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Early terrestrial arthropods: a fragmentary record

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[Plate 1]

The earliest unequivocal terrestrial fossils are uppermost Silurian (Přídolí) myriapods, presumed to be pioneer decomposers. Descendants of their marine ancestors may be discernible in the Cambrian lobopod *Aysheaia* (recently challenged). Known euthycarcinoids are too late except as survivors from such a lobopod ancestry. Unique arthropods are also known from Cambrian and Ordovician lake deposits, but shed no light on origin of terrestrial forms.

Among relevant arthropods, only scorpions have a continuous record from Silurian aquatic to Devonian terrestrial records (eurypterids are dealt with elsewhere in this volume). Respiratory organs are unknown in Silurian forms, but at least three types of gills may have existed by the Devonian, arguing for great diversification by then, and possible multiple colonization of the land. Trace fossils suggest some Devonian scorpions were amphibious, while development of a pre-oral tube indicates they were adapted for feeding out of water. Morphology of Silurian forms implies they were aquatic, solid feeders.

The presence of Silurian fungivorous microarthropods is indicated by Ludlow faecal pellets containing fungal hyphae. The terrestrial decomposer niche was occupied, and soils therefore in existence, by then. Constant humid microclimates created by early land plants were important in enabling land colonization by arthropods otherwise susceptible to desiccation. Mamayev's gravitational hypothesis provides an explanation for evolution of hexapody from uniramians clambering up and over early land plants.

Plants of the Siegenian Rhynie Chert show pathological features that may indicate terrestrial plant–animal interaction by that time, as do other lines of circumstantial evidence. Energy costs incurred by plants producing anti-herbivore and anti-detritivore defences have therefore probably been significant in ecosystems since the Devonian.

Recent major backwards extensions in time of terrestrial arthropods prove that the terrestrial geological record is still poorly sampled. Givetian Gilboa shows that, as with early plants, much can be hoped for from study of cuticle fragments. New finds should be sought in pre-Devonian equivalents of the Carboniferous Mazon Creek delta plain facies.

The earliest land animals are, of course, unknown. This account deals only with some aspects of the invertebrate, principally arthropod (worms have been summarized by Conway Morris *et al.* 1982), transition to the land as currently known from the Siluro-Devonian fossil record, and updates an earlier account (Rolfe 1980). It does not attempt to review all the possible steps and routes taken by animals, or their origins and adaptations, that might have occurred in that early colonization of land. These have, in any case, been dealt with recently by Little (1983). Even Little's book does not deal with the important first land colonization, which must have included desert prokaryotes. 'The indirect interaction of communities of microbes – prokaryote and eukaryote – to alter environmental conditions suggests that the modern era was in full swing prior to the appearance of the hypertrophied familiars we hold so dear: most invertebrates, vertebrates and plants' (Margulis 1981, p. 151). The Gaia hypothesis, that the lower atmosphere of the Earth has been highly modified by life to support more life, that is, that life makes much of its own environment (Margulis 1981, p. 348), is important in setting the scene in which our hypertrophied familiars make their first terrestrial appearance.

Discoveries of early terrestrial invertebrate fossils are so few and far between that generalizations therefrom are rarely possible, or wise. New finds have a habit of pushing back the origin of main groups. Thus, the land fauna recently found by Bonamo & Grierson (Rolfe 1982*a*, *b*; Shear *et al.* 1984) has taken the first record of at least centipedes (and perhaps also the earliest insects and amblypygid arachnids) back from the Upper Carboniferous to Middle Devonian – from 300 Ma to 380 Ma. This immediately falsifies Little's (1983, pp. 222–223) correlation of the appearance of centipedes with the great development of terrestrial forests in the Carboniferous: a reasonable conclusion in the light of the then recent verification of Upper Carboniferous centipedes (Rolfe 1980, p. 150). That such large leaps can still occur indicates how poor is the present sampling of the inevitably poorly represented terrestrial geological record.

