* 1975). More direct evidence comes from the early Carboniferous where several types of coprolites have been shown to contain spores and pollen (Scott *et al.* 1985; Rothwell & Scott 1988; Rex & Galtier 1986). An important question to ask is whether such feeding behaviour would lead to dispersal of the plant. Some aspects of this topic have already been discussed elsewhere (see Scott *et al.* 1985).

Chaloner (1976) showed that the viability of *Pteridium* spores in the faeces of locusts (*Locusta migratoria*) is reduced by only 50%, illustrating the possible importance of this method of plant propagule dispersal. It is clear that only one experiment does not prove a point. We considered, therefore, to broaden the range of these experiments, firstly by repeating the original experiments and then including millepedes and cockroaches as potential dispersal agents as the millepedes have a fossil record from the Devonian, and the cockroaches from the Upper Carboniferous. These data have been published in Chaloner *et al.* (1991*b*). The *Pteridium* spores used in these experiments showed an initial viability of 75%, somewhat lower than in the original Chaloner (1976) experiments. Viability of spores in the locust faecal pellets was reduced to 5%. This is considerably lower than that recorded by Chaloner (1976) (50%) but nevertheless it is significant. This difference may be due to a change in the feeding protocol, using bran as carrier for the fern spores rather than the carbohydrate paste biscuits of the earlier work. It seems likely that destruction of the spores by mastication will be very dependent on the mechanical properties of the food on which the spores are consumed (see Bernays 1991). For the giant African millepedes the viability of faecal spores was 8%

but for the cockroaches no spores germinated. Even a small percent survival of the spores passing through the gut may represent, for the plant, carried to a new habitat, ample compensation for those 'destroyed' and so used as food by the insect carrier.

The viability of spores passing through the guts of several arthropod groups, we believe, is highly significant. It is also interesting to note here that both Christiansen (1964) and Kuhnelt (1976) report spores and pollen remaining viable after passing through the guts of Collembola (whose fossil record is from the early Devonian (Whalley & Jarzembowski 1981)), but no supporting data was presented. An interesting observation relating to the physiology of pollen eating (and hence to spore eating) has been made by Haslett (1983). He shows that adult hoverflies produce an environment within the gut which induces germination of *Ranunculus* pollen, so that it gains digestive access to the thin-walled pollen tube. There is, therefore, no need for any exine 'cracking' in the eating process, to obtain nourishment from the pollen. However, the rapid germination of angiosperm pollen is clearly being exploited here, and it seems less likely that this strategy could be exploited to obtain nourishment from spore eating.

We believe that the advent of spore feeding from the Devonian was as important to plants as to arthropods, adding an advantage of propagule dispersal to the plants. We repeat Southwoods (1973) observation that spore or pollen feeding is more nutritious for the arthropod than leaf feeding, which does not occur until later in the fossil record.

(*b*) *Reproduction*

The connection between pollen feeding and effecting pollination (see §4*c*) is more circuitous than spore feeding as a means of dispersal, but it is genuine none the less. The process of pollen feeding brings the insect into contact with pollen, and ensuing fortuitous transport of pollen on the outside of the insect may lead to an active pollination role. We have already mentioned the Upper Carboniferous coprolite comprising a *Feraxotheca* pollen organ. In addition, coprolites from the Upper Carboniferous have also been found containing '*Monoletes*' pollen belonging to a pteridosperm (Scott 1977). However, the pollen in the gut is 'what got away'. It has been widely thought that some pteridosperms may have been animal pollinated. It is interesting to note in this context that the giant anthropod *Arthropleura* has been found with abundant *Monoletes* pollen stuck to its leg segments, and hence potentially contributing to pollen transport (externally), leading Scott & Taylor (1983) to hypothesize that 'Perhaps *Arthropleura*, brushing through the floodplain scrub, acted as a pollinator for the medullosan seed ferns that were living there'. Pollen feeding would enhance the probability of pollen carrying, even though the pollen actually eaten would have been totally lost to the plant's reproductive success.

Our knowledge concerning Permian or Mesozoic interactions of this type are entirely lacking. However, the potential of spores especially adhering to an arthropods body has also received some attention in the literature, especially the potential use of hooks for attachment. Kevan *et al.* (1975) figure early Devonian spores with grapnel-like hooks which may have been used for the attachment to early arthropods. Chaloner (1984) further notes the appearance of fleshy gymnosperm seeds during the Palaeozoic and suggests this as an adaptation to biotic seed dispersal.

As a potential biproduct of this interactive behaviour is the transfer of disease. There is evidence such as the presence of fungi in insect-induced wounds (see, for example, Kevan *et al.* (1985) and Sherwood-Pike (1990)).

(*c*) *Pollination*

The origin, 'explosive' diversification, and rise to terrestrial global domination of the angiosperms seems to have been closely associated with their biotic pollination, if not indeed triggered by it. The coevolution of flower structure and the biotic pollination vector has probably received more attention than any other aspect of plant–animal interaction (see reviews in Faegri & Van der Pijl (1979), and the fossil evidence of the evolutionary story in Crepet & Friis (1987) and Crepet *et al.* (1991)).

Biotic pollination seems to have been derived from a pollen-feeding pattern in some antecedent gymnosperm group. This must, in turn, presumably have been derived from spore feeding in free-sporing plants, which pre-dated the origin of the seed. A likely scenario is that of Coleoptera (or possibly flies belonging to the Tipulidae or Mycetophidae) being involved in pollen feeding in Jurassic gymnosperms, possibly of the Bennettitales, and so functioning incidently as pollinators in the way outlined above. Obvious adaptations strengthening this bond of pollen-feeding insect with pollen-bearing seed-plant, would have been enclosure of the ovules in an infolded seed-bearing leaf (the angiosperm carpel) to protect the limited number of ovules from predation by the pollinator, while making ample pollen available as 'reward' for the visit. If the ovules were already borne within a hermaphrodite structure (as in the Bennettitales) then insect visits to feed on pollen would inevitably also bring pollen from other plants into the proximity of the ovules. There is circumstantial evidence that pollination may have been biotic in the Bennettitales (see, for example, Crepet & Friis (1987)). Indeed that group may have been close to the immediate precursors of the angiosperms. However, it is also possible that the Bennettitales developed the hermaphrodite configuration in parallel and in advance of that in the angiosperms, as a response to the same selective pressures of a pollinating vector.

Enclosure of the ovules within a conduplicate carpel (ovary) with associated pollination onto a stigma, and pollen tube growth through sporophytic tissue of a style to reach the ovule, would have favoured two further angiosperm attributes. Of these, probably the most important was the use of a pollen–stigma recognition mechanism, to develop elaborate incompatibility systems, favouring outbreeding. The presence of a tectate or semi-tectate exine in Cretaceous angiosperm pollen (a feature associated with the pollen carrying 'signalling substances' within the wall) suggests that this mechanism of pollen–stigma recognition was adopted early in the history of the angiosperms.

Pollination onto a stigma (rather than directly into the micropyle, as in gymnosperms) would have offered the early angiosperms the process of 'pollen competition' where the competing male gametes, in adjoining pollen tubes, vie for successful zygote formation.

There appears to be a strong link, then, within the angiosperms between adoption of biotic pollination and the several angiospermous features of hermaphrodite flower, enclosed ovules, a pollen 'recognition system' and pollen competition. Circumstantial evidence for involvement of insects in pollination in the living cycads and possibly Gnetales (Faegri & Van der Pijl 1979) suggests that biotic pollination itself may have been the first step and that this must have arisen independently in more than one gymnosperm line. An enormous range of specializations, associated with entomophily, are seen in the early fossil history of the angiosperm flower. The appearance of nectaries, at first as a rather nondescript receptacular disc, but followed before the end of the Cretaceous by more specialized secretory structures (Friis & Crepet 1987) is one of the most explicit of all the observable adaptations to biotic pollination. Floral modifications (fusion of petals to form a floral tube or a 'spur' as a nectar-store, and asymmetry of the flower) all follow in the fossil record, in a range of different forms, representing adaptations to restrict access to specific pollinators and orient the approach of the pollinating insects to pollen or nectar, so as to maximize pollination efficiency (Crepet & Friis 1987).

Looking to the fossil insect record for plausible pollinators, beetles were already diverse in the Lower Cretaceous, and were clearly available for unspecialized flowers such as the Albian *Archaeanthus*, comparable to *Magnolia* in their large, open actinomorphic flower structure.

The Hymenoptera, usually cited as the insect group most involved in angiosperm pollination, have also been reported from the Cretaceous. Furthermore, members of this group have been found fossil, with evidence of pollen still present in their gut contents (Krassilov & Rasnitzen 1982). However, because the pollen present in that case is clearly gymnospermous, this can only be invoked to implicate the Hymenoptera in pollen eating rather than angiosperm pollination *per se*.

(*d*) *Plant-aided insect reproduction*

The most important role of a plant in arthropod reproduction is by providing a suitable site for the laying of eggs and growth of the offspring. In this context palaeontological evidence of leaf mines and leaf galls already presented shows the complexity of this inter-relationship. Evidence of eggs on the undersurface of a leaf or on the external surface of a plant is very scarce and only two specimens have been documented. One occurs as possible insect eggs on fragments of an *Equisetites arenaceus* sheath from the Lower Keuper (Triassic) of Germany (Greyer & Kelber 1987). Another specimen occurs as possible insect eggs on the undersurface of an angiosperm leaf from the Cretaceous (Dakota Formation) of Central North America (Stephenson 1991).

5. COEVOLUTION

Although much has been written concerning such interactions between plants and animals of the kind discussed above, and these have often been cited by neontologists as exemplifying the process of coevolution (e.g. Feinsinger 1983), we have little direct evidence of this from the fossil record. However, it is clear from the variety and number of modern plant–arthropod interactions that there must have been a significant period of coevolution (Southwood 1973; Gilbert 1979). Strong *et al.* (1984) comment 'obviously plants have fundamentally influenced the evolution of phytophagous insects. However, phytophagous insects have probably played an important part in the evolution of plants.' Unfortunately, evidence from the fossil record must be viewed, for the most part, as circumstantial (Boucot 1990). We can show the co-occurrence of origin and diversification of different plant and animal groups as well as observe the appearance of certain morphological or anatomical features (Hughes & Smart 1967; Smart & Hughes 1973). We cannot, however, ever be sure that arthropod species A coevolved with plant species B. The fossil record can provide some broad hints and support for coevolutionary theory, and can give evidence of timing of recognizable events.

The suggestion that spore–pollen feeding is a more primitive state than leaf feeding (Southwood 1973) is borne out by the fossil record. Likewise marginal feeding appears earlier than non-marginal feeding, so bearing out the suggestion of Edwards & Wratten (1983). These authors also consider that interrupted feeding occurs because of a chemical response by the plant to feeding and hence must be a more advanced character. It is clear from the fossil record that interrupted feeding occurs more commonly in the Cretaceous than before that time.

Chemical response by plants to phytophagy has also been considered by Cooper-Driver (1978, 1985). In her papers she argues that the insect groups which most commonly feed on ferns are members of more primitive families, and supports the idea that these groups coevolved with the ferns from an early stage and have evolved strategies to tolerate the toxins produced. Whereas this speculation appears to us to be sound, we have no morphological or chemical evidence from the fossil record to support the hypothesis.

A much wider consideration concerns the pattern and type of the interaction evidence. It is clear that interactions between arthropods and plants are found as soon as these groups are established upon land. The first increase in types of interaction including leaf feeding, extensive wood boring and even leaf mining coincides with the major Upper Carboniferous radiation of insects. We must mention, however, that the Permian origin and diversification of beetles has no evident importance in the plant fossil record and we might, for example, have expected some evidence for a diversification in the wood-boring habit at that time. It seems that closer search for insect damaged plants in the Permian and Triassic is needed.

The rapid radiation of the angiosperms and several insect groups during the mid-late Cretaceous is also marked by a rapid increase in the diversity and occurrences of interactions, as seen in the fossil record (figure 53). Of particular importance is the diversification in leaf-mining and gall production which coincides with the diversification of Lepidoptera, Hemiptera and Diptera. Leaf-mining and gall production appear, therefore, to have evolved early in the history of these groups and have developed in parallel through the Cretaceous and Tertiary. The close interactions between insects and flowering plants in terms of pollination syndromes is also clear from the fossil record, even as far back as the mid-Cretaceous (Crepet & Friis 1987; Crepet *et al.* 1991). Even here, however, evidence is circumstantial in that no fossil flower has been preserved with an insect trapped in the moment of pollination. Unfortunately we know of no records of pre-Tertiary amber which captures such an interaction.

We note the suggestion of Brown & Lawton (1991) that the shape of angiosperm leaves, and expressly the leaf margin character, has been strongly influenced by selective pressure exerted by leaf margin feeding behaviour of herbivores. It has long been recognized that the entire (smooth) leaf margin in angiosperms is broadly correlated with the syndrome of large-leaf, drip-tip and evergreen texture associated with lowland tropical forest. These features contrast with the typically non-entire (toothed, lobed) margin, small-size and lack of a drip-tip shown by the soft-textured leaves of temperate deciduous forest trees. This broad

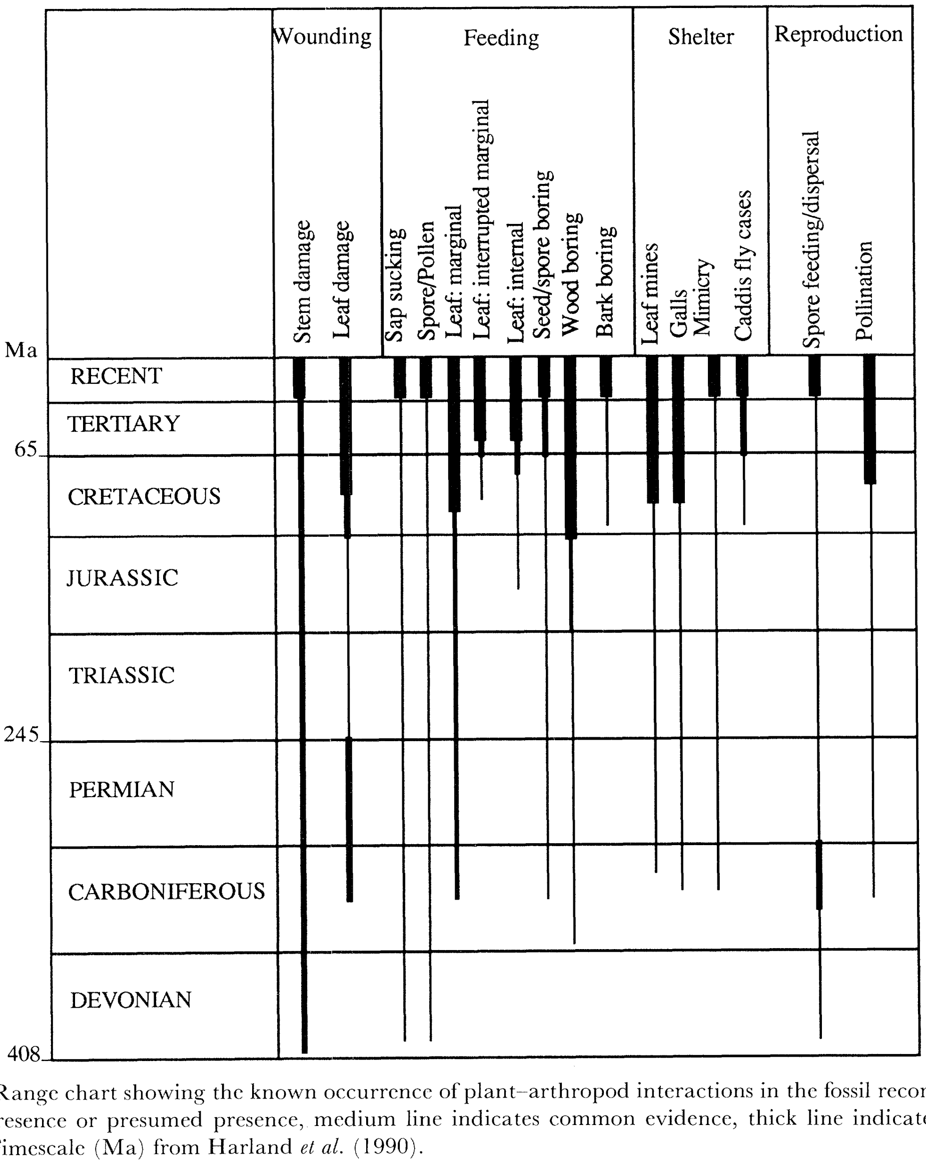


Figure 53. Range chart showing the known occurrence of plant–arthropod interactions in the fossil record. Thin line indicates presence or presumed presence, medium line indicates common evidence, thick line indicates abundant evidence. Timescale (Ma) from Harland *et al.* (1990).

correlation of leaf physiognomy with climate has been used by palaeobotanists as a basis for palaeoclimatic interpretation of fossil leaf assemblages (see, for example, Wolfe (1978); Chaloner & Creber (1990)). 'Evergreen texture' (with thick cuticle overlying tough, often fibrous leaf tissue) has an evident adaptive value in the strategy of retention of leaves over a period of 3–4 years, as against the soft-textured, 'disposable', short-lived leaves of deciduous trees. However, the causal basis for the relationship of leaf margin type to climate has always appeared somewhat enigmatic. Brown & Lawton's work now suggests that the non-entire leaf margin is merely reflecting the need for the soft-textured (and so more edible) leaf to adopt a feature which discourages marginal leaf feeding by herbivorous insects. In this we have a more complex relationship between plant, animal and climate than has been recognized hitherto. The correlation between climate and leaf margin appears to have arisen indirectly through the mediation of the selective pressure of insect leaf feeding, rather than as a structural response to the climatic environment.

We take the view that, generally speaking, the fossil record may support or refute existing coevolutionary theories, but has only rarely been used to erect new hypotheses, as in the case of Retallack & Feakes (1987) suggestion of the occurrence of terrestrial faunas preceding terrestrial plants, based on the study of fossil soils.

6. PALAEOZOIC AND MESOZOIC INTERACTIONS: CONCLUSIONS

Despite the scattered and incomplete nature of the evidence, we see compelling reasons to believe that plant–arthropod interactions developed as soon as both groups spread onto the land. The fossil record shows a diversification of interactions through time, as well as an increase in complexity of each of the several types of interaction. It also provides evidence of the evolution of behaviour in various arthropod groups. In general, diversification of interactions coincides with the radiation of a particular insect, and in some cases, plant groups. Major innovations in behaviour occur in the early Devonian, late Carboniferous and mid-Cretaceous, which all may be linked to the origin and diversification of terrestrial arthropods. There is good fossil evidence for the evolution of feeding behaviour, the use of plants for shelter and more circumstantial evidence for the interactions concerned with transport and reproduction (figure 53). In general there appears to be a mix of the development of new behaviour in old groups and new groups with new behaviour but this topic needs further investigation.

Evidence for feeding on plants by arthropods is diverse. Leaf eating appears for the first time in the Upper Carboniferous, where leaves show marginal eating. Several authors have, however, commented on the lack of evidence of herbivory in the Palaeozoic, i.e. feeding on living plant tissues (e.g. Strong *et al.* 1984; Shear & Kukalova-Peck 1990). It is possible that detritivory was relatively more important than herbivory in Carboniferous time. Perhaps as we understand more of the problems of arthropods feeding on living plant tissues (see papers in Chaloner *et al.* (1991)) it becomes surprising that we find any evidence of herbivory in the Carboniferous. In the mid-Cretaceous non-marginal leaf feeding becomes common and is particularly well seen in angiosperm leaves. In addition, interrupted marginal feeding is also commonly found. This type of feeding pattern has been linked to plants producing chemical defences against herbivory and suggests a more complex interaction.

Evidence from arthropod gut contents and coprolites implies that litter feeding and spore feeding appeared before leaf feeding, as suggested by Southwood (1973). As yet we have little direct evidence of seed feeding (but see Collinson & Hooker 1991).

Leaf mining, a more specialized form of feeding which also involves shelter and protection for the animal does not appear until the late Palaeozoic and does not become common until the mid-Cretaceous which coincides with the evolution of several insect groups which contain the major extant miners. It also coincides with the advent and diversification of angiosperms.

Wood boring appears also to be a more advanced mode of life, as the digestion of woody tissue appears only possible because of the activity of symbiotic microorganisms. We illustrate here the oldest recorded bored wood from the Lower Carboniferous, and note that such borings occur more commonly from the later Carboniferous.

Wound reactions in plant tissues from the early Devonian may suggest the early evolution of sap sucking. Morphological features of several insect mouthparts suggest that this type of behaviour became more common from the Upper Carboniferous.

Although there is rare and equivocal evidence for the use of plants by arthropods for shelter from the early Devonian it is not until the evolution of galls that direct evidence for this behaviour becomes available. Although some galls have been found from the late Palaeozoic, it is not until the mid-Cretaceous that they become common, especially on angiosperm leaves. Again, this coincides with the evolution of several insect families which are known to be gall producers at the present day.

The area of transport and reproduction is one of the most interesting but also one where direct evidence is more difficult to obtain. Our experiments using living arthropods, including insects, suggest that if an animal was feeding on spores some of these remain viable even after passing through the gut. Spore feeding, therefore, would not only be of importance to the arthropod providing a good nutritional source but also for the plant, as spores would be transported to new and favourable habitats and hence spread the species. There is equivocal evidence that some arthropods may have been involved with the pollination of some seed plant groups such as the Carboniferous pteridosperms and the Jurassic cycads.

The evolution of angiosperm–insect interactions, which clearly had far-reaching effects, appear from the mid-Cretaceous. The diversity of interactions between the two groups in modern biota is well documented and it is clear that the synchronous, rapid diversification of both insects and angiosperms in the Cretaceous is more than just fortuitous. Several floral features, including the evolution of nectaries and several corrola types may be linked to insect pollination. It is clear from the evidence presented here that there is extensive evidence for plant–arthropod interaction in the Palaeozoic and Mesozoic, but there are many gaps in our knowledge which may be filled by future work.

We thank Deborah Parsons and Geoff Prior for their help with the modern arthropod experiments, Kevin de Souza for photographic help and Sandra Muir for drawing some of the figures. Angela Lyon kindly typed the manuscript. We thank Dr Paul Whalley, Professor David Dilcher, Professor Thomas N. Taylor, Dr Margaret Collinson, Dr Paul Selden and Dr Richard Fortey for helpful discussion and encouragement. We thank Professor Thomas Taylor, Professor Gar Rothwell, Professor David Dilcher and Dr Peter Crane, Dr Chris Hill and Dr Richard Fortey for access to collections. A.C.S. thanks the Royal Society for travel funds to Australia, China and Argentina. We thank Dr J. Genise for showing us some of his unpublished material. J. S. gratefully acknowledges the receipt of a NERC research studentship.

APPENDIX 1. EVOLUTION OF PLANTS AND INSECTS: AN OVERVIEW

For a full appreciation of the modern ecosystem with its variety of plant and insect species some understanding of the evolution and diversity of both groups is essential. Unfortunately, the fossil record is far from complete and the first appearance in the record may long post-date the actual origin of the groups. Green algae and cyanobacteria must have existed in suitable terrestrial habitats long before vascular plants colonized the land (Edwards *et al.* 1986; Stewart 1983; Thomas & Spicer 1987; Chaloner 1988; Taylor 1988*a*) although there is no unequivocal evidence to support this hypothesis. Spores (Gray 1985) and cuticle (Gray *et al.* 1982), believed to be of land plant origin, have been found in sediments of Middle Ordovician age and possible conducting tubes occur as early as the Lower Silurian (Taylor 1988*a*). Chaloner (1967) has based the origin of land plants, using the spore evidence, to lie somewhere in the Lower to Middle Silurian, although the earliest land plant megafossils have only been found in younger Wenlockian deposits (Taylor 1988*a*; Edwards & Burgess 1990).

(*a*) *Early terrestrial land plants and arthropods*

Lang (1937) described, under the name *Cooksonia*, what was then the earliest land plant in the late Silurian (Pridoli) of the Welsh Borders and South Wales. Fossils probably assignable to that genus have been found in older Wenlock (mid-Silurian) strata in Ireland (Edwards 1980; Edwards & Feehan 1980; Edwards & Fanning 1985) but they lack evidence of xylem, stomata and spores all of which have been securely demonstrated in younger basal Devonian plants. *Cooksonia* persisted well into Early Devonian times (Edwards *et al.* 1986). More elaborate plants (lycopods) have been reported from Australia in rocks of Ludlow age but their age remains controversial (Chaloner 1988; Selden & Edwards 1989).