DERIVATION OF SOME EARLY LAND ARTHROPODS

There is very little direct evidence for such derivations in the fossil record: most of the terrestrial organisms appear in the fossil record fully fledged. One is therefore obliged to resort to deduction and induction from the distribution, comparative anatomy and physiology of the extant fauna, or to hypothesis, with the geological record serving as a constraint on timing. The results of this approach are summarized by Little (1983).

The great diversity of arthropods present in the Middle Cambrian Burgess Shale (Whittington 1980, 1981 *b*) hints at the vast reservoir of marine arthropods that must have existed. Experience of that fauna suggested to Whittington (1981 *a*) that morphologically discontinuous soft-bodied taxa were also very numerous. The terrestrial emergence and expansion of uniramian and chelicerate stocks (Bergström 1978; Whittington 1979, figure 2) rather than other arthropods may therefore have been fortuitous. The breaching of the land barrier would then have the characteristics of the 'sweepstakes' route recognized by the palaeobiogeographer. By rapidly and effectively filling the newly available terrestrial niches, these arthropod stocks seem to have prevented later attempts by other arthropod groups, although crustaceans have also made significant inroads (Little 1983). Other stocks that had the potential to make the transition remained in the sea to be filtered out by subsequent selection (Whittington 1980, p. 146; 1981 *a*, p. 86).

Another reservoir of aquatic arthropods from which colonization of the land might have taken place existed in freshwater lakes (Bergström 1978, pp. 44–46). Such deposits, of low fossilization potential, are known (cf. Boucot & Janis 1983, p. 268) from the Ordovician of Tennessee (Caster & Brooks 1957) and the Upper Cambrian of Siberia (Bergström 1980, p. 91, figure 2). Both sites yield unique arthropods, of little obvious relevance to origin of terrestrial forms. Stocks of relevant arthropods may yet be found elsewhere in comparable situations.

EARLY FAUNAS

The faunas of Siegenian Rhynie (400 Ma) and Emsian Alken (390 Ma) have recently been summarized elsewhere (Rolfe 1980). The newly discovered Givetian Gilboa (380 Ma) is more diverse than Rhynie, but resembles it in being almost wholly terrestrial and composed largely of carnivores (Shear *et al.* 1984). It includes a possible machilid thysanuran, a bristle-tail such as today is a saprophytic litter and soil feeder, eats marine detritus or scrapes algae off rocks (Gerson 1977, p. 237). A mite is also present that can be referred to the extant saprophagous family Ctenacaridae. The possible presence of a scutigeromorph centipede is surprising, since these present-day hunters of fast-moving prey such as spiders and flies have been thought of as highly advanced (Manton 1977, p. 35). As with the Gilboa craterostigmatomorph centipede, a return to older views of their primitive nature may be required.

MYRIAPODS, INSECTS AND PROTOLOBOPODS

The role of the Middle Cambrian *Aysheaia* as a primitive lobopod (Bergström 1978; Whittington 1979, 1980, 1981*a*; Rolfe 1980, p. 118; Little 1983, p. 127) has recently been challenged, and comparison suggested instead with elasipodid echinoderms or polychaetes (McKenzie 1983), though a defence has been made (Robison 1984). Tardigrades, thought to be related to ancestral lobopods and potentially important because of their ability for cryptobiosis, are now known to include marine species, largely from nearshore and interstitial environments (McKenzie 1983), which enhances their role as possible early members of the land fauna (Rolfe 1980).

True myriapods are first known from alluvial fan and flood plain deposits (Morton 1979) of the Old Red Sandstone, although there are several earlier ambiguous specimens (Rolfe 1980, pp. 122–123). Since the body form of myriapods is today strongly correlated with habit (Manton 1977), it is possible to induce a variety of habits for these earliest forms. Flat-backed forms may have been litter-splitters, while rounder bodied types were burrowers. All imply the presence of decaying vegetation and thus perhaps soils. A summary of work currently under way on these forms is given by Almond (this symposium).

There is some doubt about the exact age of these earliest records. Dr B. J. Bluck (personal communication) points out that lavas above the myriapod-yielding strata near Oban have recently been dated *ca.* 410 Ma (Thirlwall, in Clayburn *et al.* 1983). On currently accepted time scales, this is topmost Silurian, Pridolí (for example, Harland *et al.* 1982, p. 16). A similar radiometric age has been obtained from well above the myriapod-bearing beds of Stonehaven, but J. Richardson, unpublished, states that the associated sediments yield Gedinnian spores, casting doubt on a Přídolí assignment for the Oban age. Nevertheless, a pre-Gedinnian age for the Stonehaven finds seems likely, which could thus be Přídolí.

The ultimate origin of myriapods is of much interest since their ancestry is shared with that of insects. Such an ancestor probably had many pairs of legs, was small and weakly sclerotized and lived interstitially, a specification which, like cephalocarid crustaceans, means they will be difficult to find fossilized (Little 1983, pp. 152, 159). The discovery of minute fossil crustaceans in the Cambrian, by Müller (1982), shows that the search for such ancestors is not futile. Some aquatic uniramian characters are shown by the incomplete Cambrian *Serracaris* (Briggs 1978), and this form, perhaps significantly, has other features linking it with trilobites. Apart from *Aysheaia*, uniramian ancestors are conspicuous by their absence from the Burgess Shale fauna (Briggs 1983, p. 15). Other descendants may have remained and evolved in the sea and thus be found fossil to bear witness to that ancestry: Carboniferous euthycarcinoids may represent such a stock (Schram & Rolfe 1982).

It is interesting to find possible insects, machilid thysanurans, in the Gilboa assemblage (Shear *et al.* 1984), and collembolans at Rhynie (Whalley & Jarzembowski 1981), along with the predatory trigonotarbid and amblypygid arachnids. These 'cryptozoic complex' arachnids were thus established in a predator:prey relationship early on, a relationship that probably gave impetus to the development of flight in hexapods. The Carboniferous explosion of winged insects, in turn, provided increased prey for the arachnids that engendered them, a striking example of the more rapid evolution of prey than predator (Bakker 1983), and of the persistence of habits (Manton 1977, pp. 33–34). This led to the increase of arachnid orders in the Carboniferous (Rolfe 1980, p. 137; Little 1983, p. 126), although more of these are now turning up in the Devonian (Shear *et al.* 1984).

Scorpions

There is one terrestrial group of fossil arthropods with immediately apparent aquatic forebears, the scorpions, which is beginning to yield evidence of the nature of the transition to land, and which can therefore be dealt with in some detail.

Kjellesvig-Waering's results of many years work on fossil scorpions are about to be published, and most of what follows is based on that work (kindly made available by K. and A. Caster and P. Hoover).

Morphology

Only three autapomorphic characters separate scorpions from eurypterids: pedipalpal chelae, pectines and poison sting, although the latter is almost unprovable in fossils. The earliest fossil scorpions known, of Llandovery age, show the first two of these characters. From eurypterids, scorpions inherited not only the similar general body form but also the eurypterid type of many-faceted compound eyes, the five variably shaped abdominal plates (Blattfüsse of eurypterids) covering ventral gill chambers, compared with only four sternites of living scorpions, coxal gnathobases (in *Proscorpius*) and, in one key Frasnian genus from Wyoming, a vestigial median abdominal appendage. There seems little reason therefore to doubt scorpions' derivation from eurypterids (Rolfe 1982*b*; Rolfe & Beckett 1984; cf. Kraus 1976; Weygoldt & Paulus 1978; Grasshoff 1978, p. 280), as some zoologists are now willing to recognize (Simonetta & Delle Cave 1980, p. 8; Little 1983, p. 124; Shear *et al.* 1984).

Although large openings leading to a presumed gill chamber are visible in the posterior of the sternite or on the doublure of the Přídolí *Proscorpius osborni*, these were not thought by Kjellesvig-Waering to be stigmata proper.

Gills are unknown from Silurian forms, but they are thought to have been present from the nature of the ventral abdominal plates and overall resemblance to later gilled forms. Gill-like structures have been found in three Devonian genera. The filaments of the Emsian *Waeringoscorpio* (Størmer 1970) are quite different from any others, living or fossil, and remain ambiguous. Equally unusual ribbed, spongy gill plates(?) are found in the Onteora redbed form collected from New York State by Hueber. The most convincing gills of all to this writer are the tracts of a Wyoming Emsian genus that Kjellesvig-Waering later reinterpreted as free, ventral abdominal plates (Rolfe 1982*b*).