The earliest *Cooksonia* species possibly grew in fluviatile areas close to shore or on tidal flats (Edwards 1980; Edwards & Fanning 1985). It is into these environments with plants that the first terrestrial arthropods may have ventured. The earliest unequivocal fossils of terrestrial arthropods presumed to be pioneer detritivores are uppermost Silurian (Pridoli) myriapods (Rolfe 1985*a*). New discoveries from Pridoli age strata in the Welsh Borderland include our earliest evidence of diverse terrestrial arthropod faunas which include centipedes and other carnivorous forms (Jeram *et al.* 1990; Rolfe 1990). Possible millepedes (Myriapoda: Diplopoda) have also been found in slightly older Upper Silurian deposits (Almond 1985) although many other terrestrial arthropod classes did not appear until well into the Devonian. By Lower Devonian (Gedinnian) times many species of *Cooksonia* were present including *C. hemisphaerica* (Edwards & Burgess 1990). Their habitat ranges were now extending into the hinterlands and they are found in a much wider range of sedimentary rocks (Thomas & Spicer 1987). As the plants gradually covered the land, competition was to become increasingly important as new plant types evolved. Members of the Zosterophyllopsida (*Zosterophyllum myretonianum* Penhallow) first appear during the Gedinnian (Gensel & Andrews 1984) soon to be followed by the Trimerophytopsida with the appearance of *Trimerophyton* (*Psilophyton*) *robustius* (Dawson) Hopping, within Emsian deposits.

There is an absence of any terrestrial arthropod record during the Gedinnian but with the re-investigation of the Rhynie Chert beds of Scotland (Siegenian) a new picture of early Devonian life has developed (Kevan *et al.* 1975; Chaloner & MacDonald 1980). Many different types of true rhyniophytes including *Rhynia gwynne-vaughanii* Kidston and Lang and *Horneophyton lignieri* Kidston and Lang) Barghoorn and Darrah, are present along with the possible cooksonioid *Aglaophyton* (*Rhynia*) *major* (Kidston and Lang) Edwards and *Asteroxylon mackiei* Kidston and Lang, the first possible lycophyte of the Northern Hemisphere, providing a mixed and varied plant community.

Within this flora were found abundant non-myriapod terrestrial arthropods. These include many species of mites with orders Trigonotarbida and Acari of the class Arachnida (Chelicerata) (Rolfe 1980). The previous records of true spiders are now thought to be erroneous (Selden *et al.* 1991). There is also the first hexapod, *Rhyniella praecursor* Hirst and Maulik, representing the sub-class Collembola (Hirst & Maulik 1926; Scourfield 1940; Whalley & Jarzembowski 1981; Greenslade & Whalley 1986).

(*b*) *Early-Mid Devonian floras and arthropods*

A slightly younger Emsian locality on the Gaspé Peninsula, Quebec, has revealed another varied flora including trimerophytes, zosterophylls and lycophytes. It is within this plant assemblage that there is evidence of the oldest bristletail (Hexapoda: Thysanura/Archeognatha) (Labandeira *et al.* 1988), although its authenticity has been called to question by Jeram *et al.* (1990). The early evolution and radiation of these primitive arthropod types was therefore more or less contemporaneous with the evolution of the primitive vascular land plants. Close interactions and perhaps the first indications of possible coevolutionary relationships may also be suggested at this early stage (Kevan *et al.* 1975). Those interactions found within the Rhynie Chert are dealt with in more detail above, but other evidence includes the possible function of the spines found on the axes of various *Psilophyton* species (Trimerophytopsida) for example *P. princeps* Dawson and *P. crenulatum* Doran. Chaloner (1970) suggests the spines may have been glandular and repelled herbivorous invertebrates thus protecting the plants and their sporangia. This has been contested by Smart (1971) who proposes that they might have aided spore-gathering arthropods to climb the stems to reach the sporangia and therefore help disperse the spores. For whichever reason these spines were developed, they suggest a close relationship between land plants and land fauna as early as the Lower Devonian.

Major plant diversification occurred during the Middle and late Devonian (Banks 1985; Gensel & Andrews 1984) with the development of several major groups such as the progymnosperms (e.g. Aneurophytales) and also the appearance of several important plant strategies, including the appearance of the megaphyllous leaves and arborescence in some groups (Chaloner & Sheerin 1981; Scott 1984; Collinson & Scott 1987).

The increasing diversity of land ecosystems during the Middle Devonian is also reflected by the arthropod evidence found within the Gilboa deposits of New York (Givetian) (Rolfe 1982; Shear 1986; Shear *et al.* 1987; Selden *et al.* 1991). There were at least nine species of Trigonotarbida, six species of Acarina, two species of centipedes (Myriapoda: Chilopoda) one arthropleurid (an extinct group of arthropods similar in appearance to giant millepedes) and parts of compound eyes and tergite scraps attributed to the Machilidae (Hexapoda: Thysanura/Archaeognatha) (Shear *et al.* 1984).

(*c*) *Late Devonian floras*

During the Late Devonian the Aneurophytales were joined by another group of progymnosperms, the Archaeopteridales, represented by *Archaeopteris* Dawson, which first appeared in the Frasnian. These were large tree-sized plants with trunks up to a metre in diameter, capable of forming extensive forests (Scott 1980). Towards the end of the Period *Rhacophyton* and other coenopteridalean preferns coexisted with the 8 m tall *Cyclostigma kiltorkense* Haughton, (Lycopsida), the 15 m tall *Pseudobornia ursina* Nathorst and *Archaeocalamites* Stur, (both Sphenopsida). By early Carboniferous (Tournaisian) times, five Classes of vascular plants were in existence. Within the Lycopsida the primitive Drepanophycales and Protolepidodendrales became extinct at the end of the Devonian but other lycophytes such as *Cyclostigma* and *Lepidodendropsis* transgressed the Famennian–Tournaisian boundary and were joined by other members of the Lepidodendrales (Chaloner & Sheerin 1979; Taylor 1981).

The prefern *Rhacophyton* disappeared during the Tournasian and the Cladoxylales became extinct later in the Lower Carboniferous although Scott & Galtier (1985) and Galtier & Scott (1985) have shown that by the end of the Tournaisian the Coenopteridales were much more diverse and the first true ferns, the Filicales, were present.

The first seeds have been recorded from the Fammenian in the late Devonian and the pteridosperms diversified rapidly in the early Carboniferous (Rothwell & Scheckler 1989; Galtier 1989), so that by the late Tournaisian a wide diversity of plant groups living under different ecological conditions were present (Scott 1990).

(*d*) *Early Carboniferous terrestrial arthropods*

Terrestrial arthropod evolution and diversity during the Lower Carboniferous is revealed in recent work on the East Kirkton Limestone deposits. Evidence of the first unequivocal terrestrial scorpions are found in large numbers (Rolfe *et al.* 1990). Those scorpions of the Middle Devonian Gilboa sediments (Shear 1986) and earlier (Rolfe 1985*a*) are now believed to be aquatic (Kjellesvig-Waering 1986). East Kirkton also provides evidence of the earliest harvestman spider (Arachnida: Opiliones) (Rolfe *et al.* 1990) as well as several diplopods including a new chilognathan millepede which shows spiracles or respiratory pores proving the terrestrial nature of the animal (Rolfe 1988).

There are no fossil insects from East Kirkton; the first unequivocal evidence of true insects (Hexapoda: Pterygota) does not occur until the Namurian (Wootton 1981; Shear & Kukalova-Peck 1990). There are many theories on the evolution of the Pterygota (e.g. Martynov 1937; Rohdendorf & Rasnitsyn 1980) although most entomologists and palaeoentomologists agree that there were four main stages in their history (Carpenter 1969). Briefly, the first stage consists of the primitive wingless hexapod groups including the Archaeognatha and Zygentoma (collectively known as the Thysanura) and the Collembola of the Lower and Middle Devonian. These classes are believed to represent the most generalized insect-like plan. Stage two includes the evolution of the true insects or Pterygota, although the actual origin of the wings is still under much debate (Wigglesworth 1976; Wootton 1976; Kukalova-Peck 1978; Rasnitsyn 1981; Kinsolver & Koehl 1984; Shear & Kukalova-Peck 1990). The third stage incorporates the ability of some insects (the Neoptera) to articulate their wings and place them back over the abdomen when at rest (Snodgrass 1935). Those insects which cannot do this are believed to be more primitive and are placed in the Palaeoptera. The final stage in the evolution of modern insects concerns the development of a more complicated or indirect type of postembryonic life cycle. The immature insects do not resemble the adults, they are wingless, feed on different food and live in different habitats. They then undergo a non-feeding pupal phase during which reorganization of the immature tissues and organs into the adult plan takes place. This stage only occurs within the Neoptera and splits those orders with this postembryonic development into the 'Endopterygota' and those without into the 'Exopterygota'.

As Carpenter (1965) points out, those insects of the Upper Carboniferous had already attained the third stage of evolution. The majority of palaeoentomologists (e.g. Kinsolver & Koehl 1984; Wootton 1981; Carpenter & Burnham 1985) believe evidence of their origins must, therefore, lie within earlier Devonian and Lower Carboniferous sediments but there is no data to support this at present. Such an early origin is suggested by the presence of primitive non-flying hexapod groups such as the Thysanura and Collembola in Lower and Middle Devonian deposits. The highly evolved structure of the Upper Carboniferous insect wing suggests an earlier evolution and Kevan *et al.* (1975) propose that flight may have coevolved with arborescence in late Devonian plants. As stated, however, the excellently preserved fossils from the Lower Carboniferous East Kirkton site do not include any true insects. If the Pterygota had existed at this time it would be expected that some specimens would have been preserved here or at other Lower Carboniferous localities.

Scott (1980) suggests that the presence of a two level 'structure' to plant communities in the form of a ground cover ecosystem and a tree top ecosystem, existed during the middle to late Devonian. Extensive lycophyte and sphenophyte forests, did not, however, exist until middle to late Carboniferous times, and we believe it may have been the presence of such trees which provided the impetus needed for the evolution of flight within the Arthropoda.

Evidence of the terrestrial fauna from these Coal Measure forests include many carnivorous animals (Shear & Kukalova-Peck 1990). Centipedes (Myriapoda: Chilopoda) were common especially in the Mazon Creek fauna (Mundel 1979) along with many spiders (Arachnida: Aranae) some of which had inward striking (dianial) fangs, indicating their ability to kill insects (Rolfe 1985*b*) and other groups of spiders which possessed downward-striking (paraxial) jaws for attacking prey on a firm substrate, either on the ground or on tree trunks (Rolfe 1985*b*).

The first insects which make an appearance in the Namurian were members of the extinct order, the Palaeodictyoptera, for example *Patteiskya boukaerti* Laurentiaux, and *Ostrava nigra* Kukalova. They were originally believed to be the primitive basal group from which all other insects evolved. Together with five other orders they comprise the Palaeoptera and all have their origins in the Upper Carboniferous. Two orders, the Ephemeroptera (mayflies) and Odonata (dragonflies and damselflies) remain extant.

The other Carboniferous orders are, like the Palaeodictyoptera, extinct, and survived only until the end of the Permian (Carpenter & Burnham 1985). The Protodonata were very similar to the first dragonflies except for a variation in the wing venation and their great size. Carpenter (1969) described one specimen, *Meganeura monyi*, to have a wingspan not less than 63 cm. The Megasecoptera such as *Dunbaria fasciipennis* Tillyard, and Diaphanopterodea were very similar to the Palaeodictyoptera although studies have shown that members of the Diaphanopterodea could fold their wings back over their abdomens. But in this action they used a different method than that employed by the Neoptera, suggesting that wing folding must have evolved in this group independently (Kukalova-Peck 1978). It was also shown by Kukalova (1970) working on *Stenodictya laurentiauxi* of the Palaeodictyoptera, that they possessed very specialized beak-like mouthparts able to pierce plant material and feed on the sap. These appendages were subsequently found in the Megasecoptera and Diaphanopterodea suggesting these early groups were not the most primitive insects but were specialized sister groups and that perhaps the insect ancestors were more likely to belong to the Ephemeroptera.

Five orders of the exopterygote neopteran insects also appear in the Upper Carboniferous. Three of these orders became extinct at the end of the Palaeozoic. These were the Protorthoptera, for example *Gerarus latus* Handlirsch, which was the most diverse of all the extinct orders with over thirty families in the Upper Carboniferous alone (Burnham 1983) and the Caloneurodea, which some workers (e.g. Sharov 1966) place in the Endopterygota, and the Miomoptera (e.g. *Stefanomioptera* Carpenter) which were very small insects, perhaps related to the Protorthoptera.

The other two orders, the Blattodea (cockroaches) and Orthoptera (grasshoppers, katydids and crickets) (the earliest being *Oedischia* Handlirsch) remain extant. The Blattodea were apparently the commonest group of insects during the Upper Carboniferous, but this may be a false impression as they lived in habits in which their fossilization was more likely to occur.

A variety of insects capable of flight had, therefore, adapted successfully to the forest vegetation of the Upper Carboniferous. An extinct class of flightless hexapods, the Monura (a sister group of the Thysanura: Archaeognatha) also existed at the time but members such as *Dasyleptus brongniarti* Sharov were extinct by the close of the Palaeozoic.

(*e*) *Carboniferous and Permian floras*

In later Upper Carboniferous times distinct upland and lowland floras were well developed. The forests dominated by lycophytes and sphenophytes were confined to the swampy lowlands while the upland vegetation contained many kinds of spore-bearing plants, pteridosperms and other gymnosperms, most commonly *Cordaites* (Cordaitales) and the first conifers. Towards the close of the Carboniferous the giant lycophytes and sphenophytes were becoming less important components of the plant communities and large tree ferns became much more common (Phillips & Peppers 1984; Scott 1980).

During the early Permian plants adapted to dryer habitats in the uplands migrated down into the basins (Frederiksen 1972; Scott 1980). Major climatic changes resulted in the drying up of the lowland habitats with ensuing extinction of the arborescent lycophytes and sphenophytes (Chaloner 1967; Scott 1980). Thomas (1985) takes this idea further by noting their inability to grow in the compacted soils which surrounded their lowland swamps. All the other members of the Sphenophyllales (such as *Sphenophyllum* Brongniart) also became extinct during the Permian but the smaller Equisitales survived as did the small Sellaginellales (Lycopsida) which survive to the present day.

Scott (1980) reviewing the ecology of Upper Palaeozoic floras noted the presence of five plant communities in the Permian of Europe (based on Barthel 1976), and Ziegler (1989) recognizes at least ten biomes or phytogeographic regions on a global basis. Within these varied associations the true ferns were becoming much more abundant, the last of the preferns disappearing earlier in the Period. Seed plants continued to diversify with not only the Pteridospermales, but also Cordaitales and Coniferales, including the transition conifers, the Voltziales, with a number of specimens (e.g. *Pseudovoltzia* and *Lebachia* Florin), from middle to late Permian.

(*f*) ***Permian insects***

All the insect orders which appear in late Carboniferous rocks survived into the Permian period where they were joined by another ten orders, all members of the Neoptera (see Shear & Kukalova-Peck 1990). The extinct Protelytroptera existed throughout the Permian but did not survive into the Mesozoic. They closely resembled present day Coleoptera but are now believed to be more probably related to the Dermaptera (earwigs) after studies on their hind wings and the noted presence of cerci (Carpenter & Kukalova 1964; Kukalova 1965). Together with the extant Psocoptera (barklice) (e.g. Lower Permian *Permopsocus congener* Tillyard), Plecoptera (stoneflies) (e.g. Lower Permian *Perlopsis filicornis* Rohdendorf), Thysanoptera (thrips) (e.g. *Permothrips longipennis* Rohdenorf) and Hemiptera: Homoptera (true bugs) (e.g. *Permaleurodes rotundatus* Becker-Migdisova) they represent members of the exopterygota.

Other extant insect orders also existed during the Permian. These included the Mecoptera (scorpion flies) (e.g. Lower Permian *Platychorista venosa* Tillyard), Neuroptera (alderflies, snake flies and lacewings) (e.g. Upper Permian *Permosialis parucinervis* Martynov), Trichoptera (caddis flies) and the Coleoptera (beetles) (e.g. *Tshekardocoleus magnus* Rohdendorf). The earliest members of these orders are also the first unequivocal endopterygotes of which both adult and immature stages are known. The order Glosselytrodea is the only endopterygote group which has become extinct. It is also the only extinct insect order which survived the Palaeozoic–Mesozoic boundary and is found well into the early Jurassic. These insects (e.g. *Permoberotha villosa* Carpenter) resemble present day Neuroptera in both venation and other details of wing structure (Carpenter & Burnham 1985).

It was within the Permian that the insects reached their maximum morphological diversity (Carpenter 1977; Carpenter & Burnham 1985). This may in part be due to the inability of early spiders to trap insects aerially by orb-webs, the first evidence of which does not occur until the Cretaceous (Selden 1990). Aerial predators other than the insects are not known until the Triassic (Rolfe 1985*b*) and so the reasons for the severe decline in insect diversity at the close of the Palaeozoic are not fully understood, but only 13 out of the 21 Permian orders survived into the Mesozoic.

(*g*) ***Late Palaeozoic – early Mesozoic floras***

The late Palaeozoic – early Mesozoic flora was dominated by a variety of gymnosperms. However the Northern and Southern Hemispheres were developing distinct types of vegetation distinguished by their dominant gymnosperms. The floras of the Southern Hemisphere were dominated in the Permian by many species of the Glossopteridales such as *Glossopteris* and *Gangamopteris* but by Triassic times these were replaced by other gymnosperm orders including the Corystospermales (e.g. *Rhexoxylon* and *Pteruchus*) (Thomas & Spicer 1987). Both Glossopteridales and Corystospermales were endemic to Gondwanaland. Other orders transgressed both Hemispheres. The Triassic Peltaspermales and Caytoniales had a world-wide distribution, as did the Ginkgoales which survive to the present day.

The Cycadales and Cycadeoidales only become common from the Triassic onwards but both groups had their origin in the Palaeozoic. This latter group, with their hermaphrodite flower-like reproductive organs, developed to dominate many plant communities, forming vegetation very different to that of the late Palaeozoic.

It could have perhaps been this change in the flora, dominated by thick-cuticled forms unsuitable for the highly evolved piercing-sucking mouthparts of the Palaeodictyoptera and their allies, which caused these insect orders to become extinct. The Hemiptera on the other hand, with their relatively unspecialized piercing mouth apparatus were able to take advantage of the available niche and were able to expand in the form of the sub-order, Heteroptera (leaf hoppers) (e.g. *Paraknightia magnifica* Evans).

(*h*) ***Triassic insects***

With the new types of vegetation new groups of insects were also evolving. All of the three new orders which appeared during the Triassic originated in the glossopterid-dominated Southern Hemisphere, although they later migrated into the Northern Hemisphere. The exopterygote order, the Phasmida (stick insects) is known from the Triassic of Australia (Martynov 1928; Martynova 1962) and the other endopterygote groups, the Diptera (true flies) (e.g. Triassic *Dictyodiptera multinervis* Rhodendorf) (Rhodendorf 1974) and the Hymenoptera (sawflies, ants, wasps and bees) (e.g. Triassic *Archexyela crosbyi* Riek) soon radiated into the Northern Asian plains (Rohdendorf 1964; Rasnitsyn 1964, 1969, 1975).

(*i*) *Mesozoic floras and insects*

The cycads and cycadeoids flourished in the Jurassic, with various species such as *Cycadeoidea* (Crepet 1974), *Beania* Harris, *Williamsoniella coronata* Thomas and *Williamsonia sewardiana* Sahni (Thomas & Spicer 1987) (all members of the Bennettitales) playing important roles in the vegetation. Some new types of gymnosperms such as *Czechanowskia* (Czechanowskiales) were short-lived whereas the Coniferales became more important and their extant sister group, the Taxales, first appeared with *Palaeotaxus rediviva* Florin. The Hymenoptera and Diptera diversified rapidly during this Period and were joined by only one new group, an exopterygote Order, the Dermaptera (earwigs) (e.g. Upper Jurassic *Semenoviola obliquotruncata* Martynov).

The late Mesozoic was also a time of considerable floristic changes (Axelrod 1970). The majority of palaeobotanists believe the origins of the present day dominant plant group, the Angiospermopsida, lie somewhere in the Lower Cretaceous (Stewart 1983; Thomas & Spicer, 1987; Upchurch & Wolfe 1987; Friis & Crepet 1987; Taylor 1988*b*) although this is still very much under debate and a few authors believe their origins lie earlier in the Mesozoic (Axelrod 1961, 1970; Hughes 1976).

An actual definition of what distinguishes an angiosperm from all the other plant groups based on fossils still remains unsatisfactorily answered (Friis *et al.* 1987; Thomas & Spicer 1987; Doyle & Donoghue 1987; Taylor 1988*b*) and so early possible fossil evidence remains difficult to attribute to angiosperm origin (Crane 1985; Taylor 1988*b*). Friis & Crepet (1987) and others believe the presence of true flowers and fruit define the angiosperm condition, as floral structures provide the majority of characters used in angiosperm systematics. The earliest fossil flowers were small and simple (Crane, Friis & Pedersen 1986). Both unisexual and bisexual flowers were present by the late Albian (Middle Cretaceous, 97.5–106 Ma) (Friis & Crepet 1987). Some of these have been attributed to the dicot families Chloranthaceae and Platanaceae (Crane *et al.* 1986; Friis & Crepet 1987). Earlier evidence for the evolution of these families is provided by dispersed pollen and leaves.

Other pollen evidence suggests that angiosperms may have been present in the late Hauterivian (Lower Cretaceous) (Brenner & Crepet 1987, Hughes *et al.* 1991). Vegetative evidence in the form of fossil angiosperm leaves and wood occur in several localities of Barremian–Aptian age (Hickey & Doyle 1977; Taylor 1988*b*).

The fossil evidence so far suggests that many of the earliest angiosperms were entomophilous (Friis & Crepet 1987; Crepet & Friis 1987) and perhaps it was this reproductive relationship with the insects which made the angiosperms successful. The major anthophilous insect orders, the Coleoptera, Diptera, and Hymenoptera and to a lesser degree the Thysanoptera underwent major radiation during this Period (Zherikhin 1980) and the important angiosperm pollinating order, the Lepidoptera (moths and butterflies) evolved at this time (Whalley 1986). Some smaller groups, such as the Isoptera (termites) also appeared during the Cretaceous (e.g. *Valditermes brenanae* Jarzembowski) when both dicotyledons and monocotyledon angiosperms were present.

Towards the close of the Mesozoic there was a small decline in the relative proportion of angiosperms to other plants at the Cretaceous–Tertiary (K–T) boundary when a fern spike was produced in the palynological record (Tschudy 1981; Upchurch & Wolfe 1987). The cause for the great extinction phenomenon at this time, mainly involving animal groups, is a popular topic for speculation. This may, of course, reflect a response to the loss of pollination vectors, or simply a migratory response of anaemophilous forms successfully challenging entomophilous plants under changing climatic conditions. The suggested decrease in entomophilous angiosperms is not reflected by the insect diversity, although their actual numbers may have been depleted.

APPENDIX 2. MAJOR MATERIAL STUDIED IN MUSEUM COLLECTIONS

1. Natural History Museum, London (BMNH)
   (Collections of Devonian–Tertiary plants and insects)
2. National Museum of Scotland (Royal Scottish Museum)
   (Collections of Carboniferous plants)
3. Field Museum of Natural History, Chicago, U.S.A.
   (Collections of Carboniferous, Cretaceous, Tertiary plants and insects)
4. Indiana University, Biology Collections, Bloomington, Indiana U.S.A.
   (Collections of Cretaceous and Tertiary plants)
5. National Museum of Czechoslovakia, Prague, Czechoslovakia
   (Collections of Cretaceous and Tertiary plants)
6. Geological Collections, University of Queensland, Brisbane, Queensland, Australia
   (Collections of Permian and Triassic plants)
7. Queensland Museum, Brisbane, Queensland, Australia
   (Collections of Permian and Triassic plants)
8. Natural History Museum, Sydney, New South Wales, Australia
   (Collections of Carboniferous, Permian and Triassic plants)
9. Natural History Museum, Buenos Aires, Argentina
   (Collections of Jurassic and Cretaceous plants)

REFERENCES

Almond, J.E. 1985 The Silurian–Devonian fossil record of the Myriapoda. *Phil. Trans. R. Soc. Lond.* B **309**, 227–237.

Alvin, K.L., Barnard, P.D.W., Harris, T.M., Hughes, N.F., Wagner, R.H. & Wesley, A. 1967 Gymnospermophyta. In *The fossil record*. Chapter 6 (ed. W. B. Harland *et al.*), pp. 247–268. Geology Society of London.

Axelrod, D.I. 1961 How old are the angiosperms? *Am. J. Sci.* **259**, 447–459.

Axelrod, D.I. 1970 The evolution of flowering plants. In *The evolution of life* (ed. S. Tax) pp. 227–305. University of Chicago Press.

Banks, H.P. 1981 Peridermal activity (wound repair) in an Early Devonian (Emsian) trimerophyte from Gaspé Peninsula, Canada. *Palaeobotanist* **28–29**, 20–25.

Banks, H.P. 1985 Early land plants. *Phil. Trans. R. Soc. Lond.* B **309**, 197–200.

Barthel, M. 1976 Die Rotliegendeflora Sachsens. *Abh. Staatlichen Mus. Mineral. Geol. Dresden* **24**, 1–190.

Baxendale, R.W. 1979 Plant-bearing coprolites from North American Pennsylvanian coal balls. *Palaeontology* **22**, 537–548.

Beerbower, R., Scheckler, S. & Van Valkenburgh, B. 1987 An entangled bank – The Smithsonian conference on the evolution of terrestrial ecosystems. *Palaios* **2**, 526–527.