Pectines of these aquatic forms are more variable than in the living forms, and the question of a possible change in function of these distinctive organs has been referred to elsewhere (Rolfe & Beckett 1984).

Størmer (1970, 1976, 1977) pointed out that the development of a pre-oral chamber for external digestion of prey was as decisive a factor for adaptation in terrestrial arthropods, as it was in vertebrates. The lack of anterior production of coxae and presence of a large sternum in most Silurian scorpions where they can be traced suggests that no such pre-oral chamber existed in Silurian forms or in *Waeringoscorpio*, all of which therefore were probably marine forms. Instead, gnathobasic coxae and large chelicerae occur, implying the ingestion of solid rather than the externally digested liquid food which would readily dissipate in an aquatic environment. Such a condition is found today in Xiphosura and some mites (Hammen 1977, p. 312). Maxillary lobate coxae exist in Emsian forms, which suggests scorpions were liquid feeders by then. Possessing gills, such scorpions could only leave the water for short periods, like land crabs (Little 1983, pp. 83–106). One Přídolí form shows this development earlier, and Kjellesvig-Waering believed this preadaptation began at least that early, and that the Devonian rise of predatory fishes and eurypterids gave selection pressure for such amphibious forms. Other changes in morphology correlated with the transition included, in due course, reduction and eventual loss of the sub-sternite abdominal plates and gills, dispersal of lateral faceted eyes into individual eyes, backward displacement of median eyes from the anterior border, and the loss of pre-pectinal plate and first abdominal plate, so that modern scorpions only have sternites 2–5 developed.

A large stridulation organ occurs on the pedipalpal coxa of the metre-long Gedinnian *Praearcturus*, which might be thought of as a peculiarly terrestrial adaptation, yet such organs occur in extant aquatic insects where they are used for communication or defence, as well as in the aquatic or amphibious Triassic scorpion *Mesophonus*. In living scorpions, stridulation is not used for intraspecific communication, but for defence. In land crabs stridulation is used to communicate, and can be transmitted to the substrate for threat, appeasement or sexual display. Some male crabs attract females to their burrows by stridulating (Little 1983, pp. 87, 100, 104, 121–122).

Occurrence

The eight Silurian scorpions known, largely come from sediments that range from offshore marine to restricted marine situations (Rolfe & Beckett 1984). One of these has recently been reinterpreted as a brackish–estuarine intertidal situation (Boucot & Janis 1983), but only two records of Silurian scorpions are from the more proximal regions of deltaic and fluvial environments, and these are of Downtonian age. The record shows a landward shift with the eight Devonian scorpions, shortly to be published under seven genera (Kjellesvig-Waering 1984). Only *Palaeoscorpius* comes from the deep marine Hunsrückschiefer, and *Waeringoscorpio* from the Alken land-locked lagoon, communicating with the sea only at high tide. All other records are either from estuarine channel-fill or fluvial deposits. The unusual Onteora redbed scorpion actually occurs among zosterophylls buried at the site where they grew (Hueber & Grierson 1961), perhaps on point bars in broad river channels (Scott *et al.* 1976) or, like most Old Red plants, forming dense monotypic stands near water on flood plains (Edwards, this symposium).

Trace fossil evidence

Palaeohelcura trackways (Rolfe 1980, pp. 131, 147), thought to have been left by large scorpions such as *Brontoscorpio* or *Praearcturus*, are known from Gedinnian localities in Antarctica. Opinion varies as to the exact environment of deposition of these strata: trackways occur on foreset beds deposited in active channels or on tidally emergent sandflats laced with channels. Bradshaw (1982 and personal communication) prefers to regard the trackways as having been made subaquatically, but agrees they could have been left during periods of temporary emergence. The sediments have also been interpreted as the products of monsoonal flood or even aeolian dunes (Bradshaw 1982, pp. 621–622, 626).

Comments

Habits deduced from morphology, and habitat deduced from sedimentology, receive confirmation from trace fossils that scorpions were amphibious by the early Devonian.

The multiplicity of gill types (if they are indeed gills), suggests different evolutionary derivations from within the scorpion complex, perhaps implying multiple independent colonization of the land, as others have suggested for the chelicerates as a whole (Bergström 1978; Dubinin 1957; Sharov 1966; Hammen 1977; Grasshoff 1978; Kraus 1976; Manton 1979; Little 1983, p. 126). The very wide distribution of records of Devonian amphibious scorpions across the Laurussian plate (Boucot & Gray 1983), from Wyoming to England at least, may be a further reflection of this diversity.

Of Kjellesvig-Waering's (1984) 21 superfamilies of scorpions, six are present in the Silurian, and an additional three enter in the Devonian. Only one of those 21 superfamilies survives today. This suggests that great changes occurred in scorpions in quite widely separated Silurian seas, since the classification reflects mainly the nature of the covering of the respiratory apparatus, whether by abdominal plates or sternites proper and, to a lesser extent, the development of the oral tube, as reflected in the coxosternal configuration.

It remains unclear whether the existence of the wide floodplains bordering Old Red landmasses, traversed by many braided streams, provided ideal opportunities merely for the *preservation* of these amphibious scorpions, or whether this was the actual environment in which that transition took place, as it is tempting to believe.

The preadaptations of eurypterids for avoiding desiccation (Rolfe 1980; Selden, this symposium) were inherited by scorpions, and hence it has been suggested that they could colonize land directly (Little 1983, p. 126). Some may have passed directly over beaches, others via river systems, to achieve this end.

TRACE FOSSILS

Trace fossils can be of great value in analysing habits and habitat of past terrestrial life, since they are autochthonous. Unless associated with their body-fossil maker, interpretation of that maker may be ambiguous, especially with the current lack of neoichnology for relevant terrestrial forms (Rolfe 1980). In addition, there may be room for various interpretations of the exact depositional regime of the containing sediments. Progress is, however, possible. Thus, the *Beaconites* tubes that are rapidly becoming recognized as a widespread feature of Old Red facies, have been shown by Allen & Williams (1981 *a*, *b*) to occur in flood plain sediments, in and near active river channels where a moist environment was provided. The animal as yet remains unknown, but the tubes range up to 250 mm across (Allen & Williams 1981 *b*), and may be associated with a surface body-drag groove, impressions of appendages and presumed faecal pellets up to 12 mm in diameter (Allen & Williams 1981 *a*). This association favours an arthropod origin (Rolfe 1980; Allen & Williams 1981 *b*; Bradshaw 1982) which, if true, confirms the burrowing habit of early terrestrial arthropods in seeking increased relative humidity and avoiding temperature extremes. The groove and tracks suggest a chelicerate of some kind (for example, Briggs & Rolfe 1983), but faecal pellets would normally be sufficient to exclude comparison with most living chelicerates, that are liquid feeders. Living *Limulus* is a solid feeder and produces columnar faeces (Kaestner 1968, p. 79), and induction of liquid-feeding from the repertoire of the limited extant fauna must be guarded against. Some evidence for solid ingestion by early chelicerates has been given (Rolfe & Beckett 1984), and more is expected shortly from C. D. Waterston's study of complete '*Cyrtoctenus*'. Eurypterids are obvious candidates. Another possibility is that such burrows were produced by scorpions, and extant scorpion burrows (Kaestner 1968, p. 109) might be investigated to that end.

Progress has also been made on the significant Lower Old Red ichnocoenosis from Dunure (Rolfe 1980, pp. 131–133, figure 4). Pollard *et al.* (1982) have recognized several of the Dunure ichnotaxa elsewhere in a more fully understood sedimentological context, and at least some of them they attribute to ephemeral aquatic benthonic arthropods, inhabiting temporary pools, low bars and mud-flats, rather than to fully terrestrial arthropods. Reinterpretation of the environment of deposition of the Dunure deposit suggest a more subaqueous origin than previously envisaged, and the most myriapod-like trackways come from the deepest of the shallow water siltstones (Pollard & Walker 1984). This might be significant, of course, as evidence of locomotor preadaptation by amphibious forms. The variety of arthropods represented at this transitional site of ephemeral lakes in the distal region of a braided river plain promises to yield further information on such key forms.