Bernays, E.A. 1991 Evolution of insect morphology in relation to plants. *Phil. Trans. R. Soc. Lond.* B **333**, 257–264.

Berry, E.W. 1923 Pathological conditions among fossil plants. In *Paleopathology: an introduction to the study of ancient evidences of disease* (ed. R. L. Moodie), pp. 99–109. Urbana, Illinois: University of Illinois Press.

Berryman, A.A. 1986 *Forest insects: principles and practice of population management.* (279 pages.) New York: Plenum.

Blair, K.G. 1943 Scolytidae (Col.) from the Wealden Formation. *Entomologists' mon. Mag.* **79**, 59–60.

Boucot, A.J. 1990 *Evolutionary paleobiology of behavior and coevolution.* (727 pages.) Amsterdam: Elsevier.

Brenner, G.J. & Crepet, W.L. 1987 Paleotropical evolution of angiosperms in the Lower Cretaceous of northern Gondwana. *Palynology* **11**, 220.

Brongniart, C. 1876 Perforations observées dans deux moreaux de bois fossile. *Annls Soc. ent. Fr.* 5 ser, **18**, 215–220.

Brown, V.K. & Lawton, J.H. 1991 Herbivory and the evolution of leaf size and shape. *Phil. Trans. R. Soc. Lond.* B **333**, 265–272.

Brues, C.T. 1936 Evidences of insect activity preserved in wood. *J Paleontol.* **10**, 637–643.

Brues, C.T. 1946 *Insect dietary.* Cambridge, Massachusetts: Harvard University Press.

Burnham, L. 1983 Studies on Upper Carboniferous insects: 1. The Geraridae (Order: Protorthoptera). *Psyche* **90**, 1–57.

Butler, E.J. & Jones, S.G. 1949 *Plant pathology.* London: Macmillan.

Carpenter, F.M. 1965 Studies on the Carboniferous insects from Commentry, France. Part V. The genus Triplosoba. *Psyche* **70**, 120–128.

Carpenter, F.M. 1971 Adaptations among Palaeozoic insects. *Proc. North Am. Paleontol. Convention (1969)* **1**, 1236–1251.

Carpenter, F.M. 1977 Geological History and evolution of the insects. *Proc. 15th Int. Congr. Entomol.* 1976, 63–70.

Carpenter, F.M. & Burnham, L. 1985 The geological record of insects. *A. Rev. Earth Planet. Sci.* **13**, 297–314.

Carpenter, F.M. & Kukalova, J. 1964 The structure of the Protelytroptera, with description of a new genus from Permian strata of Moravia. *Psyche* **71**, 183–197.

Chaloner, W.G. 1967 Spores and land plant evolution. *Rev. Palaebot. Palynol.* **1**, 83–93.

Chaloner, W.G. 1970 The rise of the first land plants. *Biol. Rev.* **45**, 353–377.

Chaloner, W.G. 1976 The evolution of adaptive features in fossil exines. In *Evolutionary significance of the exine* (ed. I. K. Ferguson & J. Muller), pp. 1–14. Academic Press.

Chaloner, W.G. 1984 Plants, animals and time. *The Palaeobotanist* **32**, 197–202.

Chaloner, W.G. 1988 Early land plants – the saga of a great conquest. In *Proc. XIV Int. Bot. Congr.* (ed. W. Greuter & B. Zimmer), pp. 301–316, Konigstein/Taunus: Koeltz.

Chaloner, W.G. & Creber, G.T. 1990 Do fossil plants give a climatic signal? *J. Geol. Soc. Lond.* **147**, 343–350.

Chaloner, W.G., Harper, J.L. & Lawton, J.L. 1991*a* The evolutionary interactions of animals and plants. *Phil. Trans. R. Soc. Lond.* B **333**, 177–305.

Chaloner, W.G. & MacDonald, P. 1980 *Plants invade the land.* (18 pages.) Edinburgh: H.M.S.O.

Chaloner, W.G., Scott, A.C. & Stephenson, J. 1991*b* Fossil evidence for plant–arthropod interactions in the Palaeozoic and Mesozoic. *Phil. Trans. R. Soc. Lond.* B **333**, 177–186.

Chaloner, W.G. & Sheerin, A. 1979 Devonian megafloras. The Devonian System. *Spec. Pap. Palaeontol.* **23**, 145–161.

Chaloner, W.G. & Sheerin, A. 1981 The evolution of reproductive strategies in early land plant. In *Evolution today* (ed. G. C. E. Scudder & J. L. Reveal), pp. 93–101. Pittsburgh: Hunt Institute for Botanical Documentation.

Christiansen, K. 1964 Bionomics of Collembola. *A. Rev. Entomol.* **9**, 147–178.

Cichan, M.A. & Taylor, T.N. 1982 Wood-borings in *Premnoxylon*: Plant-animal interactions in the Carboniferous. *Palaeontol. Palaeoclimatol. Palaeoecol.* **39**, 123–127.

Cleal, C.J. & Shute, G.H. 1991 The Carboniferous pteridosperm frond *Neuropteris heterophylla* (Brongiart) Sternberg. *Bull. Br. Mus. nat. His. (Geol.)* **46**, 153–174.

Collinson, M.E. & Hooker, J. 1991 Fossil evidence of interactions between plants and plant-eating mammals. *Phil. Trans. R. Soc. Lond.* B **333**, 197–208.

Collinson, M.E. & Scott, A.C. 1987 Factors controlling the organization and evolution of ancient plant communities. In *Organization of communities, past and present* (ed. J. H. R. Gee & P. S. Giller), pp. 399–420. Oxford: Blackwell Scientific Publications.

Condon, M. & Whalen, M.D. 1983 A plea for collection and preservation of herbivore and pathogen damaged plant materials. *Taxon* **32**, 105–107.

Conway-Morris, S. 1981 Parasites and the fossil record. *Parasitology* **82**, 489–509.

Cooper-Driver, G.A. 1978 Insect-fern associations. *Entomol. exp. appl.* **24**, 310–316.

Cooper-Driver, G.A. 1985 Anti-predation strategies in pteridophytes – a biochemical approach. *Proc. R. Soc. Edinb.* **86B**, 397–402.

Crane, P.R. 1985 Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann. M. bot. Gdn* **72**, 716–793.

Crane, P.R., Friis, E.M. & Pedersen, K.P. 1986 Lower Cretaceous angiosperm flowers: fossil evidence on early radiation of dicotyledons. *Science, Wash.* **232**, 852–854.

Crane, P.R. & Jarzembowski, E.A. 1980 Insect leaf mines from the Palaeocene of southern England. *J. nat. Hist.* **14**, 629–636.

Creber, G.T. & Ash, S.R. 1990 Evidence of widespread fungal attack on Upper Triassic trees in the southwestern U.S.A. *Rev. Palaeobot. Palynol.* **63**, 189–195.

Crepet, W.L. 1974 Investigations of North American cycadeoids: the reproductive biology of Cycadeoidea. *Palaeontographica* B **148**, 144–169.

Crepet, W.L. 1979 Insect pollination: a palaeontological perspective. *BioScience* **29**, 102–108.

Crepet, W.L. 1984 Advanced (constant) insect pollination mechanisms: patterns of evolution and implications vis-a-vis angiosperm diversity. *Ann. Mo. bot. Gdn* **71**, 607–630.

Crepet, W.L. & Friis, E.M. 1987 The evolution of insect pollination in angiosperms. In: *The origins of angiosperms and their biological consequences* (ed. E. M. Friis, W. G. Chaloner & P. R. Crane), pp. 181–201. Cambridge University Press.

Crepet, W.L., Friis, E.M. & Nixon, K. 1991 Fossil evidence for the evolution of biotic pollination. *Phil. Trans. R. Soc. Lond.* B **333**, 187–195.

Crowson, R.A. 1970 *Classification and education.* London: Heinemann Educational Books Ltd.

Crowson, R.A. 1975 The evolutionary history for Coleoptera as documented by fossil and comparative evidence. *Atti. Congesso Naz. Ital. Ent. Bologna* **10**, 47–90.

Crowson, R.A. 1985 Comments on the insecta of the Rhynie Chert. *Entomol. Gener.* **11**, 97–98.

Crowson, R.A., Rolfe, W.D.I., Smart, J., Waterston, C.D., Willey, E.C. & Wootton, R.J. 1967 *Arthropoda: Chelicerata, Pycnogonida, Palaeoisopus, Myriapoda and Insecta. The Fossil Record.* Chapter 19, pp. 499–534. Geological Society of London.

De Witt West, T. 1962 Notes on the Oliver Collection of Carboniferous plants. 3. Wound reactions in a petiole of *Ankyropteris westphaliensis* Bertrand. *Ann. Mag. nat. Hist.* **13**, 185–191.

Dijkstra, S.J. & Pierart, P. 1957 Lower Carboniferous megaspores from the Moscow Basin. *Meded. geol. Sticht.* **11**, 5–19.

Doyle, J.A. & Donoghue, M.J. 1987 The origin of angiosperms: a cladistic approach. In *The origins of angiosperms and their biological consequences* (ed. E. M. Friis, W. G. Chaloner & P. R. Crane), pp. 17–49, Cambridge University Press.

Edmunds, G.F. Jr. & Alstad, D.N. 1978 Coevolution of insect herbivores and conifers. *Science, Wash.* **199**, 941–945.

Edwards, D. 1980 Early land floras. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 55–85. Systematics Association Special Volume 15. London: Academic Press.

Edwards, D. & Burgess, N.D. 1990 Terrestrialization: Plants. In *Palaeobiology: a synthesis* (ed. D. E. G. Briggs & P. R. Crowther), pp. 60–64. Oxford: Blackwell Scientific Publications.

Edwards, D. & Fanning, U. 1985 Evolution and environment in the late Silurian-early Devonian: the rise of the pteridophytes. *Phil. Trans. R. Soc. Lond.* B **309**, 147–165.

Edwards, D., Fanning, U. & Richardson, J.D. 1986 Stomata and sterome in early land plants. *Nature, Lond.* **323**, 438–440.

Edwards, D. & Feehan, J. 1980 Records of *Cooksonia*-type sporangia from late Wenlock strata in Ireland. *Nature, Lond.* **287**, 41–42.

Edwards, D.S. 1980 Evidence for the sporophytic status of the Lower Devonian plant *Rhynia gwynne-vaughanii* Kidson and Lang. *Rev. Palaeobot. Palynol.* **29**, 177–188.

Edwards, P.J. & Wratten, S.D. 1980 Ecology of insect-plant interactions. *Inst. Biol. stud. Biol.* **121.**

Edwards, P.J. & Wratten, S.D. 1983 Wound induced defences in plants and their consequences for patterns of insect grazing. *Oecologia* **59**, 88–93.

Edwards, P.J. & Wratten, S.D. 1985 Induced plant defences against insect grazing: fact or artefact? *Oikos* **44**, 70–74.

Elton, C.S. 1973 The structure of invertebrate populations inside neotropical rainforest. *J. Anim. Ecol.* **42**, 55–104.

Faigri, K. & Van der Pijl, L. 1979 *The principles of pollination biology*, 3rd edn. (291 pages.) Oxford.

Feinsinger, P. 1983 Coevolution and pollination. In *Coevolution* (ed. D. J. Futuyma & M. Slatkin), pp. 282–310. Sunderland, Massachusetts: Sinauer Associates.

Fourcroy, M. & Braun, C. 1967 Observations on galls of *Aulax* on *Glechoma. Marcellia* **34**, 3–30.

Frederiksen, N.O. 1972 The rise of the Mesophytic flora. *Geosci. Man* **4**, 17–28.

Friis, E.M., Chaloner, W.G. & Crane, P.R. (eds) 1987 *The origins of angiosperms and their biological consequences.* Cambridge University Press.

Friis, E.M. & Crepet, W.L. 1987 Time and appearance of floral features. In *The origins of angiosperms and their biological consequences* (ed. E. M. Friis, W. G. Chaloner & P. R. Crane), pp. 145–179, Cambridge University Press.

Fritsch, A. 1882 Fossile Arthropoden aus der Steinkohlen- und Kreideformation Bohemens. *Beitr. Paläont. Öst.-Ung.* **2**, 1–7.

Galtier, J. 1989 Morphology and phylogenetic relationships of early Pteridosperms. In *Origin and evolution of gymnosperms* (ed. C. B. Beck), pp. 135–176. New York: Columbia University Press.

Galtier, J. & Scott, A.C. 1985 Diversification of early ferns. *Proc. R. Soc. Edin.* **86B**, 289–301.

Gensel, P.G. & Andrews, H.N. 1984 *Plant life in the Devonian.* New York: Praeger Publishing.

Gerson, U. 1979 The associations between pteridophytes and arthropods. *Fern Gaz.* **12**, 29–45.

Geyer, G. & Kelber, K.P. 1987 Flugelreste und Lebensspuren von Insekten aus dem Unteren Keuper Mainfrankens. *Neues Jb. Geol. Paläont. Abh.* **174**, 331–355.

Gilbert, L.E. 1979 Development of theory in the analysis of insect-plant interactions. In *Analysis of ecological systems* (ed. D. J. Horn, G. R. Stairs & R. D. Mitchell), pp. 117–154. Ohio State University Press.

Gillanders, A.T. 1908 *Forest entomology.* (422 pages.) Edinburgh: W. Blackwood & Sons.

Gray, J. 1985 The microfossil record of early land plants: advances in understanding of early terrestrialization. In *Evolution and environment in the late Silurian and early Devonian* (ed. W. G. Chaloner & J. Lawson) (*Phil. Trans. R. Soc. Lond.* B **309**), pp. 167–195. London: The Royal Society.

Gray, J., Massa, D., Boucot, A.J. 1982 Caradocian land plant microfossils from Libya. *Geology* **10**, 197–201.

Greenslade, P.J.M. 1988 Reply to R. A. Crowson's comments on Insecta in the Rhynie Chert. *Entomol. Gener.* **13**, 115–117.

Greenslade, P.J.M. & Whalley, P.E.S. 1986 The systematic position of *Rhyniella praecursor* Hirst & Maulik (Collembola). The earliest known Hexapod. *2nd Int. Sem. Apterogota*, pp. 319–332. Italy: University of Sienna.

Grogan, W.L. & Szadziewski, R. 1988 A new biting midge from the Upper Cretaceous Cenomanian amber from New Jersey, U.S.A. Diptera, Ceratopognidae. *J. Paleontol.* **62**, 808–812.

Hagen, H.A. 1882 Fossil insects of the Dakota Group. *Nature, Lond.* **25**, 265–266.

Hamilton, W.D. 1978 Evolution and diversity under bark. In *Diversity of insect faunas* (ed. L. A. Mound & N. Waloff) (*Symp. R. Entomol. Soc. Lond.* **9**), pp. 154–175. London: Blackwell.

Harland, W.B., Armstrong, R.L., Cox, A.V., Craig, L.E., Smith, A.G. & Smith, D.G. 1990 *A geologic time scale 1989.* (263 pages.) Cambridge University Press.

Harris, T.M. 1957 How we study fossil plants: *Caytonia. New Biology* **22**, 24–38.

Haslett, J.R. 1983 A photographic account of pollen digestion by adult hoverflies. *Physiol. Entomol.* **8**, 167–171.

Hering, E.M. 1951 *Biology of the leaf miners.* (420 pages.) The Netherlands: Junk.

Hickey, L.J. & Doyle, J.A. 1977 Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev.* **43**, 3–104.

Hill, C.R. 1987 Jurassic *Angiopteris* (Marattiales) from North Yorkshire. *Rev. Palaeobot. Palynol.* **51**, 65–93.

Hirst, S. & Maulik, S. 1926 On some arthropod remains from the Rhynie Chert (Old Red Sandstone). *Geol. Mag.* **63**, 69–71.

Hocking, B. 1975 Ant-plant mutualism: evolution and energy. In *Coevolution of animals and plants* (ed. L. E. Gilbert & P. H. Raven), pp. 78–90. University of Texas Press.

Holden, H.S. 1910 Note on wounded *Myeloxylon*. New Phytol. **9**, 253–257.

Hollick, A. 1906 Insect borings in Cretaceous Lignite from Kreischerville. *Proc. Staten Island Ass. Arts Sci.* **1**, 23–24.

Hsu Ten, Zhu Jianen, Chen, Ye, Duan Shuying, Hu Yufan & Zhu Weiqing 1974 New genera and species of late Triassic plants from Yingjen, Yunan. *Acta bot. sinica* **16**, 266–278.

Hughes, N.F. 1976 *Palaeobiology of Angiosperm origins*. Cambridge University Press.

Hughes, N.F., McDougall, A.B. & Chapman, J.L. 1991 Exceptional new record of Cretaceous Hauterivian Angiospermid pollen from Southern England. *J. Micropalaeontol.* **10**, 75–82.

Hughes, N.F. & Smart, J. 1967 Plant-insect relationships in Palaeozoic and later time. In *The fossil record* (ed. W. B. Harland *et al.*), pp. 107–117. Geological Society of London.

Jacot, A.P. 1939 Reduction of spruce and fir litter by minute animals. *J. forestry* **37**, 858–860.

Jarzembowski, E.A. 1981 An early Cretaceous termite from southern England (Isoptera: Hodotermidae). *System. Entomol.* **6**, 91–96.

Jarzembowski, E.A. 1989 A fossil aphid (Insecta: Hemiptera) from the Early Cretaceous of southern England. *Cret. Res.* **10**, 239–248.

Jarzembowski, E.A. 1990 A boring beetle from the Wealden of the Weald. In *Evolutionary paleobiology of behavior and coevolution* (ed. A. J. Boucot), pp. 373–376. Amsterdam: Elsevier.

Jeppson, L.R., Keifer, H.H. & Baker, E.W. 1975 *Mites injurious to economic plants*. University of California Press.

Jeram, A.J., Selden, P.A. & Edwards, D. 1990 Land animals in the Silurian: Arachnids and myriapods from Shropshire, England. *Science, Wash.* **250**, 658–661.

Juniper, B.E. & Jeffrees, C.E. 1983 *Plant surfaces*. (93 pages.) London: Edward Arnold.

Kelber, K.-P. & Geyer, G. 1989 Lebensspuren von Insekten an Pflanzen des Unteren Keupers, *Courier Forschungsinstitut Senckenberg* **109**, 165–174.

Kerp, J.H.F. 1988 Aspects of Permian Palaeobotany and Palynology. X. The west- and central European species of the genus *Autunia* Krasser emend. Kerp (Peltaspermaceae) and the form-genus *Rhachiphyllum* Kerp (callipterid foliage). *Rev. Palaeobot. Palynol.* **54**, 249–360.

Kerp, J.H.F. & Haubold, H. 1988 Aspects of Permian Palaeobotany and Palynology. VIII. On the reclassification of the western and central European species of the form-genus *Callipteris* Brongniart 1849 non Bory 1804. *Rev. Palaeobot. Palynol.* **54**, 135–150.

Kevan, P.G., Chaloner, W.G. & Savile, D.B.O. 1975 Interrelationships of early terrestrial arthropods and plants. *Palaeontology* **18**, 391–417.

Khan, M.B. & Harborne, J.B. 1990 Induced alkaloid defence in *Atropa acuminata* in response to mechanical and herbivore leaf damage. *Chemoecology* **1**, 77–80.

Kidston, R. & Lang, W.H. 1921 On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part IV. Restoration of the vascular cryptograms and discussion of their bearing on the general morphology of the Pteridophyta and the origin and organization of land plants. *Trans. R. Soc. Edinb.* **51**, 831–854.

Kidston, R. & Lang, W.H. 1921 On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part V. The thallophyta occurring in the peat bed; the succession of the plants through the vertical section of the beds, and the conditions of accumulation and preservation of the deposit. *Trans. R. Soc. Edinb.* **51**, 855–902.

Kinsolver, J.G. & Koehl, M.A.R. 1984 Aerodynamics, thermoregulation, and the evolution of the insect wings: differential scaling and evolutionary change. *Evolution* **39**, 488–504.

Kjellesvig-Waering, E.N. 1986 A restudy of fossil Scorpionida of the world. *Paleontogr. Am.* **55**, 1–287.

Knowlton, F.H. 1917 A fossil flora from the Frontier Formation of southwestern Wyoming. *U.S. geol. Surv. prof. Pap.* **108F**, 73–107.

Kogan, M. 1976 The role of chemical factors in insect/plant relationships. *Proc. 15th Int. Congr. Entomol. Wash.* 211–227.

Krassilov, V.A. & Rasinitsyn, A.P. 1982 A unique discovery: pollen in the intestines of early Cretaceous sawflies. *Paleontol. Zhournal* **561**(4), 83–96. [In Russian.]

Kuhnelt, W. 1955 An introduction to the study of soil animals. In *Soil zoology* (ed. D. K. McE. Kevan), pp. 3–9. London: Butterworths.

Kuhnelt, W. 1976 *Soil Biology*, 2nd edn. Michigan State University Press.

Kukalova, J. 1965 Permian Protoelytroptera, Coleoptera, and Protorthoptera of Moravia. *Sb. Geol. Ved. Paleontol.* **6**, 61–98. [In Russian.]

Kukalova, J. 1970 Revisional study of the order Palaeodictyoptera in the Upper Carboniferous shales of Commentry, France. Part II. *Psyche* **77**, 1–44.

Kukalova-Peck, J. 1974 Wing folding in the Palaeozoic insect order Diaphanopterodea (Paleoptera), with a description of new members of the family Elmoidae. *Psyche* **81**, 315–333.

Kukalova-Peck, J. 1978 Origin and evolution of insect wings, and their relation to metamorphosis, as documented by the fossil record. *J. Morphol.* **156**, 53–125.

Kuster, E. 1911 *Die Gallen der Pflanzen*. (437 pages.) Leipzig, S. Hirzel.

Labandeira, C.C. 1986 Mouthpart design and basic ways that insects have partitioned recent food reserves: implications for the macroevolutionary history of a morphologically diverse group. *Fourth North Am. Paleontol. Convention, Annual meeting, San Antonio, Texas*, p. 663. (Abstract.)

Labandeira, C.C., Beall, B.S. & Heuber, F.M. 1988 Early insect diversification: evidence from a Lower Devonian bristletail from Quebec. *Science, Wash.* **242**, 913–916.

Lang, W.H. 1937 On the plant remains from the Downtonian of England and Wales. *Phil. Trans. R. Soc. Edinb.* B **227**, 245–291.

Lawton, J.H. 1978 Host-plant influences on insect diversity: the effects of space and time. In *Diversity of insect faunas* (ed. L. A. Mound & N. Walloff). (*Symp. R. Entomol. Soc. Lond.* **9**), pp. 105–125. London: Blackwell.

Lesnikowska, A.D. 1990 Evidence of herbivory in tree-fern petioles from the Calhoun Coal (Upper Pennsylvanian) of Illinois. *Palaios* **5**, 76–80.

Lesquereux, L. 1892 The flora of the Dakota Group. *U.S. Geol. Surv. Monogr.* **17**, 1–400.

Lovendal, E.A. 1898 *De Danske Barkbiller* pp. 114–117. Kjobenhavn.

Luxton, M. 1972 Studies on the oribatid mites of a Danish beechwood soil. 1. Nutritional biology. *Pedobiologia* **12**, 434–463.

Maresquelle, H.J. & Meyer, J. 1965 Physiologie et morphogenese des galles d'origine animale (Zoocecidies). *Handbüch der Pflanzenphysiologie.* **15**(2), 280–329.

Martin, M.M. 1991 The evolution of cellulose digestion in insects. *Phil. Trans. R. Soc. Lond.* B **333**, 281–288.

Martynov, A.V. 1928 A new fossil form of Phasmatodea from Galkino (Turkestan) and on Mesozoic phasmids in general. *Ann. Mag. nat. Hist.* **1**, 319–328. [In Russian.]

Martynov, A.V. 1937 Studies on the geological history and phylogeny of the insects (Pterygota), part 1. *Trudy Paleontol. Inst. Akad. Nauk SSSR* **7**, 1–148. [In Russian.]

Martynova, O.M. 1962 Order Phasmatodea. In *Principles of palaeontology* (ed. B. B. Rohdendorf), pp. 151–160. Akad. Nauk. SSSR. [In Russian.]

Meyen, S.V. 1984 Is *Thuringia* a gymnosperm synangium or coprolite? *Z. geol. Wiss. Berlin* **12**, 269–270.

Meyer, J. 1987 *Plant galls and gall inducers.* (291 pages.) Berlin: Gebruder Borntraeger.

Miller, P.F. 1974 Competition between *Ophyiulus pilosus* (Newport) and *Iulus scandinavius* Latzel. *Symp. Zool. Soc. Lond.* **32**, 553–574.

Müller, A.H. 1982 Uber Hyponomefossiler und rezenter Insekten, erster Beitrag. *Freiberger Forschungsheft* **C 366**, 7–27.

Mundel, P. 1979 The centipedes (Chilipoda) of Mazon Creek. In: M. H. Nitecki (Editor), *Mazon Creek fossils* pp. 361–368. Academic Press, New York.

Needham, J.G., Frost, S.W. & Tothill, B.H. 1928 Leaf-Mining Insects. (351 pages.) London: Bailliere, Tindal & Cox.

Norton, R.A., Bonamo, P.M., Grierson, J.D. & Shear, W.A. 1988 Oribatid mite fossils from a terrestrial deposit near Gilboa, New York. *J. Paleontol.* **62**, 259–269.

Paulusse, J.H.M. & Jeansson, C.Y. 1977 Structuration du sol par les Diplopods étude experimentale et microscopique. *Ecol. Bull.* **25**, 484–488.

Phillips, T.L. & Peppers, R.A. 1984 Changing patterns of Pennsylvanian coal swamp vegetation and implications of climatic control on coal occurrence. *Int. J. Coal Geol.* **3**, 205–255.

Piearce, T.G. 1989 Acceptability of pteridophyte litters to *Lumbricus terrestris* and *Oniscus asellus*, and implications for the nature of ancient soils. *Pedobiologia* **33**, 91–100.

Plumstead, E.P. 1963 The influence of plants and environment on the developing animal life in Karoo times. *S. Afr. J. Sci.* **59**, 147–152.

Potonié, H. 1893 Die Flora des Rothliegenden von Thuringen. *Abh. preuss. geol. Landesanst.* **9**, 1–298.

Potonié, R. 1921 Mitteilungen uber mazerierte kohlige Pflanzenfossilien. *Z. Bot.* **13**, 79–88.

Rasnitsyn, A.P. 1964 New Triassic Hymenoptera from Middle Asia. *Paleontol. Zhournal* **1964** (1), 88–96. [In Russian.]

Rasnitsyn, A.P. 1969 The origin and evolution of Hymenoptera. *Trudy Paleontol. Inst. Akad. Nauk. SSSR.* **123**, 1–196. [In Russian.]

Rasnitsyn, A.P. 1975 Hymenoptera Apocrita of the Mesozoic. *Trudy Paleontol. Inst. Akad. Nauk SSSR* **147**, 1–132. [In Russian.]

Rasnitsyn, A.P. 1981 A modified paranotal theory of insect wing origin. *J. Morphol.* **168**, 331–338.

Raven, J.A. 1983 Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Adv. Ecol. Res.* **13**, 135–234.

Retallack, G. 1990 The work of dung beetles and its fossil record. In *Evolutionary paleobiology of behavior and coevolution* (ed. A. J. Boucot), pp. 214–226. Amsterdam: Elsevier.

Retallack, G. & Feakes, C. 1987 Trace fossil evidence for Late Ordovician animals on land. *Science, Wash.* **235**, 61–63.

Retallack, G.J. 1981 Fossil soils: indicators of ancient terrestrial environments. In *Paleobotany, paleoecology and evolution* (ed. K. J. Niklas), pp. 55–102. New York: Praeger.

Rex, G.M. & Galtier, J. 1986 Sur l'evidence d'interactions animal-vegetal dans le Carbonifère inférieur Français. *C. r. Acad. Sci., Paris* (Ser 303 (II)) **17**, 1623–1626.

Rex, G.M. & Scott, A.C. 1987 The sedimentology, palaeoecology and preservation of the Lower Carboniferous plant deposits at Pettycur, Fife, Scotland. *Geol. Mag.* **124**, 43–66.

Robaux, P., Jeanson, C.Y. & Barbier, D. 1977 Microstructures construites par un acarien *Tyrophagus putrescentiae* dans une argile. Etude experimentale et microscopique. *Ecol. Bull.* **25**, 489–493.

Robbins, E.I., Porter, K.G. & Haberyan, K.A. 1985 Pellet microfossils: Possible evidence for metazoan life in Early Proterozoic time. *Proc. natn. Acad. Sci. U.S.A.* **82**, 5809–5813.

Rohdendorf, B.B. 1964 Historical development of the Diptera. *Trudy Paleontol. Inst. Akad. Nauk SSSR* **100**, 1–311. [In Russian.]

Rohdendorf, B.B. 1974 *The historical development of the Diptera.* (360 pages.) University of Alberta Press.

Rohdendorf, B.B. & Rasnitsyn, A.P. 1980 Historical development of insects. *Trudy. Paleontol. Inst. Akad. Nauk SSSR* **178**, 1–268.

Rolfe, W.D.I. 1980 Early invertebrate terrestrial faunas. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen). pp. 117–157. London: Academic Press.

Rolfe, W.D.I. 1982 Ancient air breathers. *Field Mus. nat. Hist. Bull.* **53**, 12–16.

Rolfe, W.D.I. 1985*a* Aspects of the Carboniferous terrestrial arthropod community. *Proc. IXth Int. Congr. Carbonif. Stratigr. Geol.* (*Urbana, 1979*) **5**, 303–316.

Rolfe, W.D.I. 1985*b* Early terrestrial arthropods: a fragmentary record. *Phil. Trans. R. Soc. Lond.* B **309**, 207–218.

Rolfe, W.D.I. 1988 Early life on land: the East Kirkton discoveries. *Earth Sci. Conserv.* **25**, 22–25.

Rolfe, W.D.I. 1990 Seeking the arthropods of Eden. *Nature, Lond.* **348**, 112–113.

Rolfe, W.D.I., Durant, G., Fallick, A.E., Hall, A.J., Large, Scott, A.C., Smithson, T.R. & Walkden, G. 1990 An early terrestrial biota preserved by Visean vulcanicity in Scotland. In: *Volcanism and fossil biotas* (ed. M. Lockey & A. Rice). (*Geol. Soc. Am., spec. Pub.* **244**), pp. 13–24.

Rolfe, W.D.I. & Ingham, J.K. 1967 Limb structure, affinity and diet of the Carboniferous "centipede" *Arthropleura*. *Scott. J. Geol.* **3**, 118–124.

Rothwell, G. & Scheckler, S.E. 1989 Biology of ancestral gymnosperms. In *Origin and evolution of gymnosperms* (ed. C. B. Beck), pp. 85–134. New York: Columbia University Press.

Rothwell, G.W. & Scott, A.C. 1983 Coprolites within the marattiaceous fern stems (*Psaronius magnificus*) from the Upper Pennsylvanian of the Appalachian Basin, U.S.A. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **41**, 227–232.

Rothwell, G.W. & Scott, A.C. 1988 *Heterotheca* Benson; Lyginopterid pollen organs or coprolites? *Bull. Br. Mus. nat. His.* (Geol.) **44**, 41–43.

Rozefelds, A.C. 1985 The first records of fossil leaf mining from Australia. *Rec. N.Z. geol. Surv.* **9**, 80–81.

Rozefelds, A.C. 1988 Lepidoptera Mines in *Pachypteris* leaves (Corystospermaceae: Pteridospermophyta) from the Upper Jurassic/Lower Cretaceous Battle Camp Formation North Queensland. *Proc. R. Soc. Queensland* **99**, 77–81.

Rozefelds, A.C. & Sobbe, I. 1987 Problematic insect leaf mines from the Upper Triassic Ipswich Coal Measures of southeastern Queensland, Australia. Alcheringa **11**, 51–57.

Scott, A.C. 1977 Coprolites containing plant material from the Carboniferous of Britain. *Palaeontology* **20,** 59–68.

Scott, A.C. 1980 The ecology of some Upper Palaeozoic floras. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 87–115. London: Academic Press.

Scott, A.C. 1984 The early history of life on land. *J. biol. Educ.* **18**, 207–219.

Scott, A.C. 1990 Preservation, evolution, and extinction of plants in the Lower Carboniferous volcanic sequences in Scotland. In *Volcanism and fossil biotas* (ed. M. Lockley & A. Rice) (*Geol. Soc. Am. spec. Pub.* **244**), pp. 25–38.

Scott, A.C., Chaloner, W.G. & Paterson, S. 1985 Evidence of pteridophyte-arthropod interactions in the fossil record. *Proc. R. Soc. Edinb.* **86B**, 133–140.

Scott, A.C. & Galtier, J. 1985 Distribution and ecology of early ferns. *Proc. R. Soc. Edinb.* **86B**, 141–149.

Scott, A.C., Meyer-Berthaud, B., Galtier, J., Rex, G.M., Brindley, S.A. & Clayton, G. 1986 Studies on a new Lower Carboniferous flora from Kingswood, near Pettycur, Fife, Scotland. 1. Preliminary report. *Rev. Palaeobot. Palynol.* **48**, 161–180.

Scott, A.C. & Paterson, S. 1984 Techniques for study of plant/arthropod interactions in the fossil record. *Geobios Mémoire Spécial* **8**, 449–455.

Scott, A.C. & Taylor, T.N. 1983 Plant/animal interactions during the Upper Carboniferous. *Bot. Rev.* **49**, 259–307.

Scourfield, D.J. 1940 The oldest known fossil insect (*Rhyniella praecursor* Hirst & Maulik) – further details from additional specimens. *Proc. Linn. Soc. Lond.* **152**, 113–131.

Selden, P.A. 1990 Lower Cretaceous spiders from the Sierra de Montsech, north-east Spain. *Palaeontology* **33**, 257–286.

Selden, P.A. & Edwards, D. 1989 Colonisation of the land. In *Evolution and the fossil record* (ed. K. C. Allen & D. E. G. Briggs), pp. 122–152. London: Belhaven Press.

Selden, P.A., Shear, W.A. & Bonamo, P.M. 1991 A spider and other arachnids from the Devonian of New York, and re-interpretations of Devonian Araneae. *Palaeontology* **34**, 241–281.

Seward, A.C. 1898 *Fossil Plants*, vol. 1. Cambridge University Press.

Seward, A.C. 1923 The use of the microscope in palaeobotanical research. *Jl R. microsc. Soc.* **1923**, 299–302.

Seward, A.C. 1924 On a new species of *Tempskya* from Montana: *Tempskya knowltoni* Sp. Nov. *Ann. Bot.* **38**, 485–505.

Sharov, A.G. 1966 *Basic arthropodan stock, with special reference to insects*. Oxford: Pergamon Press.

Sharov, A.G. 1971 *Phylogeny of the Orthopteridea*. Jerusalem: Keter Press.

Sharov, A.G. 1973 Morphological features and way of life of the Palaeodictyoptera. *Doklady Chteniya Pamyati Nikolaya Aleksahdrovicha Kholodkovskogo* **23**, 49–63. [In Russian.]

Shear, W.A. 1986 A fossil fauna of early terrestrial arthropods from the Givetian (Upper Middle Devonian) of Gilboa, New York, U.S.A. *Actas X Cong. Int. Aracnol. Jaca/Espana* **1**, 387–392.

Shear, W.A., Bonamo, P.M., Grierson, J.D., Rolfe, W.D.I., Smith, E.L. & Norton, R.A. 1984 Early land animals in North America: Evidence from Devonian age arthropods from Gilboa, New York. *Science, Wash.* **224**, 492–494.

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

Shear, W.A., Selden, P.A., Rolfe, W.D.I., Bonamo, P.M. & Grierson, J.D. 1987 New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). *Am. Mus. Novitates* **2901**, 1–74.

Sherwood-Pike, M.A. 1990 Fossil evidence for fungus-plant interactions. In *Evolutionary paleobiology of behavior and coevolution* (ed. A. J. Boucot), pp. 118–123. Amsterdam: Elsevier.

Sherwood-Pike, M.A. & Gray, J. 1985 Silurian fungal remains: probable records of the class Ascomycetes. *Lethaia* **18**, 1–220.

Shorthouse, J.D. 1973 The insect community associated with rose galls of *Diplolepis polita* (Cynipidae, Hymenoptera). *Quaest. Ent.* **9**, 55–98.

Shorthouse, J.D. 1982 Resource exploitation by gall wasps of the genus *Diplolepis*. *Proc. Int. Symp. Insect-Plant Relationships* **5**, 193–198.

Shorthouse, J.D. 1986 Significance of nutritive cells in insect galls. *Proc. Entomol. Soc. Wash.* **88**, 368–375.

Skalski, A.W. 1976 A new member of the family Micropterygidae (Lepidoptera) from the Lower Cretaceous of Transbaikalia. *Paleontol. Zhournal.* **1979**(2), 90–97.

Smart, J. 1971 Palaeoecological factors affecting the Original Winged Insects. *Proc. XIII Int. Congr. Entomol., Moscow 1968* **1**, 304–306.

Smart, J. & Hughes, N.F. 1973 The insect and the plant: progressive paleontological integration. In *Insect/plant relationships* (ed. H. F. Van Emden) (Symp. R. Entomol. Soc., *Lond.* **6**), pp. 143–155.

Snodgrass, R.E. 1935 *Principles of Insect Morphology*. (667 pages.) New York: McGraw-Hill.

Solem, A. & Yochelson, E.L. 1979 North American Paleozoic land snails, with a summary of other Paleozoic nonmarine snails. *U.S. geol. Surv. prof. Pap.* **1072**, 1–42.

Southwood, T.R.E. 1973 The insect/plant relationship – an evolutionary perspective. In *Insect/plant relationships* (ed. H. F. Emden) (*Symp. R. Entomol. Soc. Lond.* **6**), pp. 3–30.

Southwood, T.R.E. 1984 Insect-plant adaptations. In *Origins and development of adaptation* (Ciba Foundation Symposium **102**), pp. 138–151. London: Pitman.

Southwood, T.R.E. 1985 Interactions of plants and animals: patterns and process. *Oikos* **44**, 5–11.

Stephenson, J. 1991 Evidence of plant/insect interactions in the Late Cretaceous and Early Tertiary. Ph.D. thesis, University of London.

Stewart, W.N. 1983 *Paleobotany and the evolution of plants*. (405 pages.) Cambridge University Press.

Stidd, B.M. 1971 Morphology and anatomy of the frond of *Psaronius*. *Palaeontographica* **134B**, 87–123.

Stopes, M.C. 1907 A note on a wounded *Calamites*. *Ann. Bot.* **21**, 277–280.

Straus, A. 1977 Gallen, Minen und andere Frasspuren im Pliozan von Willerhausen am Harz. *Verh. bot. Ver. Prov. Brandenb.* **113,** 41–80.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. 1984 *Insects on plants: community patterns and mechanisms*. (313 pages.) Oxford: Blackwell Scientific Publications.

Sukatsheva, D. 1982 Istoricheskoye Razuitiye Otryada Rucheinikov. *Tr. Inst. Akad. Nauk. S.S.S.R.* **197**, 1–111.

Taylor, T.N. 1981 *Paleobotany: an introduction to fossil plant biology*. (589 pages.) New York: McGraw Hill.

Taylor, T.N. 1988*a* The origin and evolution of angiosperms. *ISI atlas of science: animal and plant sciences*, pp. 47–50.

Taylor, T.N. 1988*b* The origin of land plants: some answers, more questions. *Taxon* **37**, 805–833.

Thomas, B.A. 1985 Pteridophyte success and past biota – a palaeobotanist's approach. *Proc. R. Soc. Edinb.* **86B**, 423–430.

Thomas, B.A. & Spicer, R.A. 1987 *The evolution and palaeobiology of land plants*. (309 pages.) London: Croom Helm.

Tillyard, R.J. 1922 Some new Permian insects from Belmont, New South Wales, in the collection of Mr. John Mitchell. *Proc. Linn. Soc. New South Wales* **47**, 279–292.

Trant, C.A. & Gensel, P.G. 1985 Branching in *Psilophyton*: a new species from the Lower Devonian of New Brunswick, Canada. *Am. J. Bot.* **72**, 1256–1273.

Tschudy, R.H. 1981 Geographic distribution and dispersal of Normapolles genera in North America. *Rev. Palaeobot. Palynol.* **35**, 283–314.

Upchurch, G.R. Jr. & Wolfe, J.A. 1987 Mid-Cretaceous to Early Tertiary vegetation and climate: evidence from fossil leaves and woods. In *The origins of angiosperms and their biological consequences* (ed. E. M. Friis, W. G. Chaloner & P. Crane), pp. 75–105. Cambridge University Press.

Uvarov, B. 1966 *Grasshoppers and locusts.* Cambridge University Press.

Van Amerom, H.W.J. 1977 *Phagophytichnus ekowsskii* nov. ichnogen. & nov. ichnosp., eine missbildung infolge von insektenfrass, aus dem Spanischen Stephanien (Provinz Leon). *Leid. geol. Meded.* **38**, 181–184.

Van Amerom, H.W.J. & Boersma, M. 1971 A new find of the ichnofossil *Phagophytichnus ekowskii* Van Amerom. *Geologie Mijnb.* **50**, 667–670.

Van Emden, H.F. & Way, M.J. 1973 Host plants in the population dynamics of insects. In *Insect/plant relationships* (ed. H. F. Van Emden) (*Symp. R. Entomol. Soc. Lond.* **6**), pp. 181–199. London: Blackwell.

Walker, M.V. 1938 Evidence of Triassic insects in the Petrified Forest National Monument, Arizona. *Proc. U.S. natn. Mus.* **85**, 137–141.

Wallace, H.R. 1973 *Nematode ecology and plant disease.* London: Edward Arnold.

Watson, J. 1977 Some Lower Cretaceous conifers of the Cheirolepidiaceae from the U.S.A. and England. *Palaeontology* **20**, 715–749.

Whalley, P. 1986 A review of the current evidence of Lepidoptera in the Mesozoic. *Biol. J. Linn. Soc.* **28**, 253–271.

Whalley, P. & Jarzembowski, E.A. 1981 A new assessment of *Rhyniella*, the earliest known insect, from the Devonian of Rhynie, Scotland. *Nature, Lond.* **291**, 317.

Wigglesworth, V.B. 1976 The evolution of insect flight. In *Insect flight* (ed. R. C. Rainey) (*Symp. R. entomol. Soc.* **7**), pp. 255–269.

Wilkinson, M. 1930 Note on a wounded lepidodendroid axis. *Mem. Proc. Manchester Lit. Soc.* **73**, 75–82.

Wolfe, J.A. 1978 A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *Am. Sci.* **66**, 694–703.

Wootton, R.J. 1976 The fossil record of insect flight. In *Insect flight* (ed. R. C. Rainey) (*Symp. R. entomol. Soc.* **7**), 235–254.

Wootton, R.J. 1981 Palaeozoic insects. *A. Rev. Entomol.* **26**, 319–344.

Wootton, R.J. 1988 The historical ecology of aquatic insects: an overview. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **62**, 477–492.

Zherikhin, V.V. 1980 In *Historical development of insects* (ed. B. B. Rohdendorf & A. P. Rasnitsyn) (*Trudy Paleontol. Inst. Akad. Nauk SSSR* **178**), pp. 1–268.

Zhou Zhiyan & Zhang Bole 1989 A sideritic *Protocupressinoxylon* with insect borings and frass from the Middle Jurassic, Henan, China. *Rev. Palaeobot. Palynol.* **59**, 133–143.

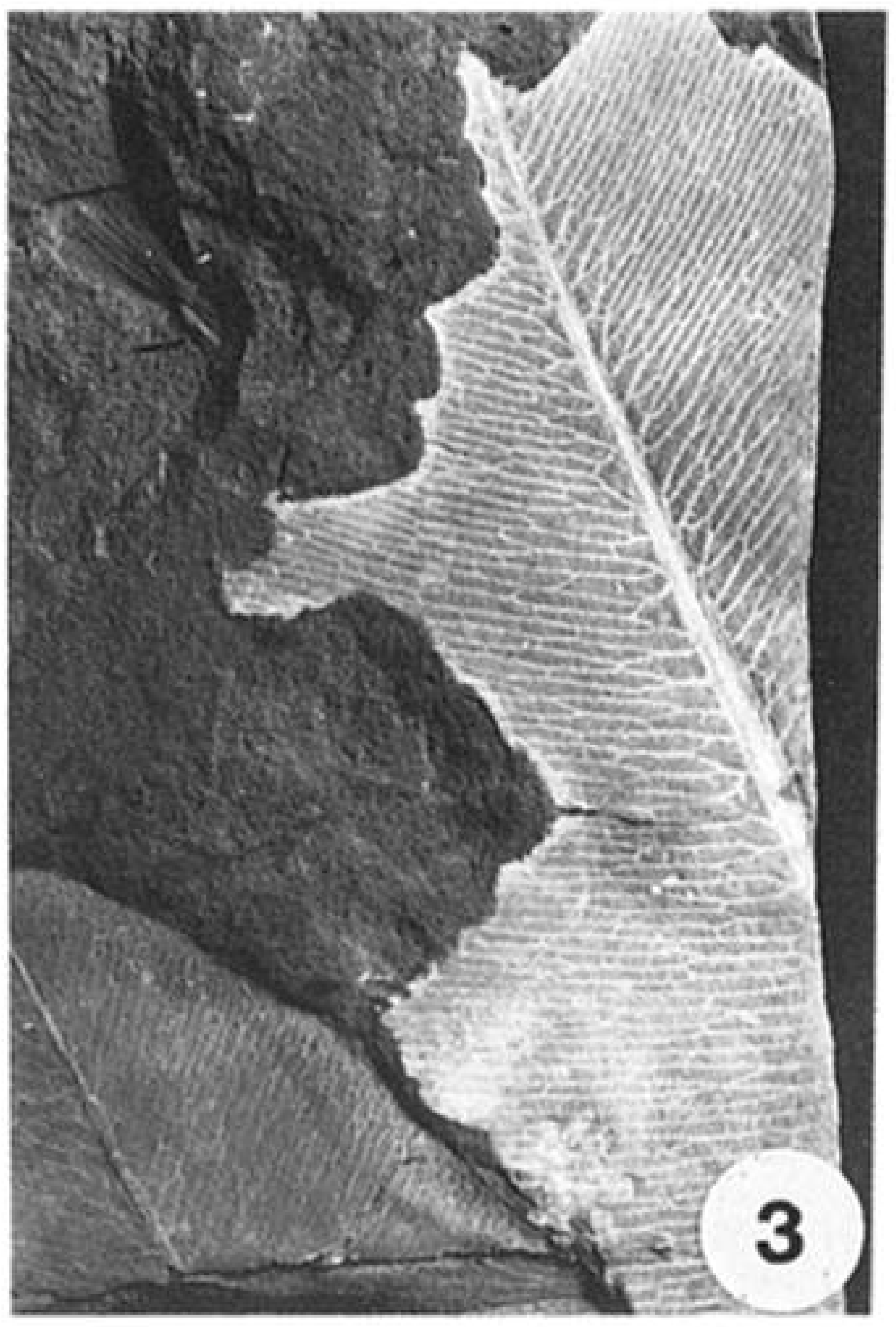
Ziegler, A.M. 1989 Phytogeographic patterns and continental configurations during the Permian Period. In *Palaeozoic palaeogeography and biogeography* (ed. W. S. McKerrow & C. R. Scotese) Memoir of the Geological Society 12.

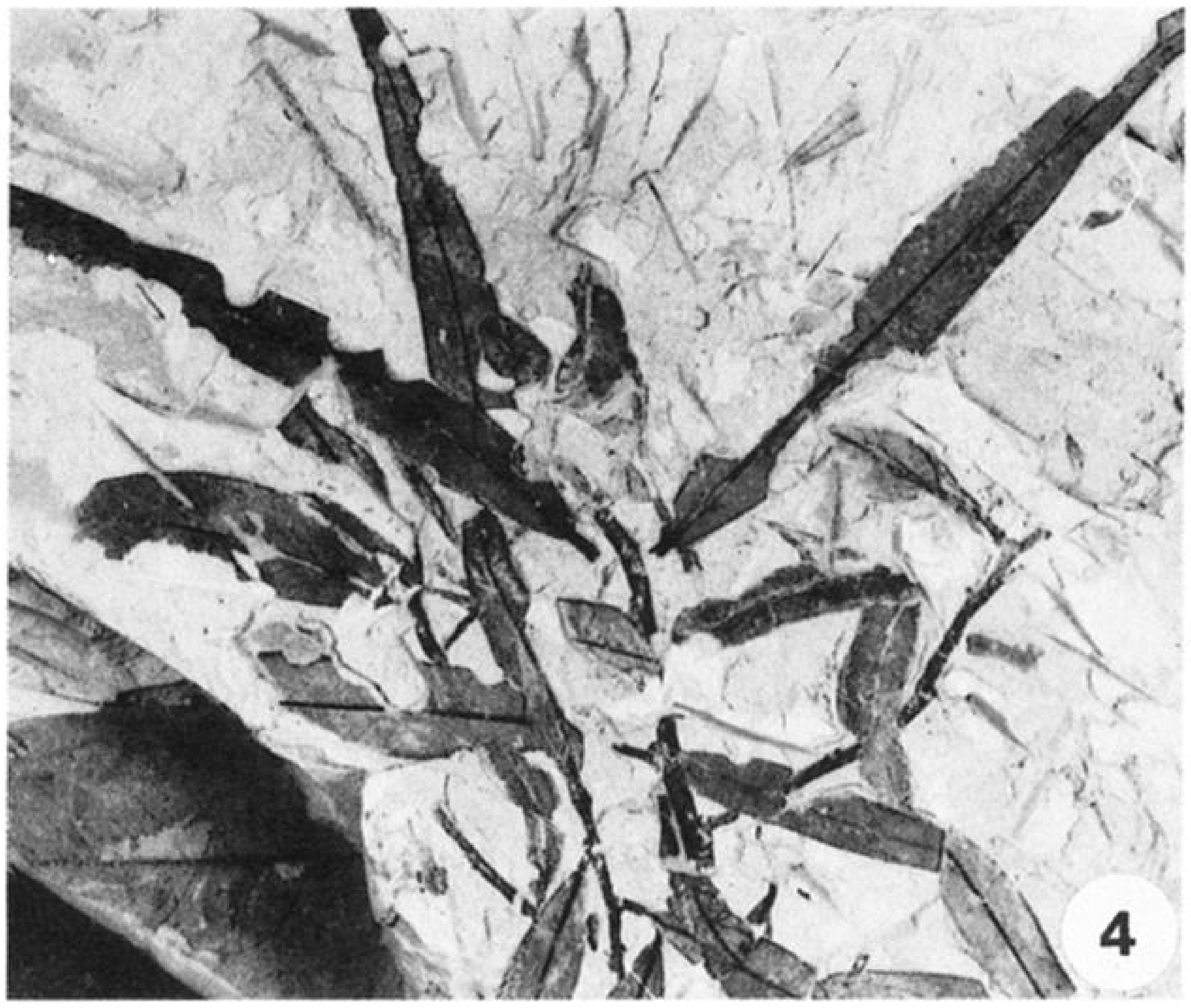
Received 30 April 1991; revised and accepted 15 October 1991

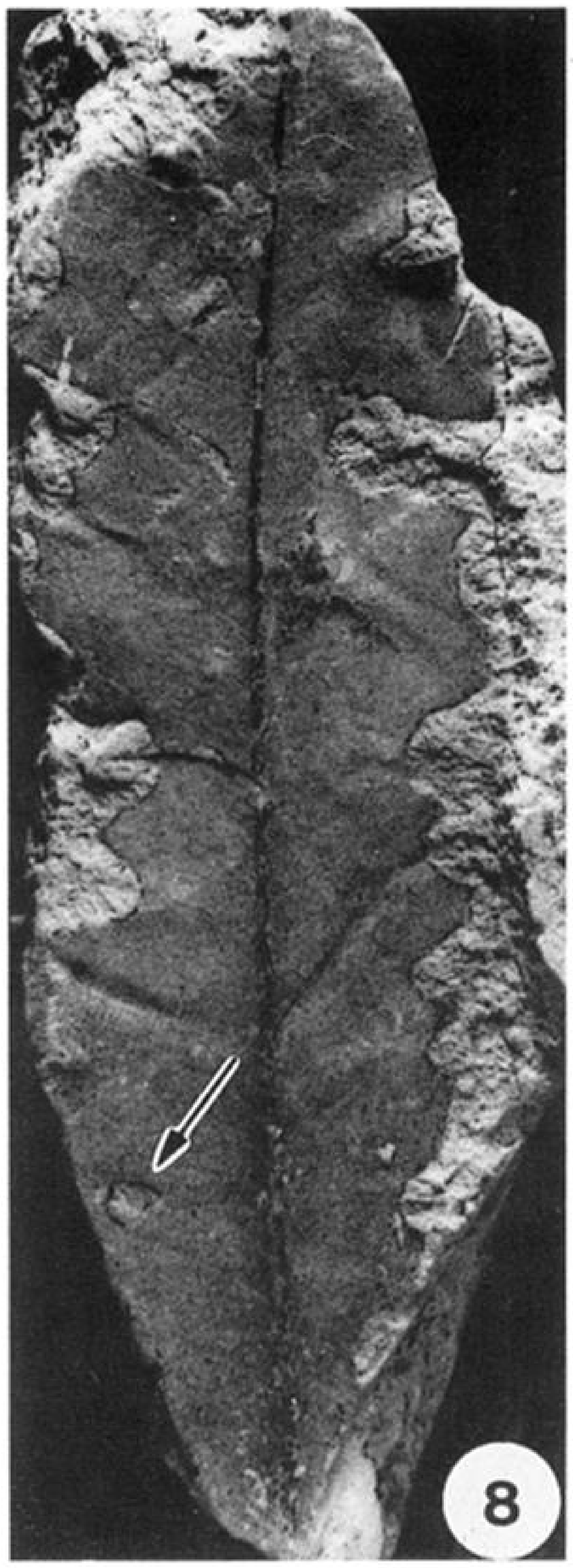
Note added in proof (8 January 1992): We have noted the absence of data for plant–arthropod interactions in the Triassic. Although not specifically dealing with this topic, an important monograph on Triassic compression floras from South Africa by Anderson & Anderson (1989) illustrates numerous damaged leaves. As we would have expected most specimens show continuous marginal feeding traces. However, in some species (e.g. *Sphenobaiera insecta* Anderson and Anderson and *S. sectina* Anderson and Anderson) the leaf tips are often missing. In addition, although no leaf galls are evident, leaf mines are common in the conifer *Heidiphyllum elongatum* (Morris) Retallack. These new data do not alter our present conclusions but reinforce the suggestion that absence of data is often more apparent than real.

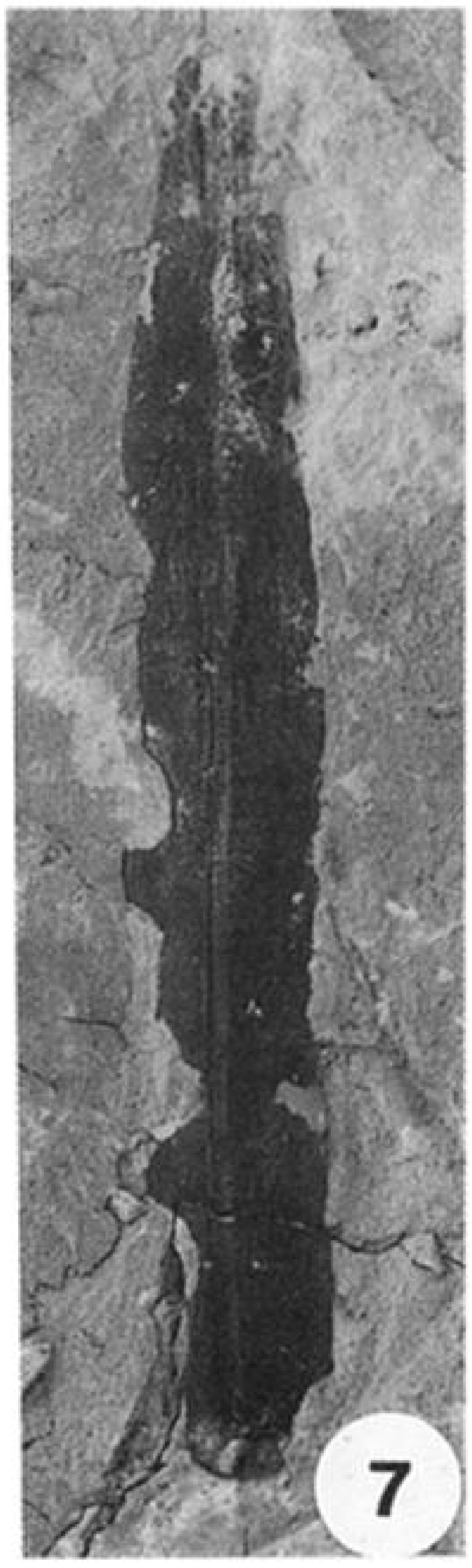
Reference

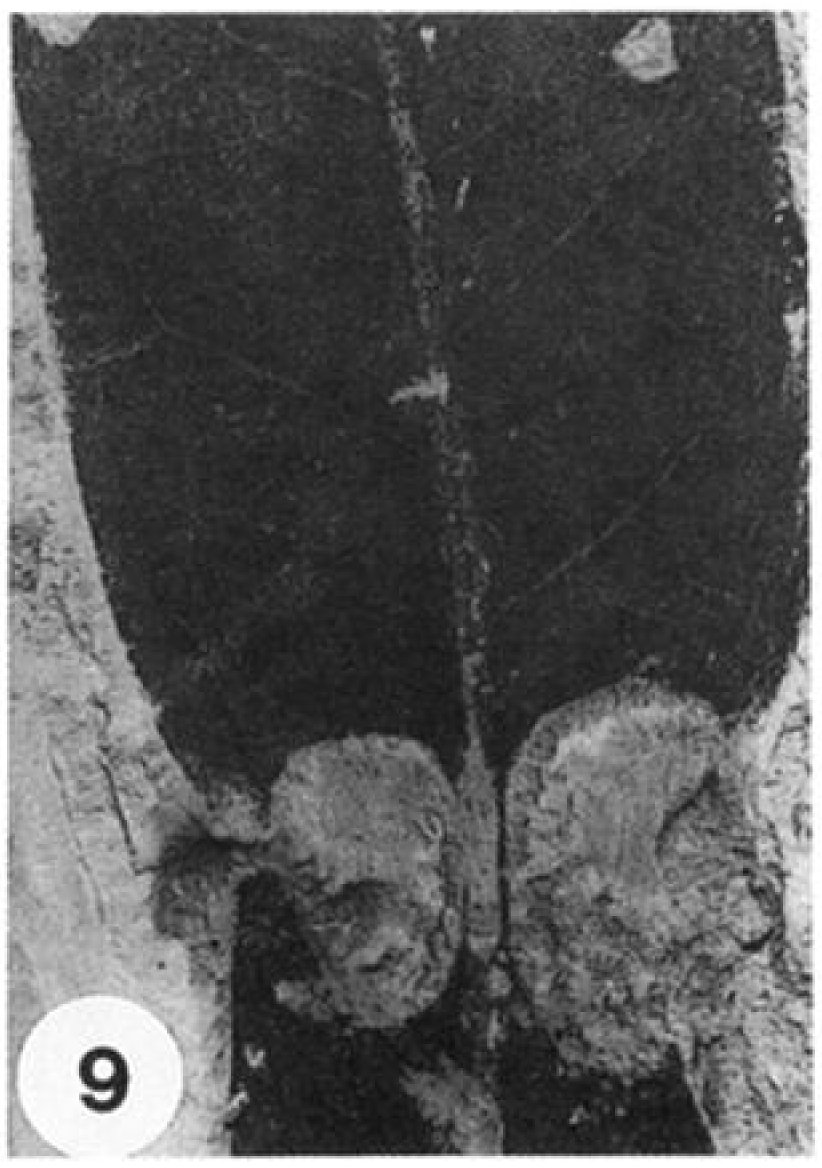
Anderson, J.M. & Anderson, H.M. 1989 *Palaeoflora of Southern Africa. Molteno Formation (Triassic)*, vol. 2 (*Gymnosperms (excluding Dicroidium)*). (567 pages.) Rotterdam: A. A. Balkema.











Figures 3–9. Examples of leaf feeding.

Figure 3. *Glossopteris* leaf with continuous marginal feeding traces, Permian, Australia. Scott Colln. Magn. × 1.

Figure 4. Lanceolate leaves showing various forms of marginal feeding types from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago, PP11050. Magn. × ½.

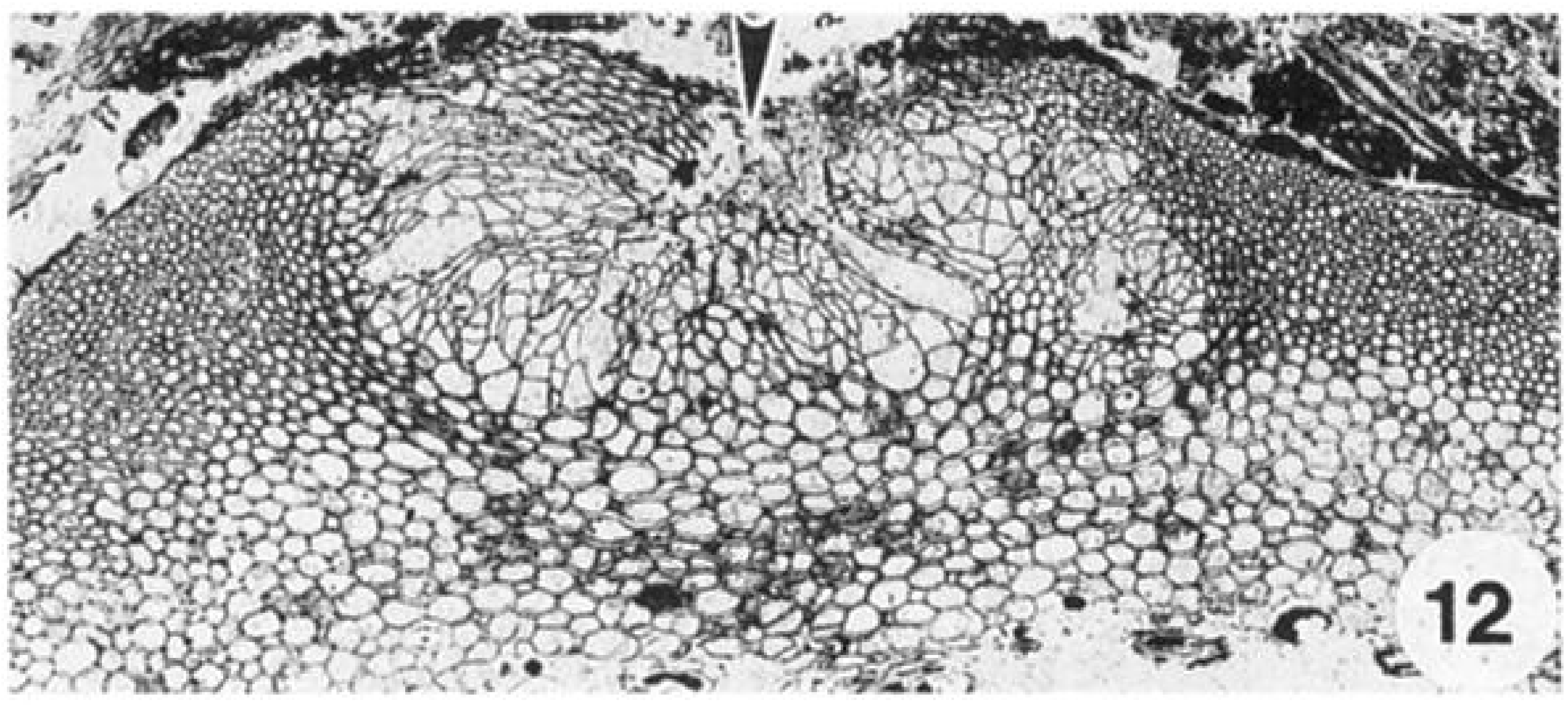
Figure 5. Detail of figure 4 showing feeding traces with thickened callus tissue. Magn. × 4.

Figure 6. Pteridosperm pinnule, *Neuropteris scheuchzeri* showing marginal feeding damage, Upper Carboniferous, Mazon Creek, Illinois, U.S.A. Field Museum of Natural History, Chicago. PP24268. Magn. × 1.

Figure 7. Continuous marginal feeding trace on cycad leaf, Middle Jurassic, Yorkshire. Scott Colln. Magn. × ¾.

Figure 8. Marginal and rare internal (arrow) feeding traces on angiosperm leaf from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. PP11525. Magn. × 1½.

Figure 9. Bud feeding on angiosperm leaf: the animal fed on this leaf while it was still in bud. Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. PP6519. Magn. × 2.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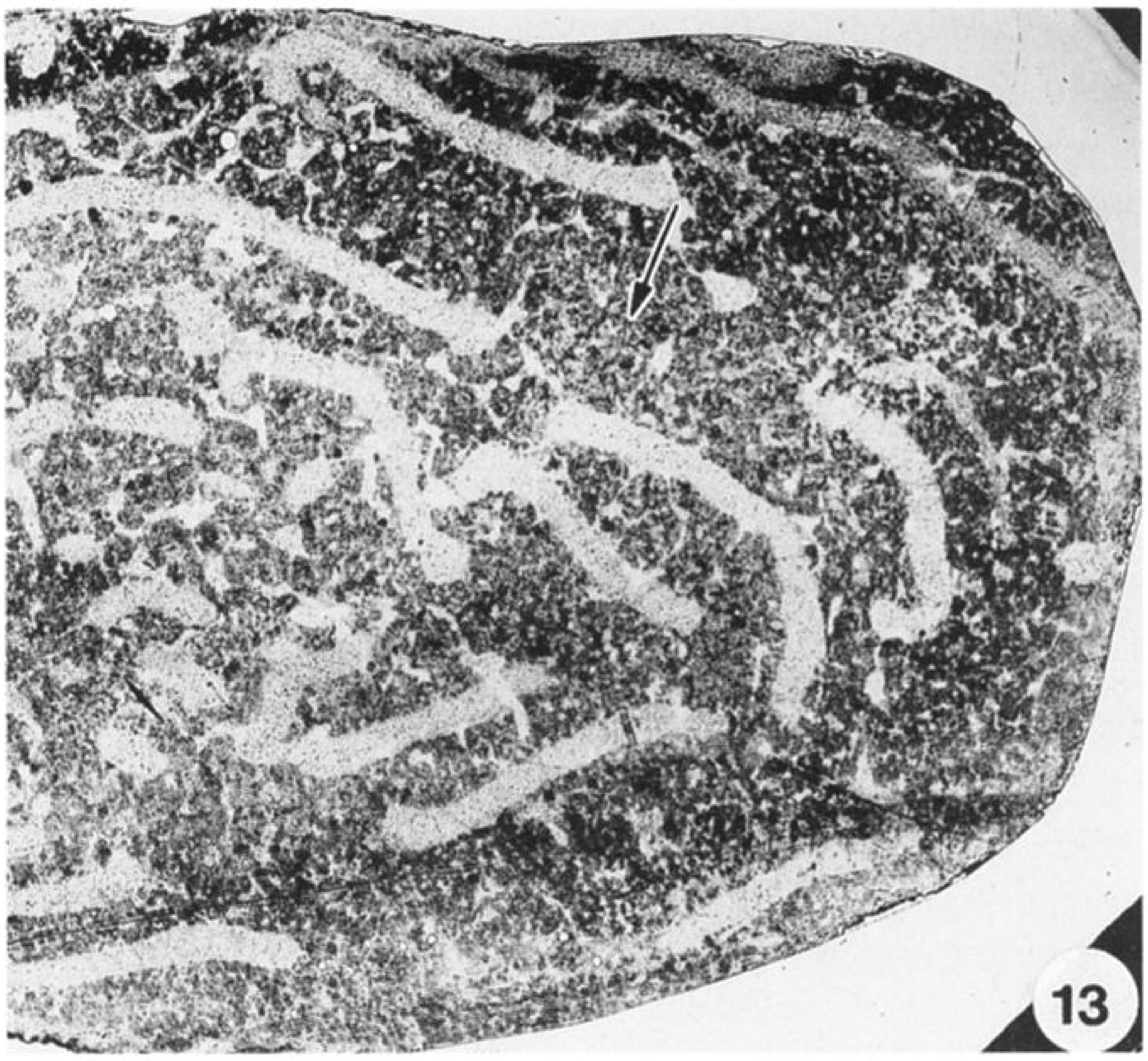
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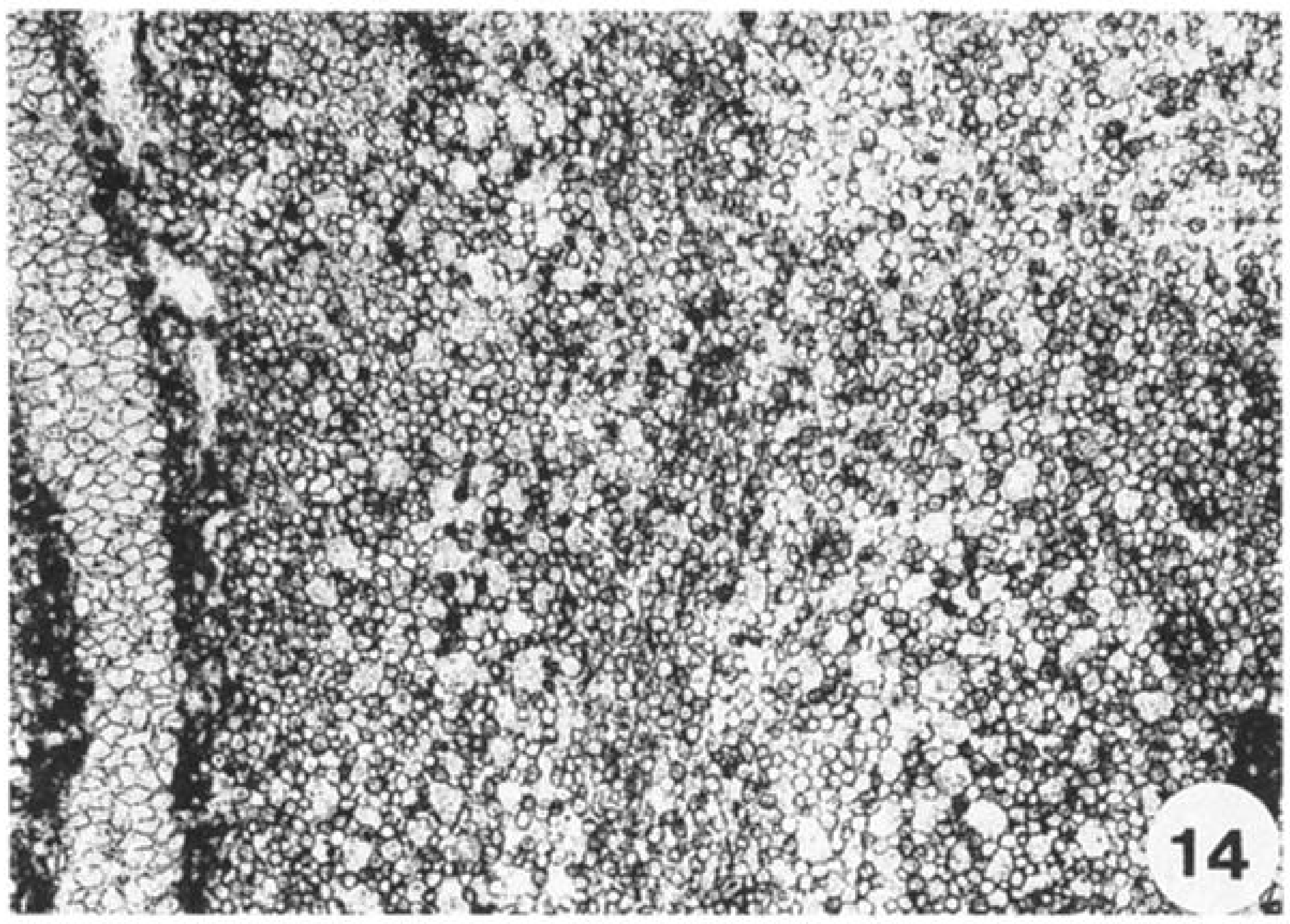
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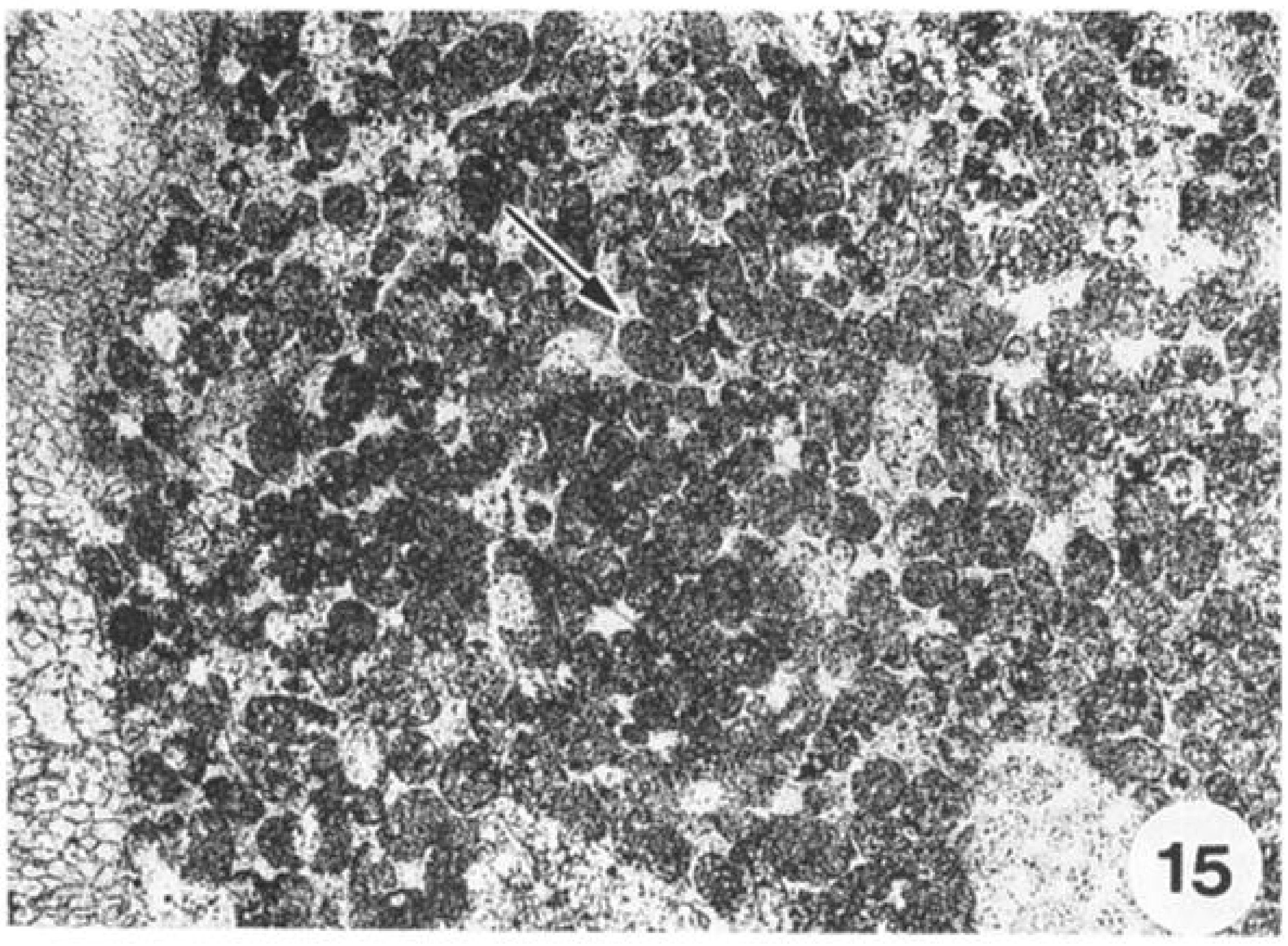
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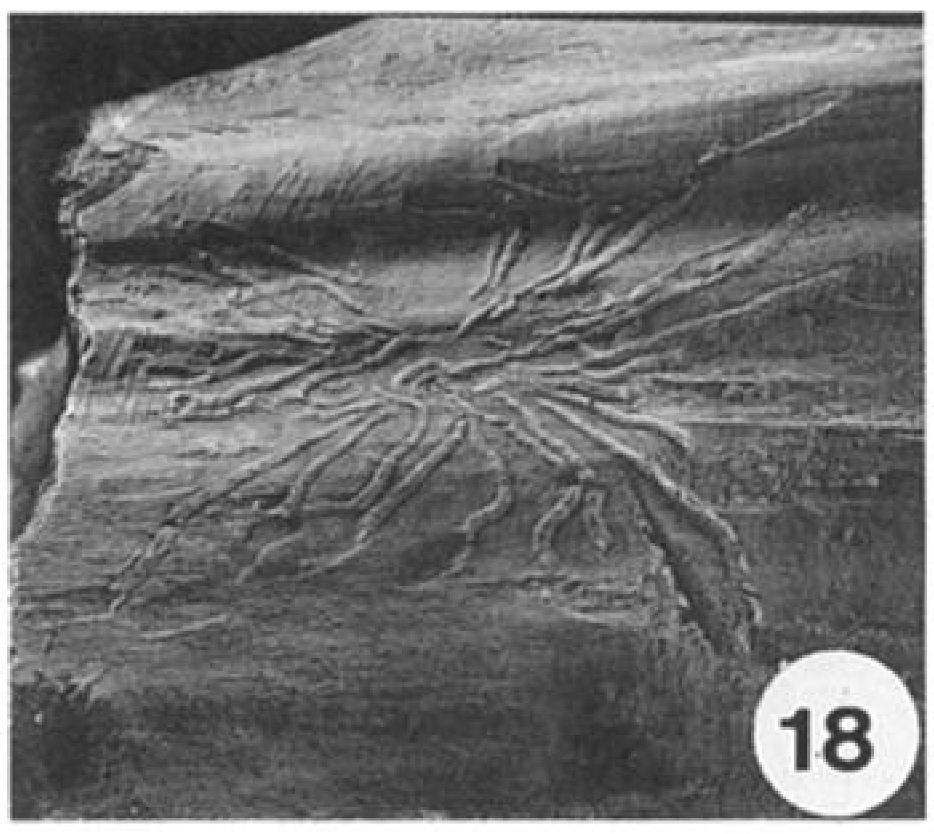
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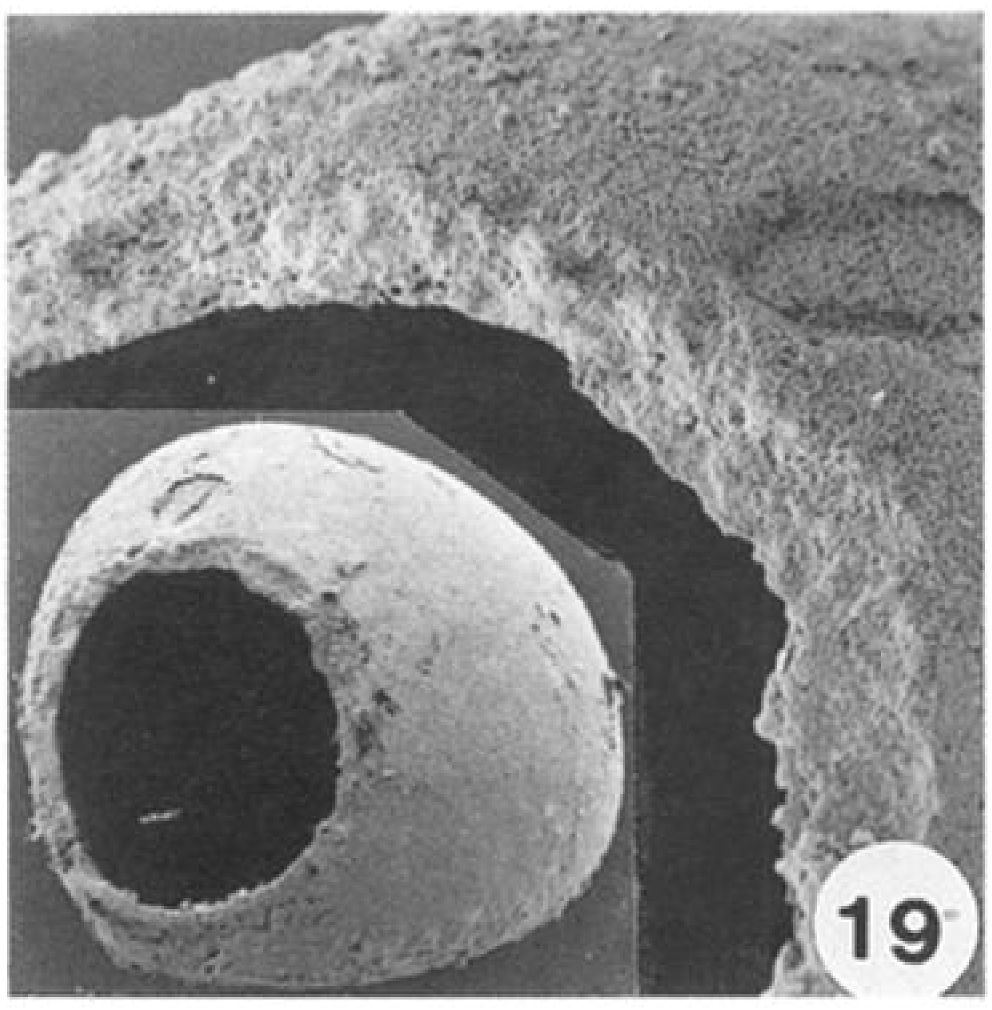
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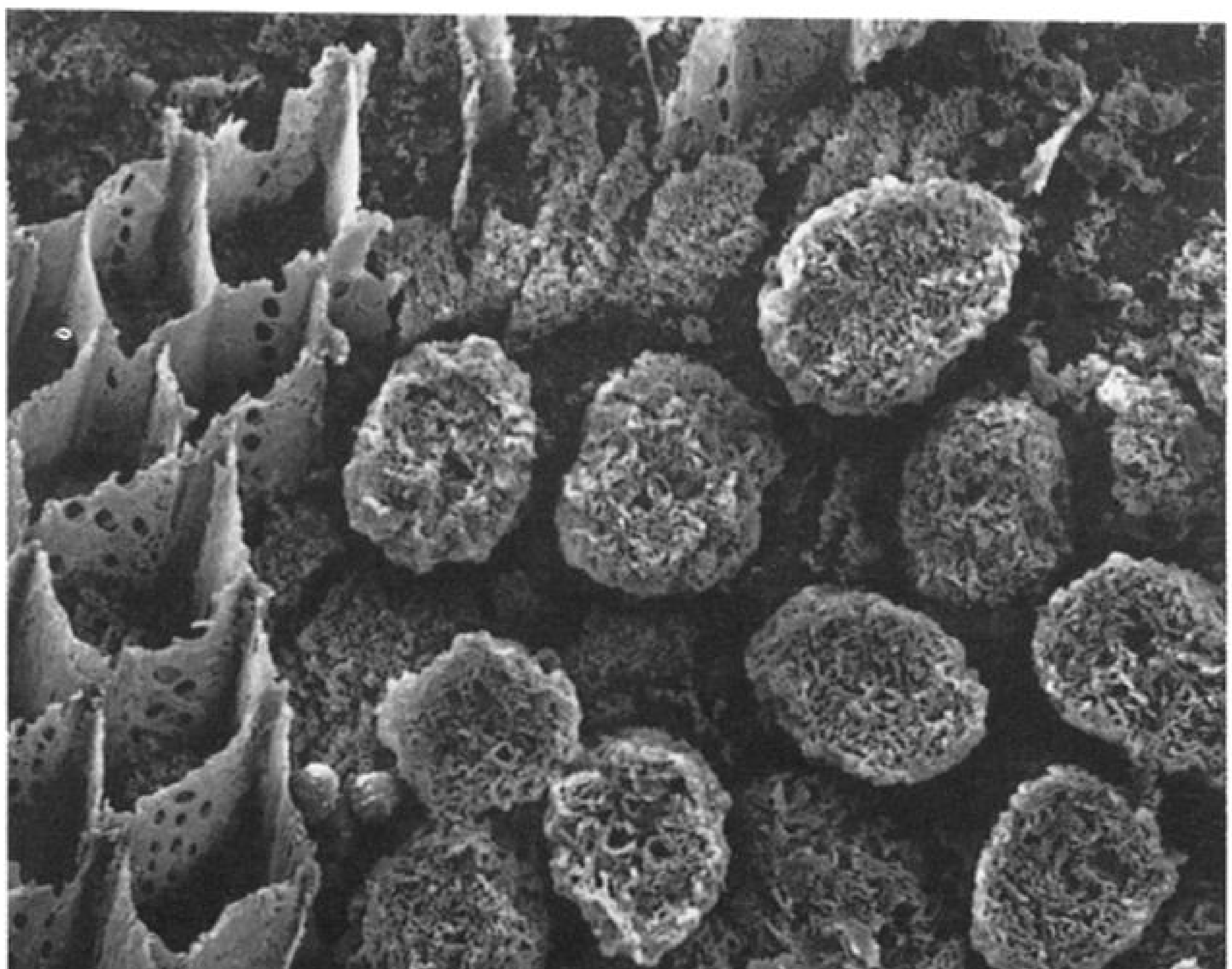
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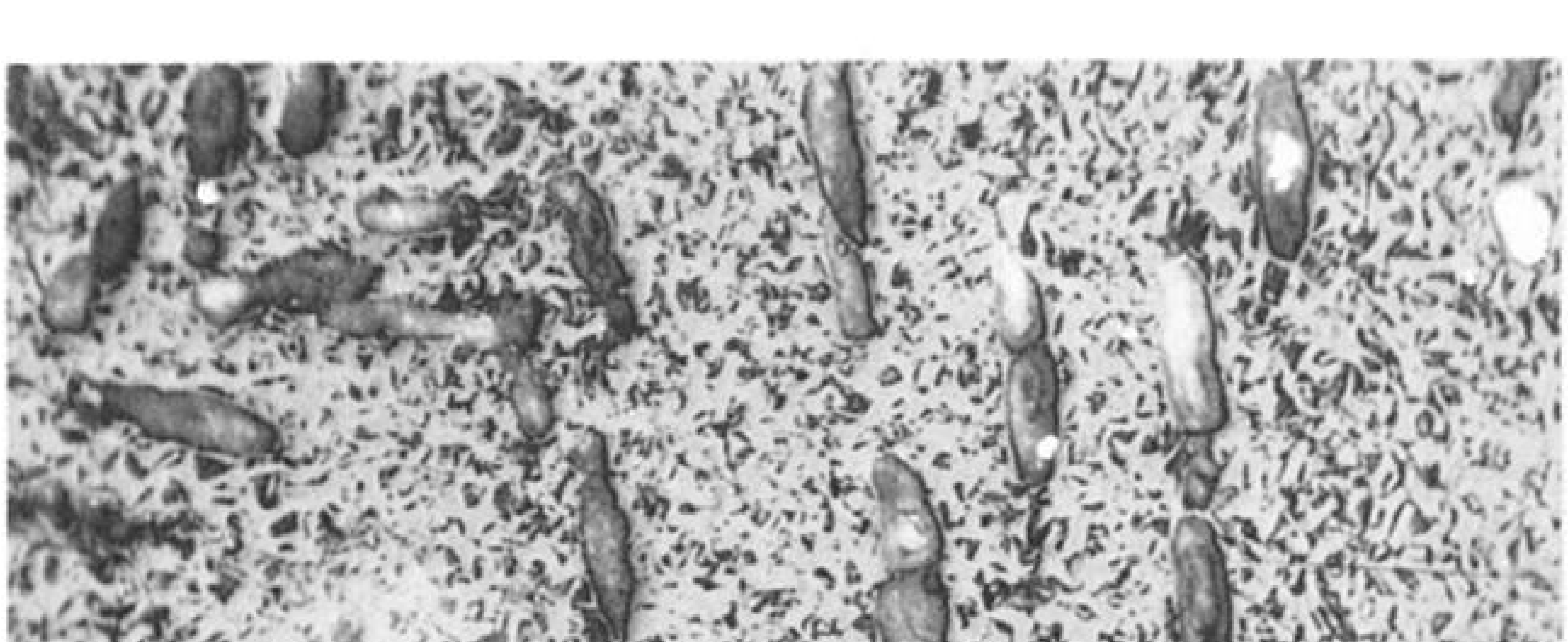
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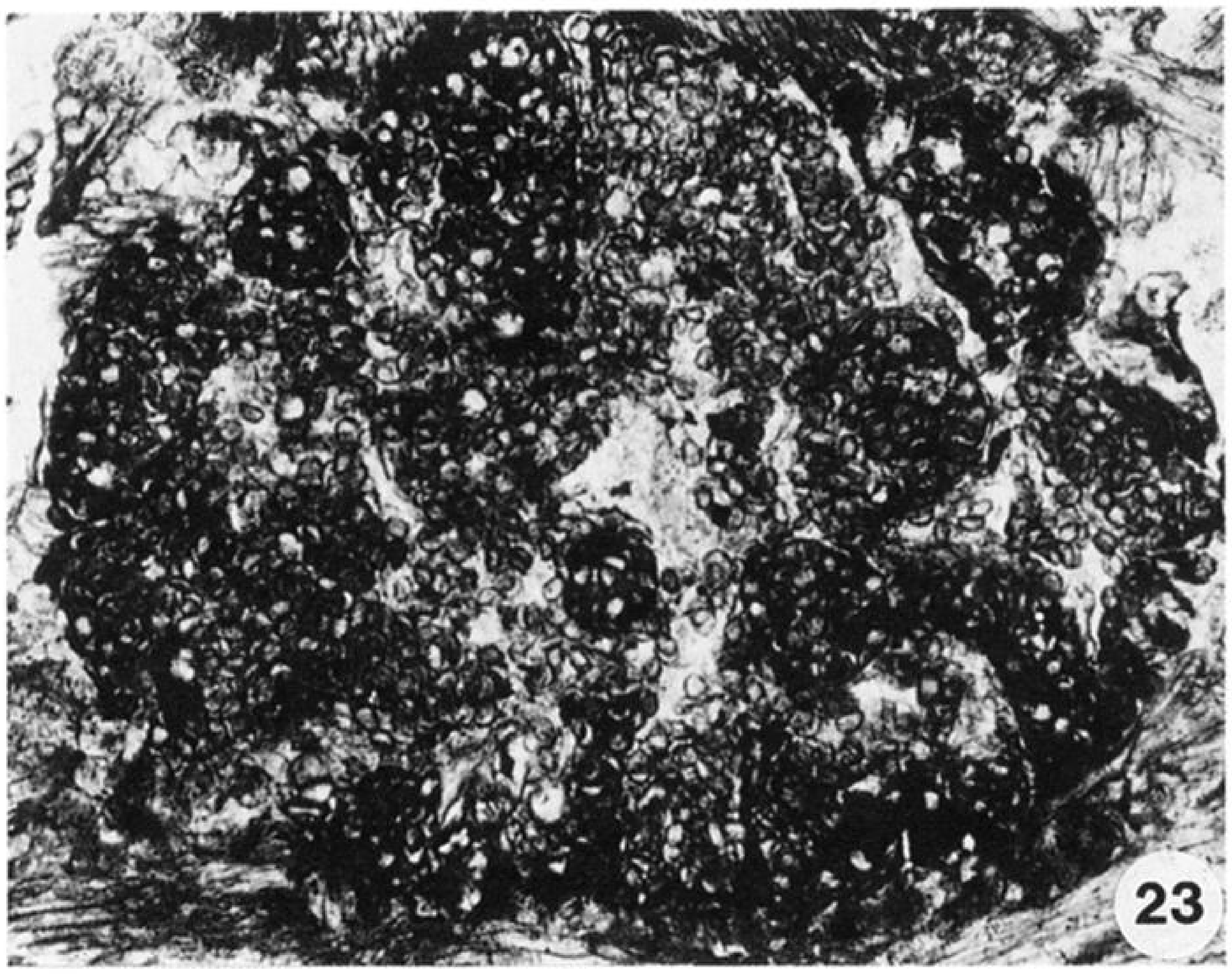
Figures 12–21. For description see opposite.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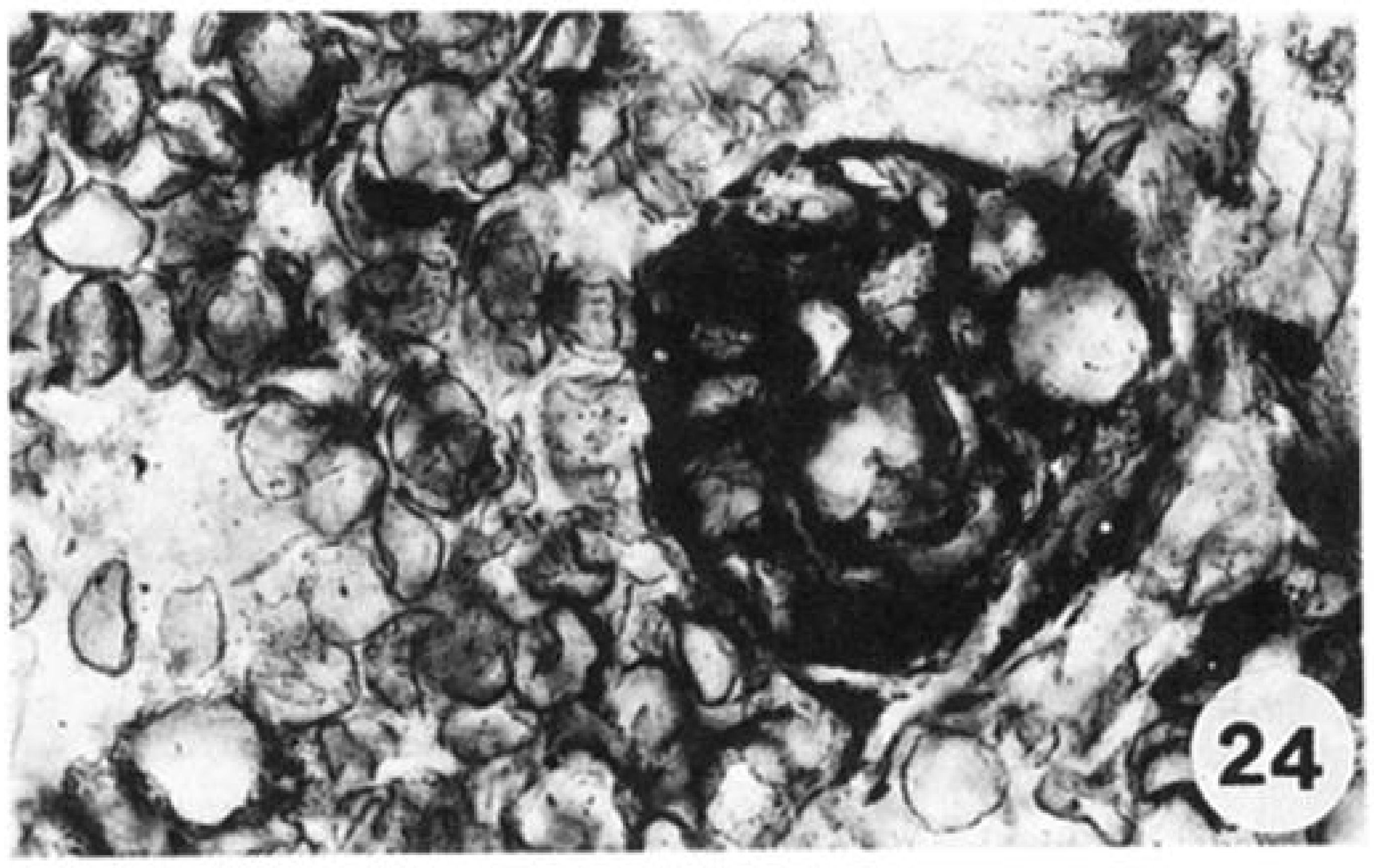
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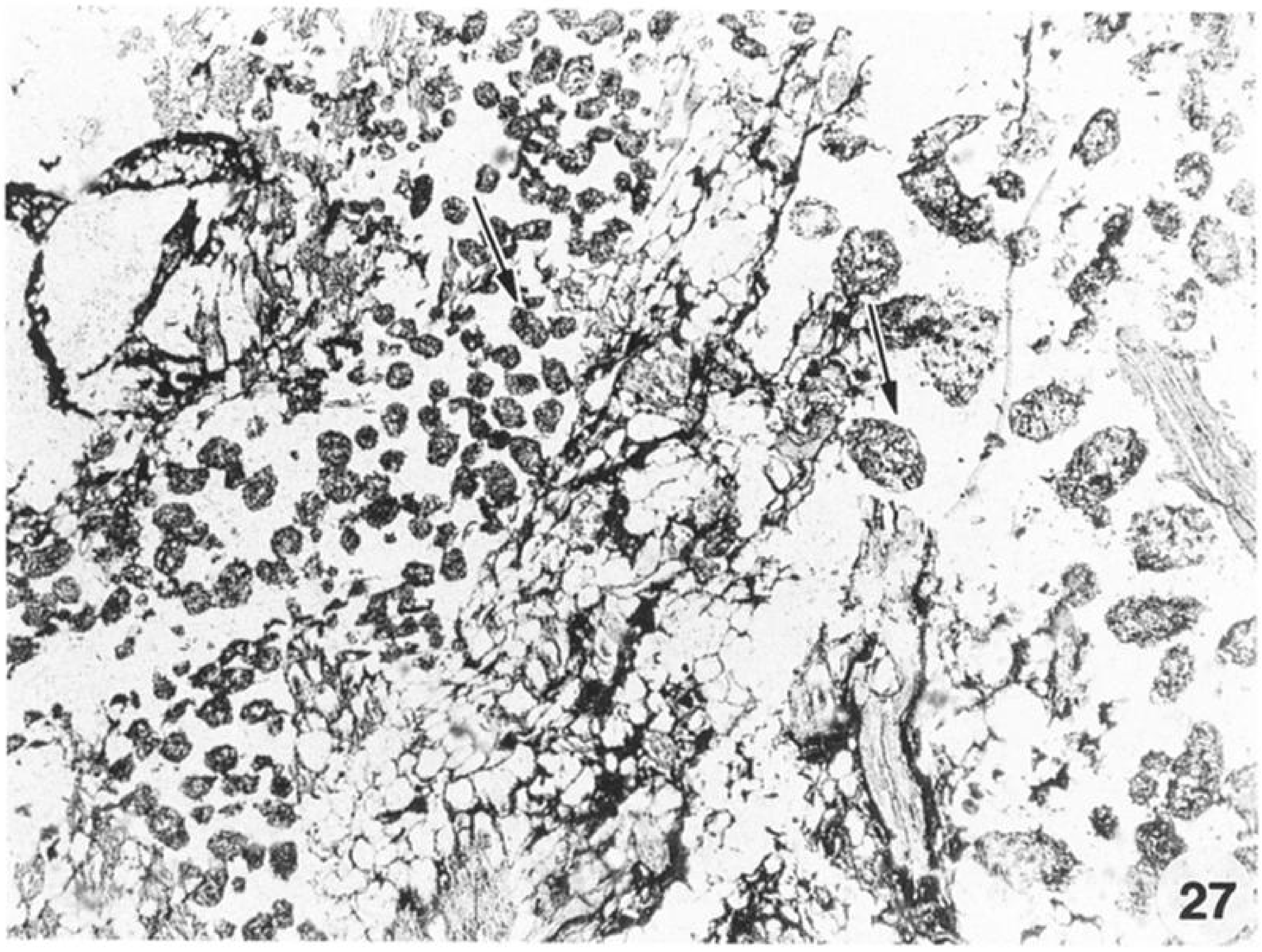
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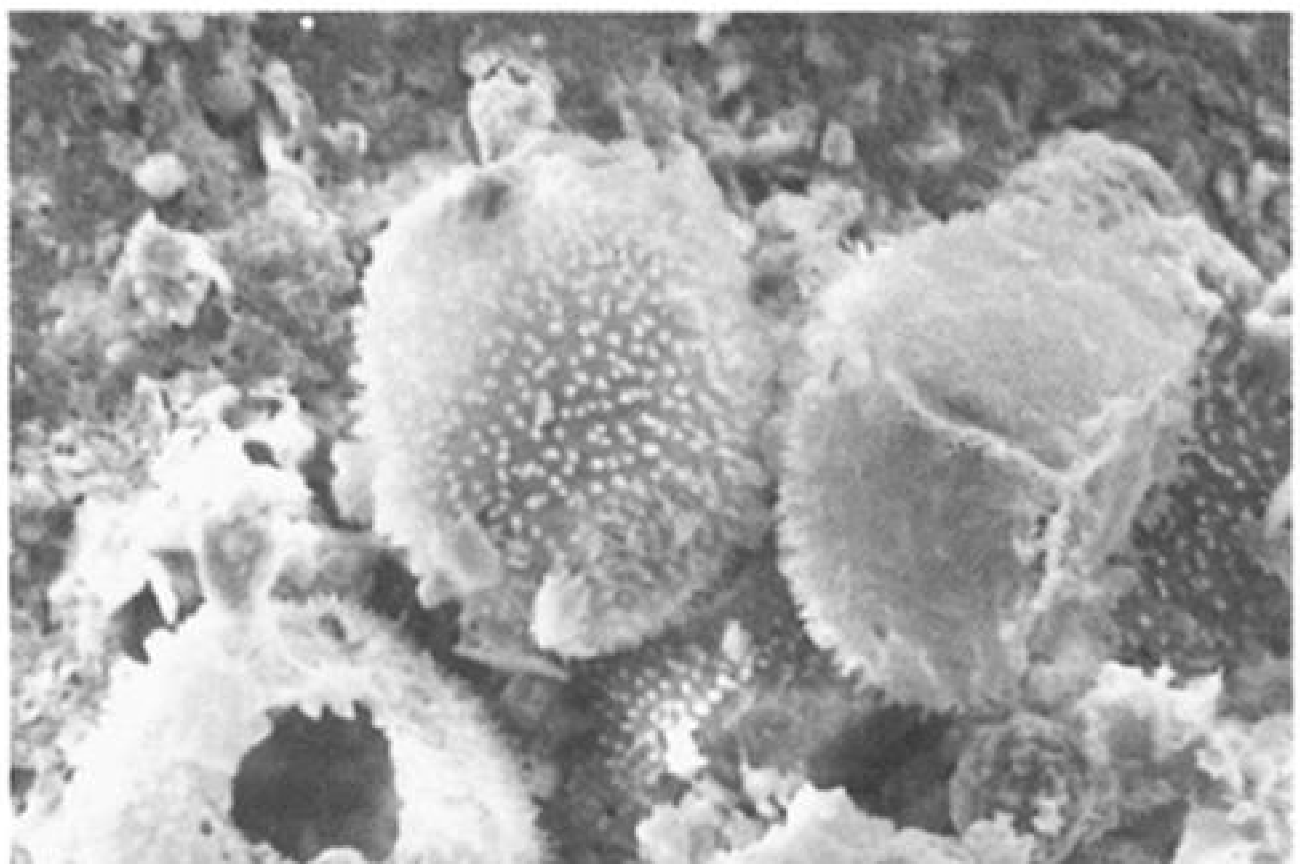
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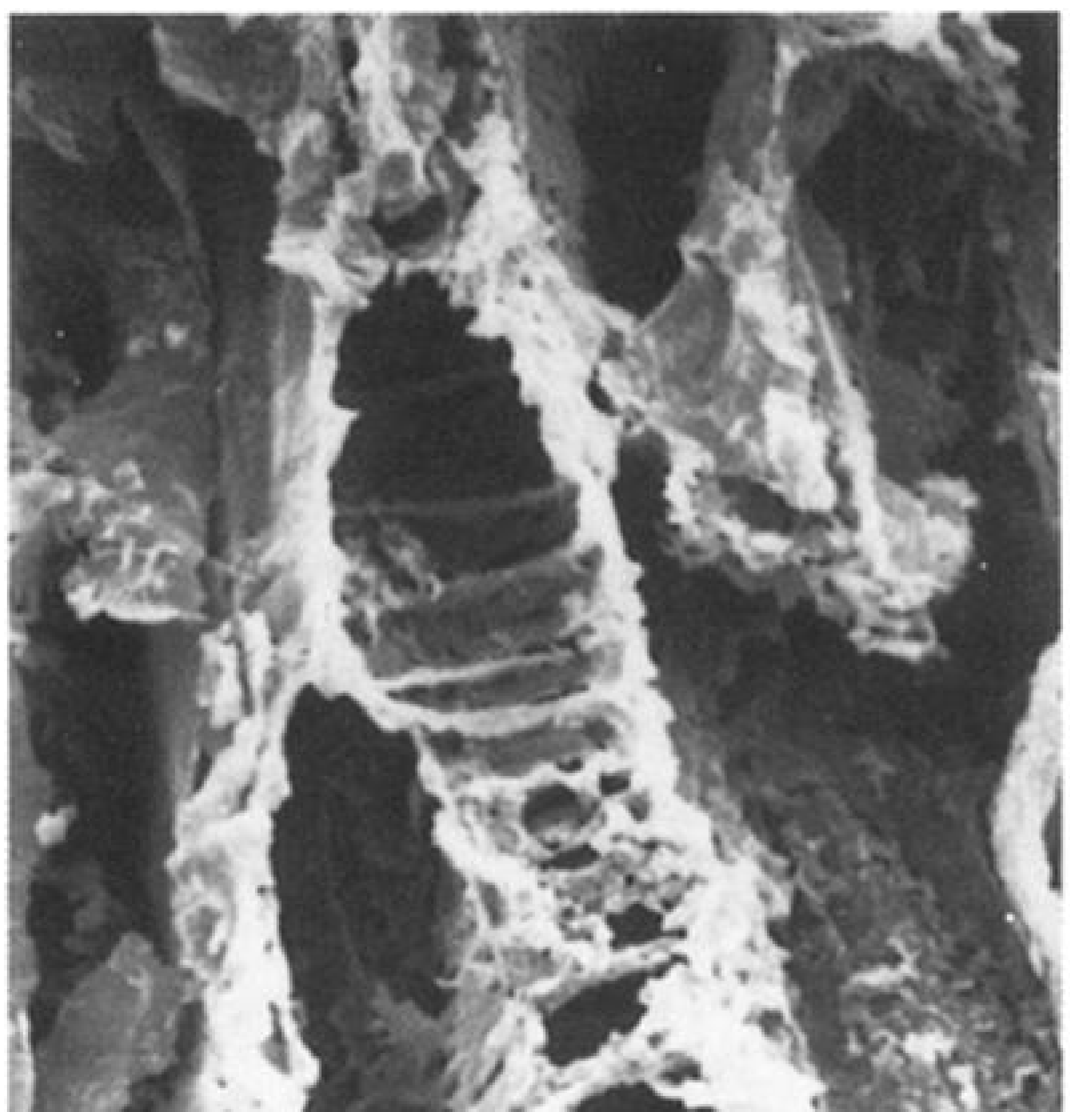
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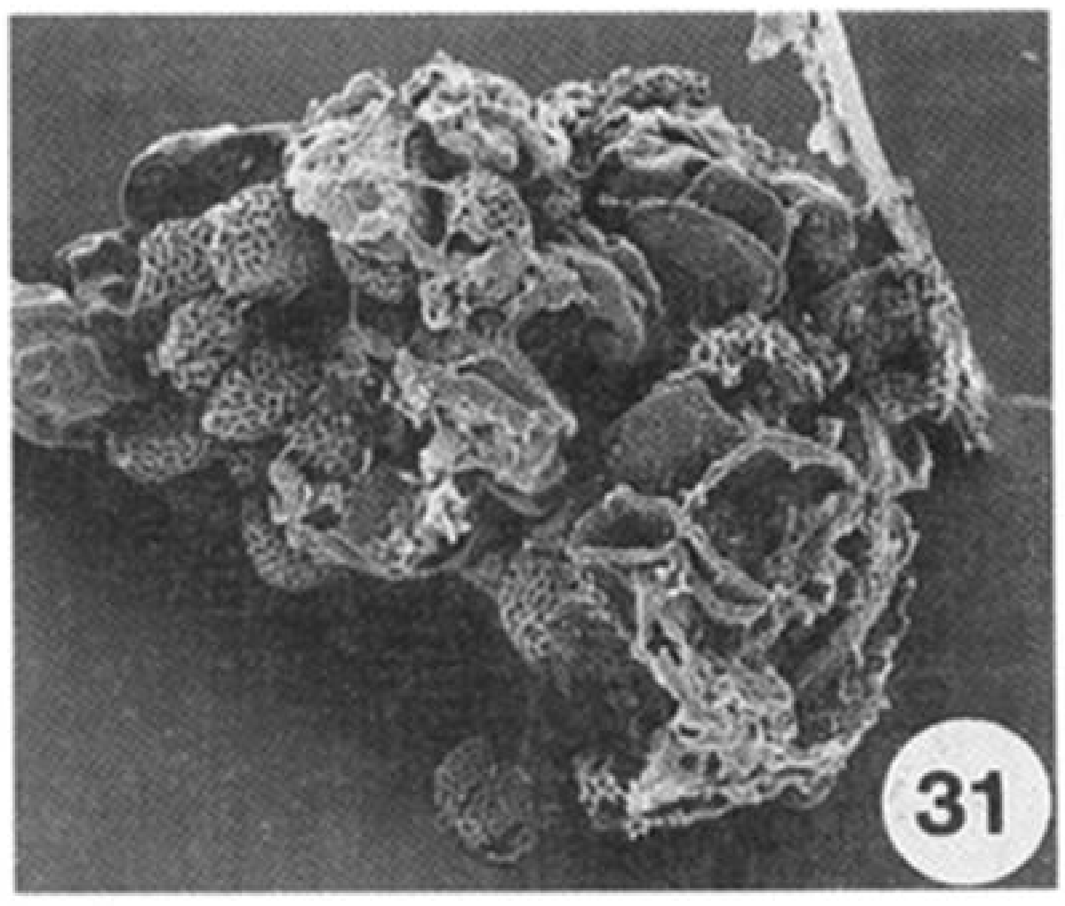
Figures 23–30. For description see opposite.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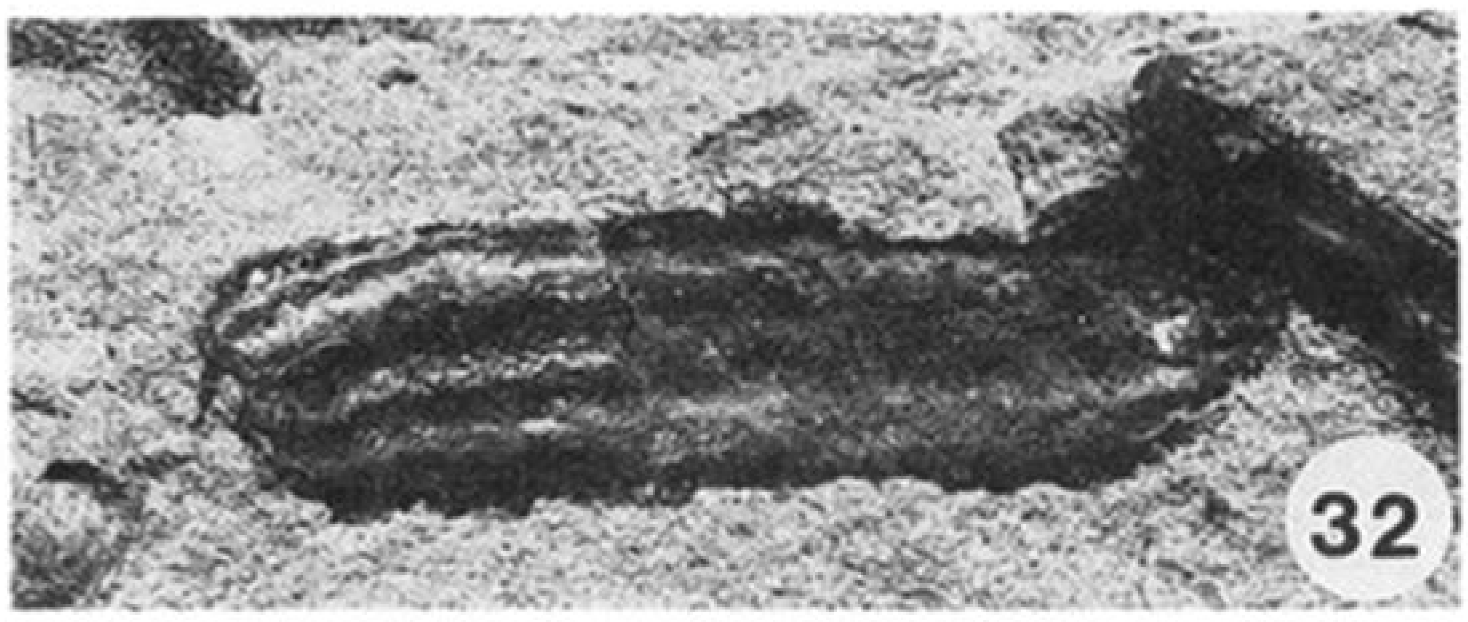
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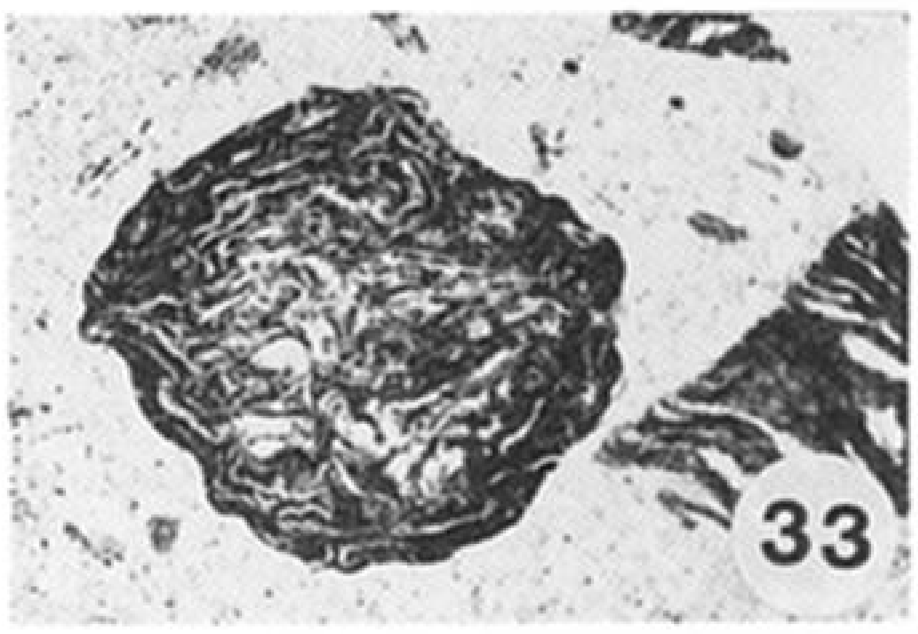
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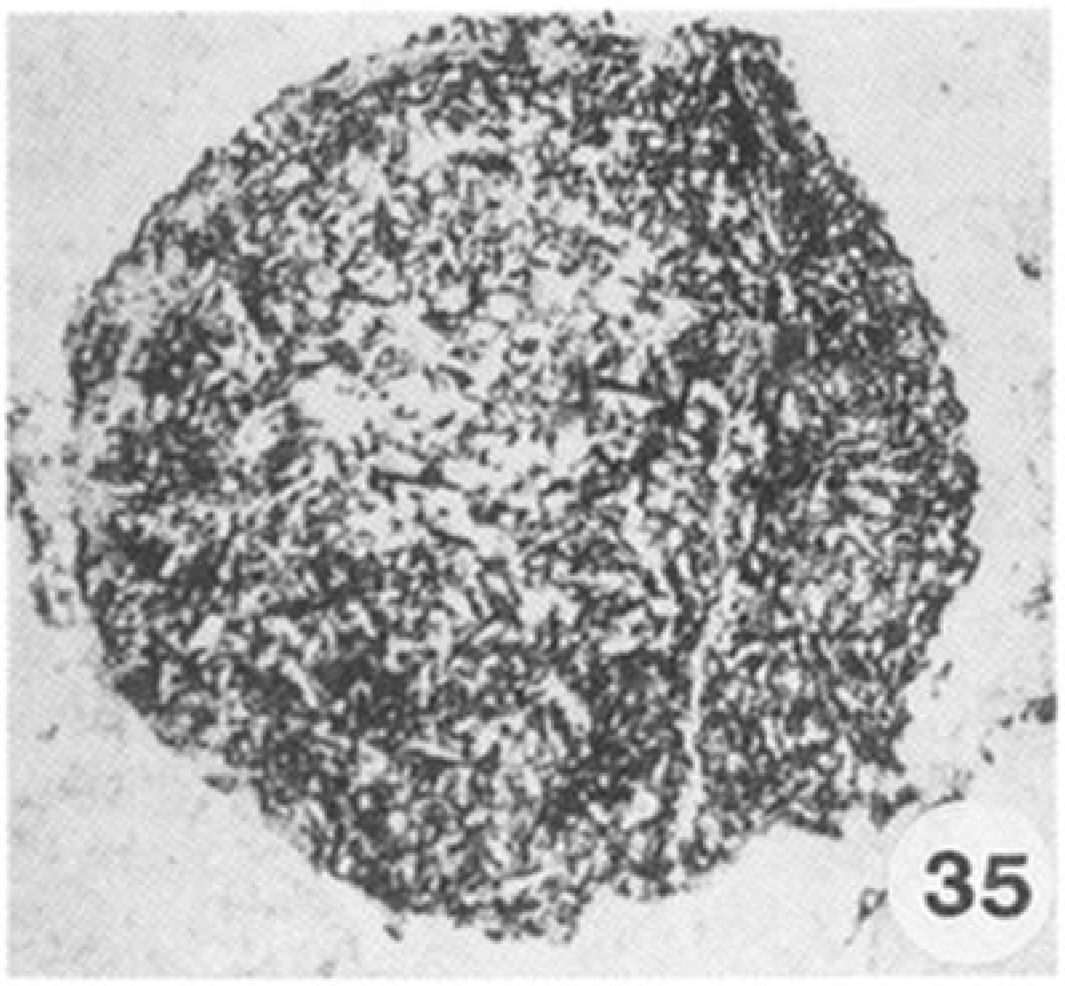
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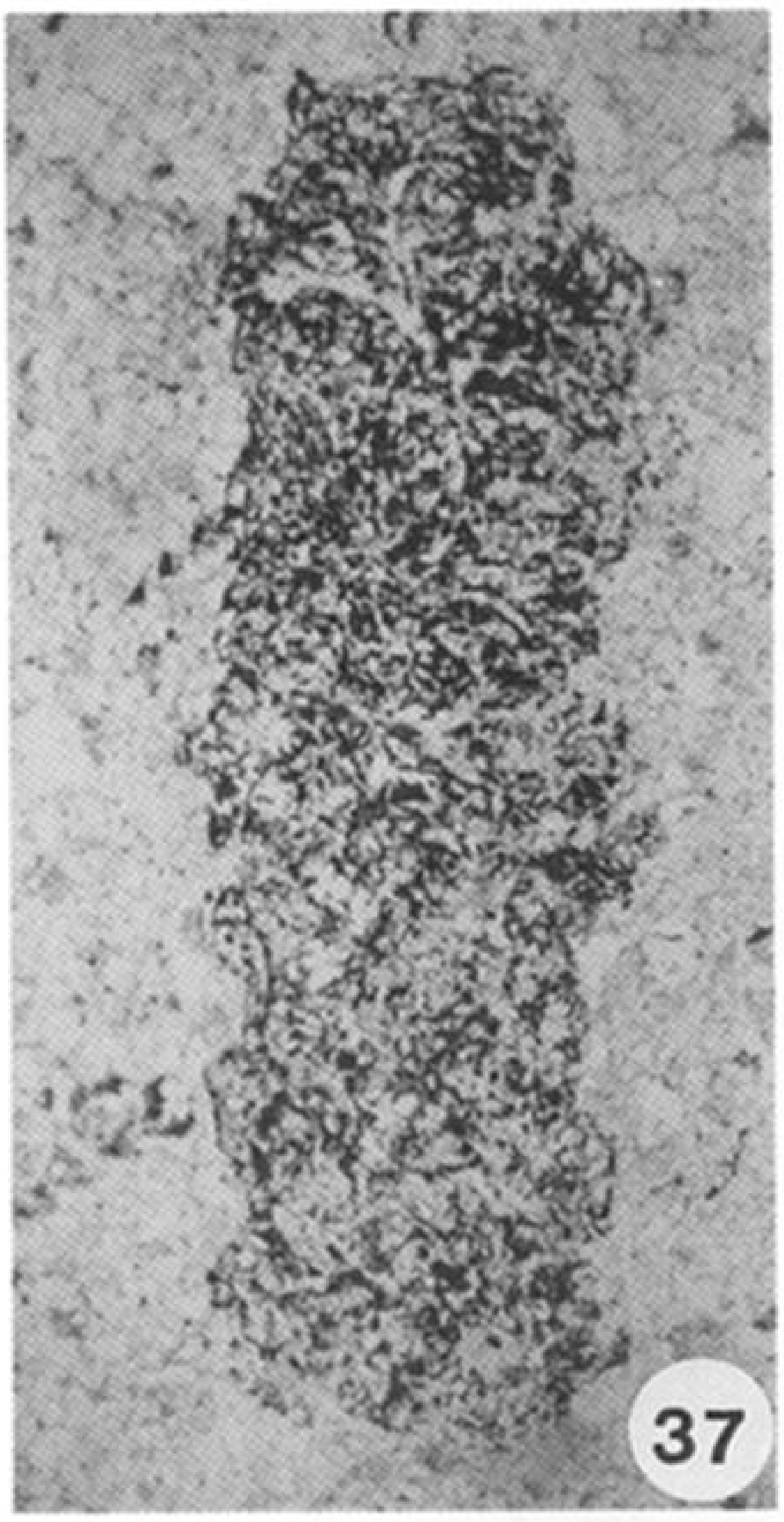
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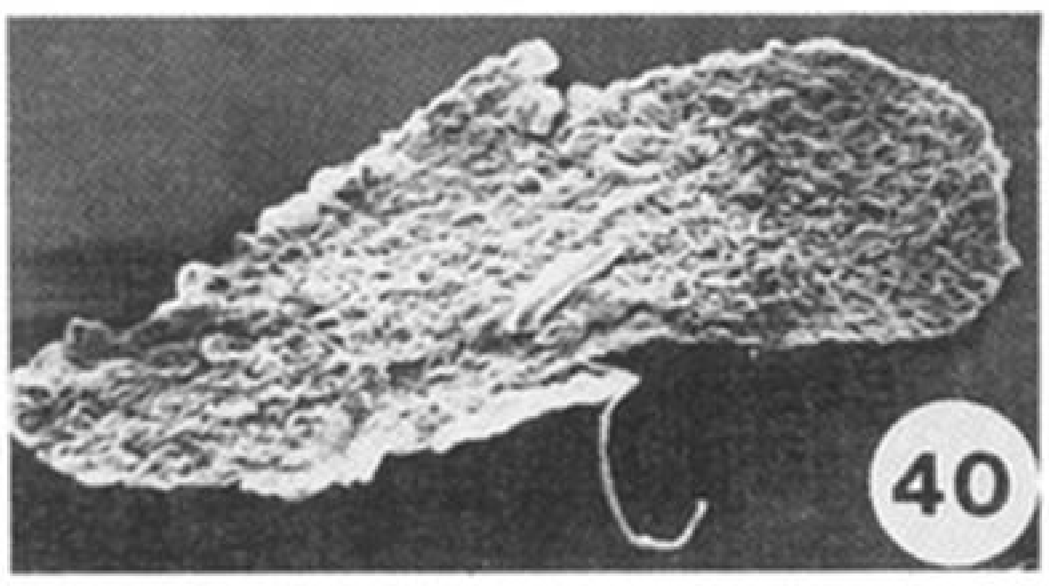
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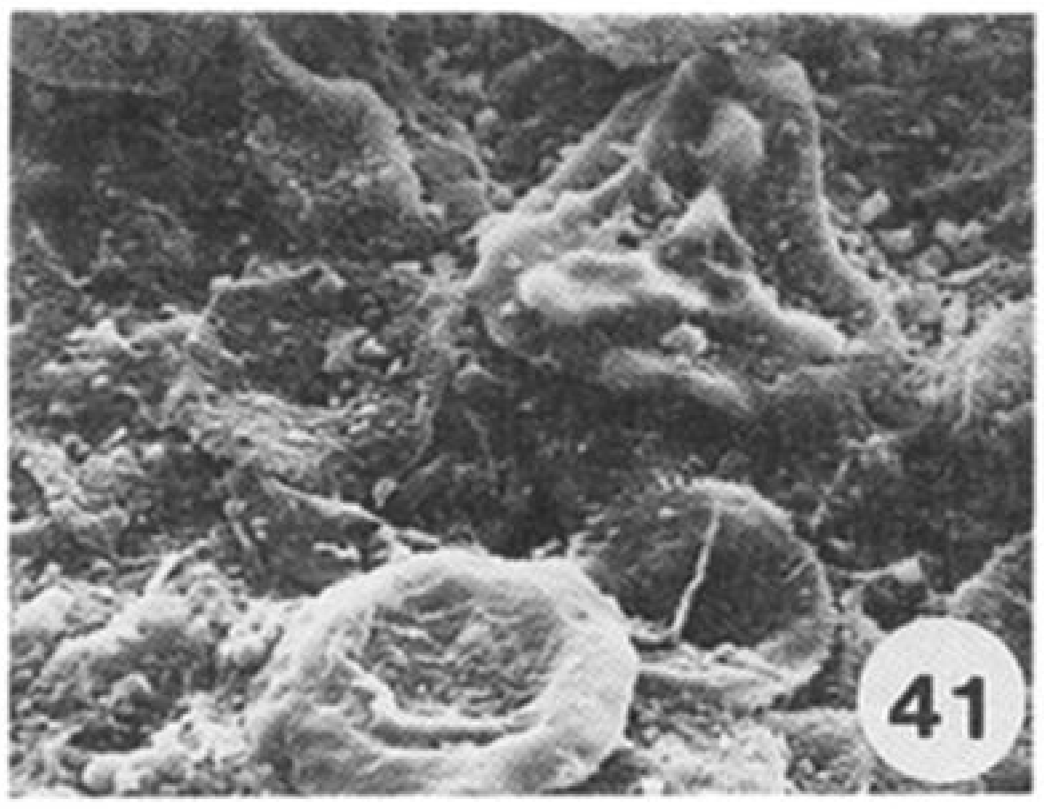
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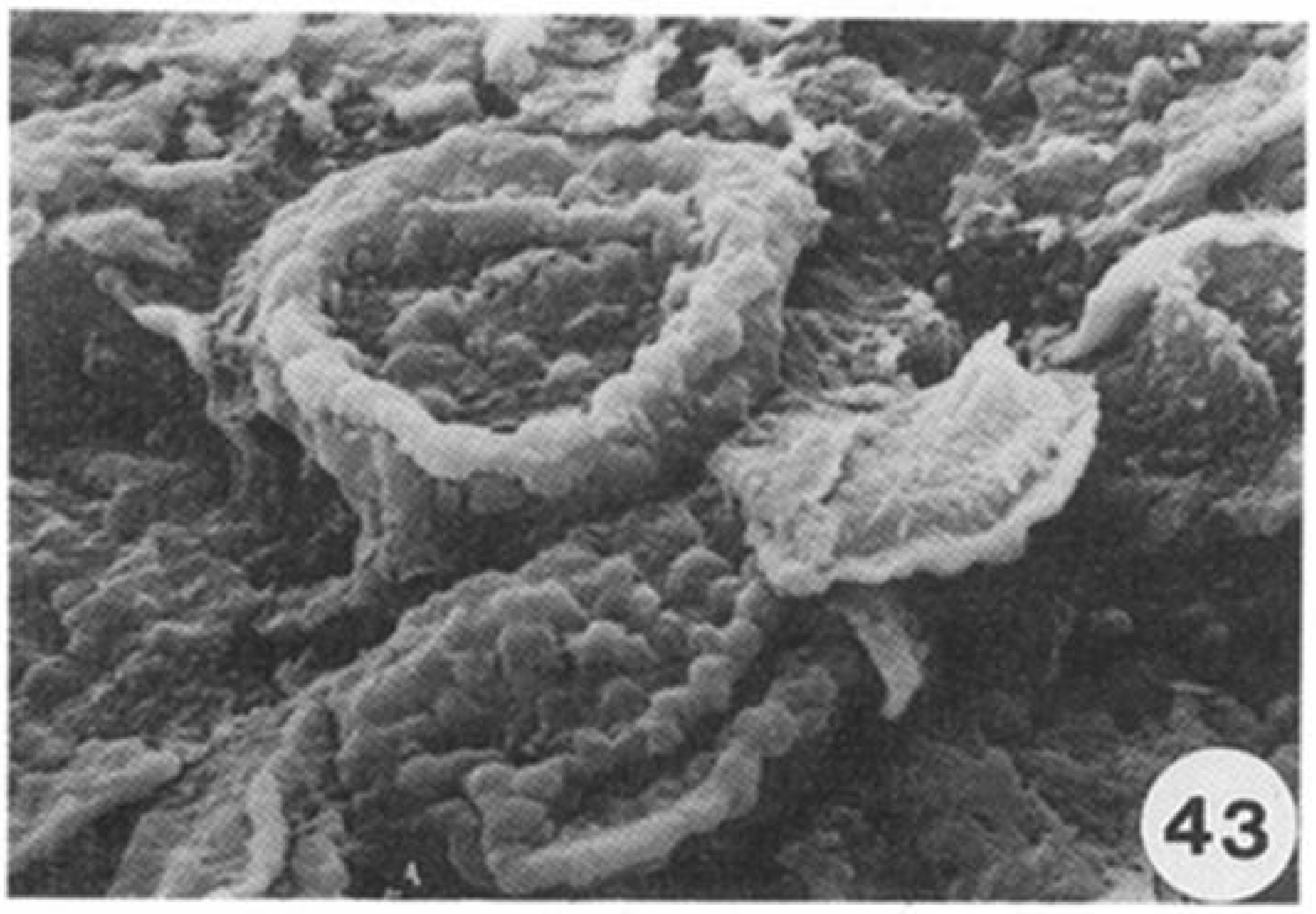
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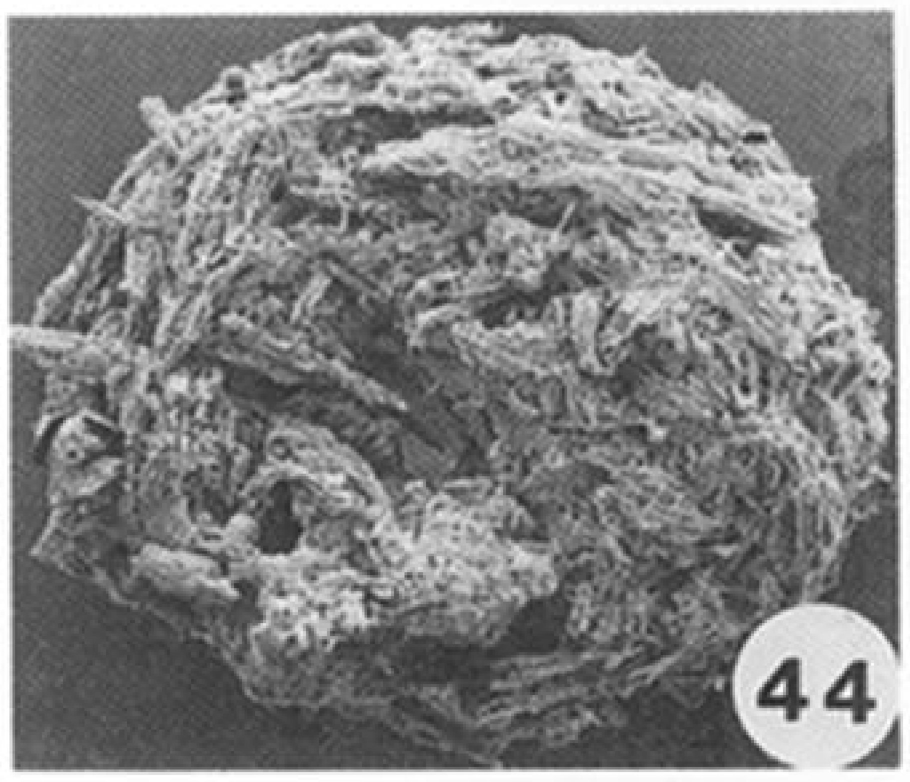
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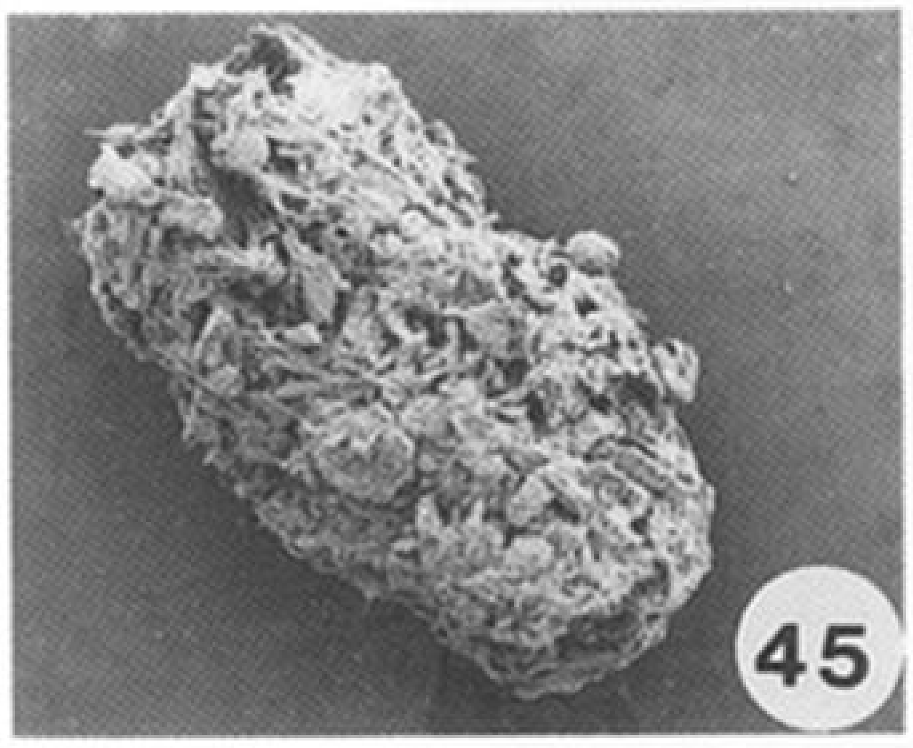
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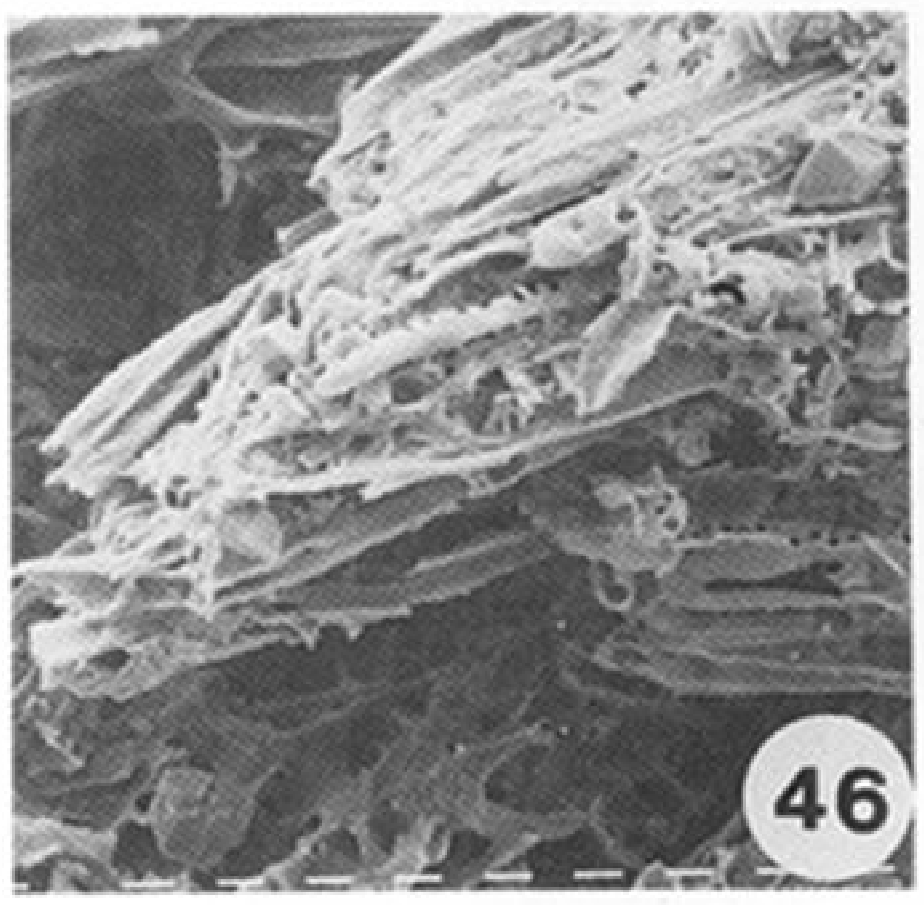
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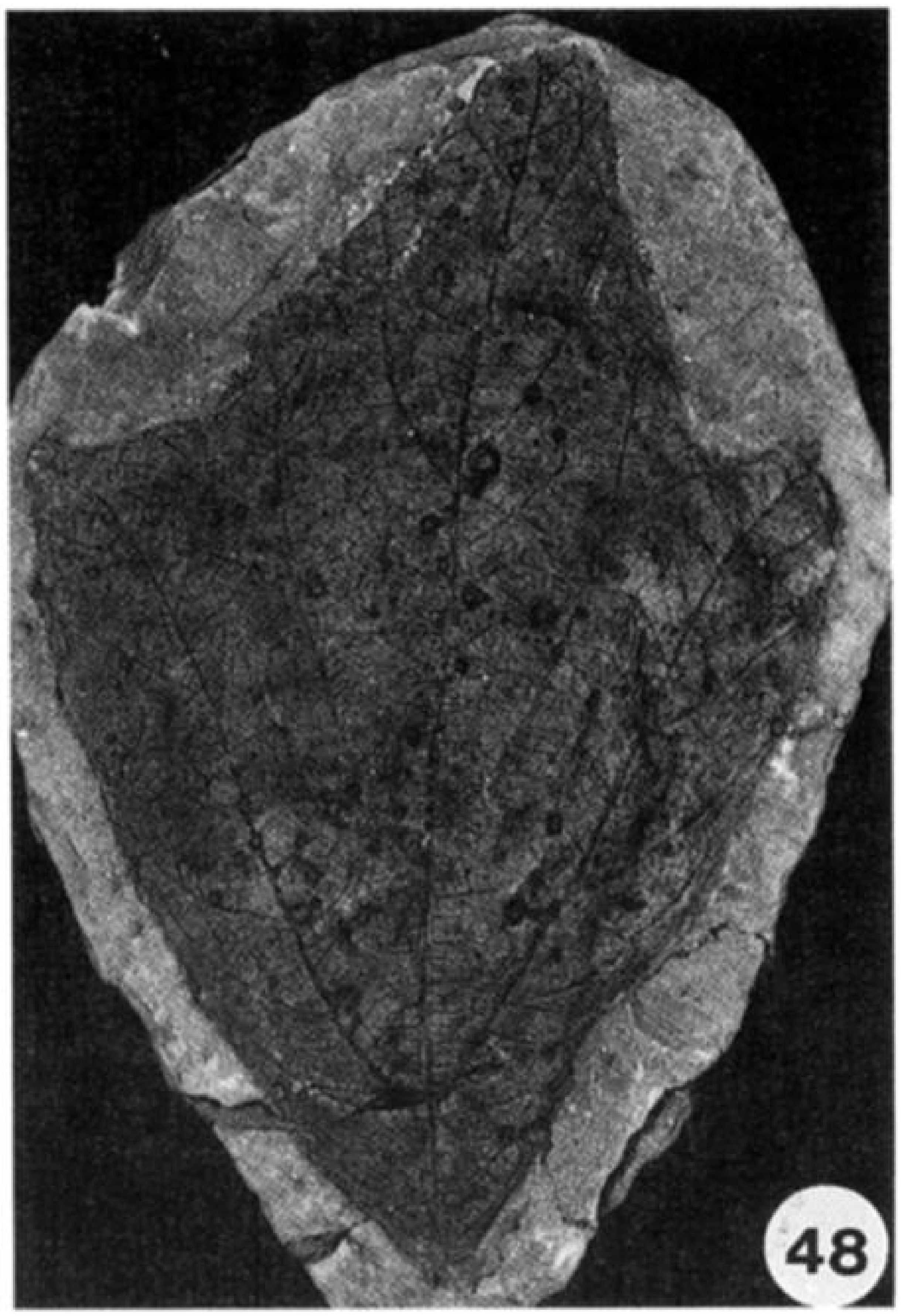
Figures 31–46. For description see opposite.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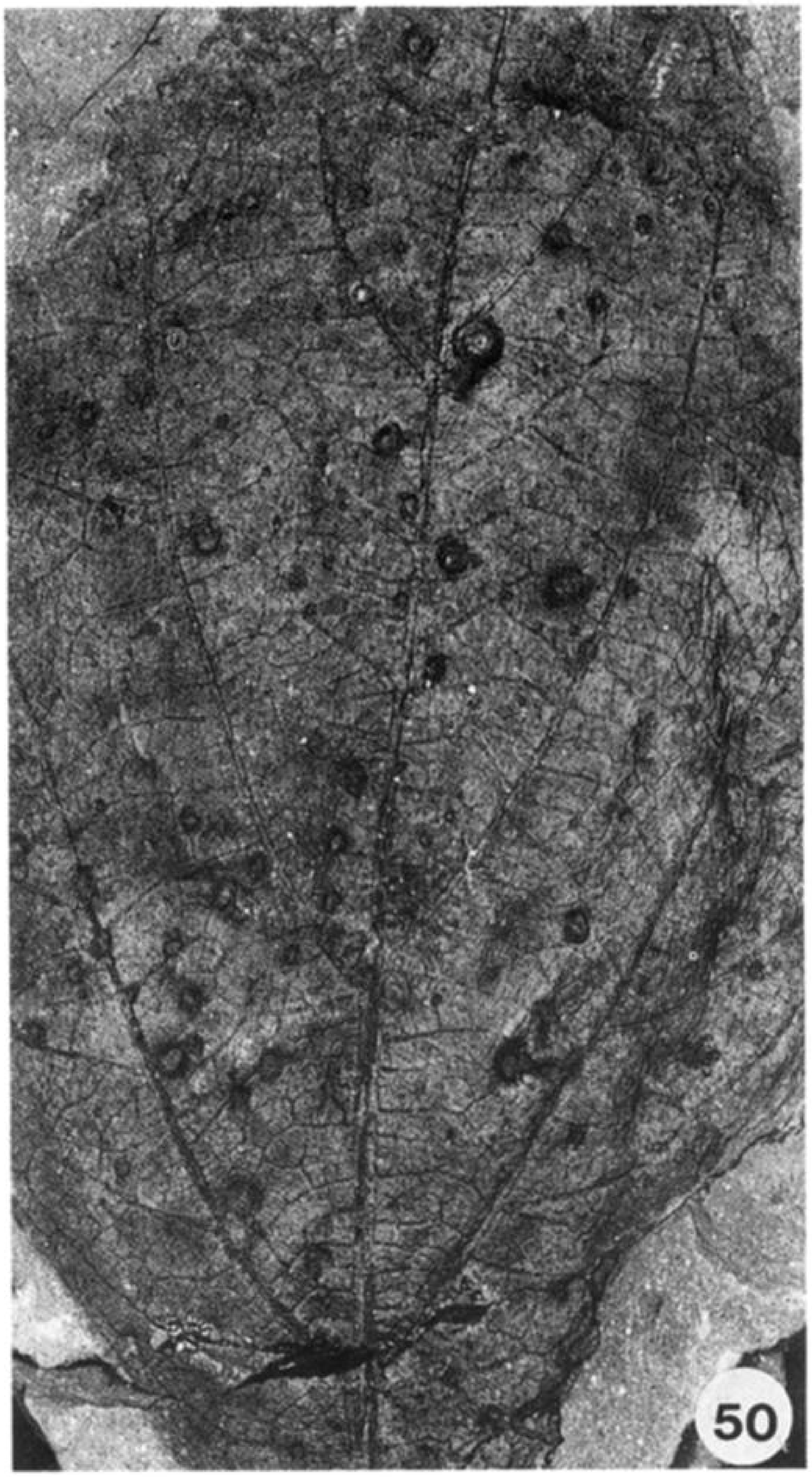
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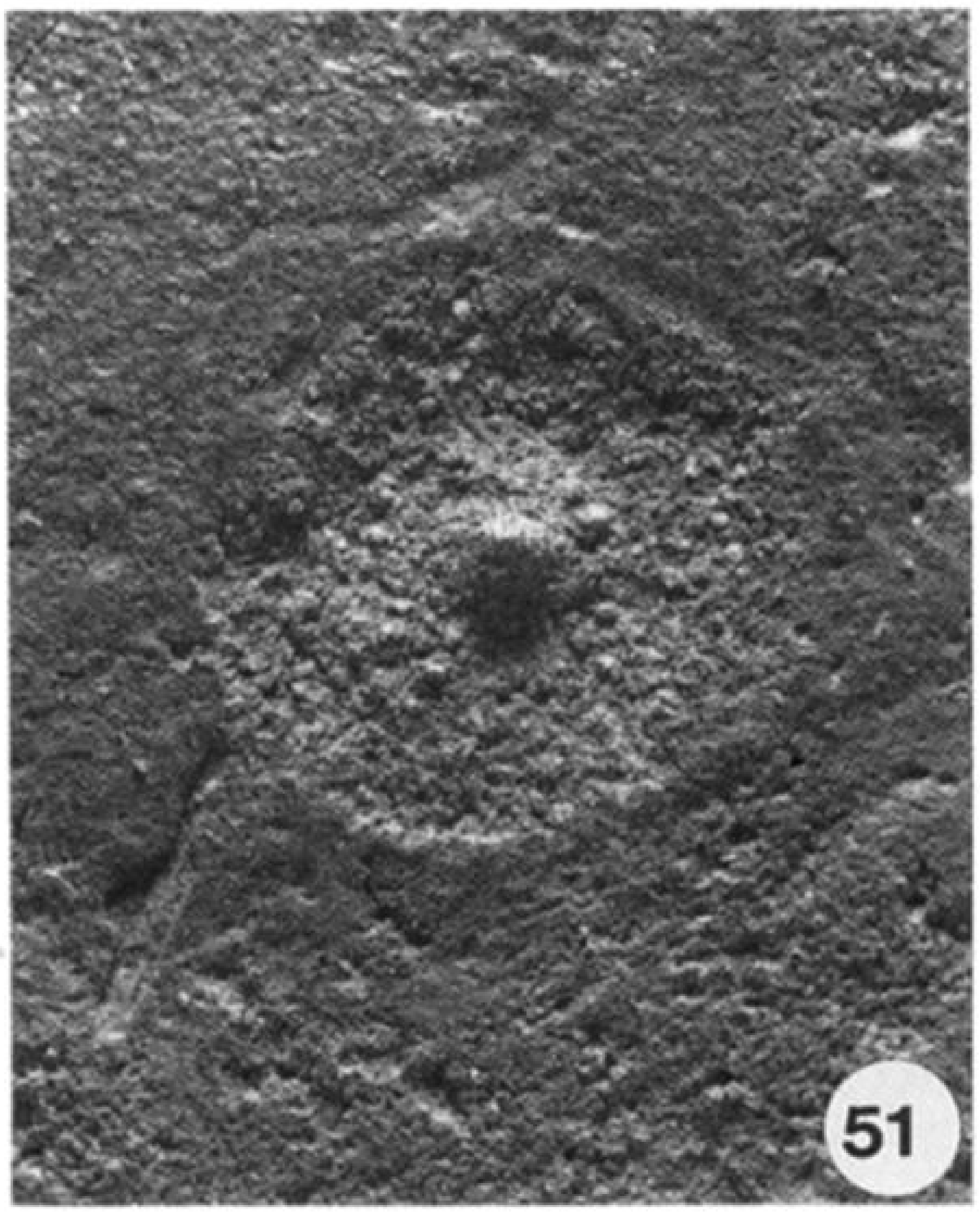
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Figures 48–52. Examples of Cretaceous galls.

Figures 48 and 50. Angiosperm leaf from the Cenomanian, Cretaceous, Vyserovice, Czechoslovakia with small cone galls, each with a central exit hole. Magn. × $\frac{1}{2}$ Natural History Museum, London. v53724. Magn. × $\frac{1}{2}$. Figure 50. Magn. × 1.

Figure 49. Angiosperm leaf with large ball gall from the Ripley Formation, Maastrichtian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago, PP14154. Magn. × 1.

Figures 51 and 52. Angiosperm leaf with spot gall with central exit hole from the Dakota Formation, Cenomanian, Cretaceous, U.S.A. Field Museum of Natural History, Chicago. UP 348. Figure 51. Magn. × 6. Figure 52. Magn. × $\frac{1}{2}$.