Palaeoecology

The importance of stands of humidifying plants close to water, as an environment encouraging emigration of aquatic animals, can hardly be over-emphasized. Microclimates within such plant stands must have varied from top to bottom. In modern *Sphagnum* bogs there are large daily fluctuations of temperature and relative humidity in the surface boundary layer, yet these factors remain practically constant in the stalk layer. Algae and bryophytes are among the first colonizers of new terrestrial habitats today, and support their own faunas. Both cryptogams and fauna are associated in similar stages of extant biotal succession series. Thus, when algal mats form on bare peat, Collembola can colonize beneath them, since high humidities are maintained (Gerson 1974, p. 36). What may be such an algal mat has been found at the Old Red locality described by Scott *et al.* (1976). The Devonian terrestrial assemblages suggest that similar coevolutionary associations had occurred between animals and plants by then (Gerson 1969, pp. 496, 499).

Extant arthropods feed on the greater variety of plants in the terrestrial than in aquatic habitats, where they are practically restricted to the available algae. They are thus primary consumers of plants in aquatic as well as terrestrial environments, and can voraciously skeletonize whole plants. Gerson (1974) documents many intimate associations of arthropods with algae, although little is known of the nature of those interactions. Sherwood-Pike & Gray (1984) suggest that 'the transition from a saprophyte on shallow water algal remains to saprophyte on detritus produced by terrestrial plants in moist environments requires little adaptation'. Similar escalations can be suggested at all points in the ecological and no doubt palaeoecological pyramid: 'when free living mites that ordinarily obtain food from fungi or decaying material find themselves on plants, in birds' nests or on animals...some may be able to feed sufficiently to survive' (Jeppson 1974, p. 5). Such generalized associations only hint at what the original mutualisms might have been, and one can speculate that the Devonian animal–plant interactions suggested by Kevan *et al.* (1975) continue habits that were carried over from their aquatic forebears. If there is any basis for Pirozynski & Malloch's (1974) theory of the origin of land plants as a symbiosis between a semiaquatic green alga and an aquatic fungus, one may make the wild speculation that early arthropods delivered the first inoculation of the one into the other.

Interaction between early arthropods and plants

The earliest direct evidence of a plant–animal association is provided by faecal pellets containing fragments of fungal hyphae, from the Ludlovian of Sweden, described by Sherwood-Pike & Gray (1985). They suggest the pellets came from a fungivorous microarthropod (collembolan, mite or milipede) that lived in a near-shore plant community. This is also the oldest evidence of the terrestrial decomposer niche occupied by higher fungi and saprophagous microarthropods, and thus for the degradation processes involved in soil formation. Such processes are well established by the Carboniferous, where much more evidence is available (Rolfe 1980, 1984; Scott & Taylor 1983; Taylor & Scott 1983). Their initiation was of great importance, however, since it is through such decomposer chains that the greatest proportion of primary production passes in the terrestrial ecosystem, in marked contrast to the marine ecosystem.

As is thought to be the case with insects, herbivory by other terrestrial arthropods probably originated from such initial detritivory. The greater the exposure of such an arthropod to a plant, the more likely a herbivore:host relationship was to arise (Little 1983, p. 223).

Kevan *et al.* (1975) present many lines of circumstantial evidence for coevolutionary development of Devonian terrestrial vascular plants, fungi and arthropods. They showed that the spores of terrestrial plants and fungi became more diverse from the Silurian to the Devonian and acquired characters such as spines and grapnel-like ornament. Such features suggest protection from or dissemination by arthropods, or both. Heterospory they interpreted as a possible response to arthropod-mediated fertilization.

The remarkable preservation of the Rhynie Chert biota has permitted observation of associations between members of this Lower Devonian, Siegenian assemblage. Similar relation-

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DESCRIPTION OF PLATE 1

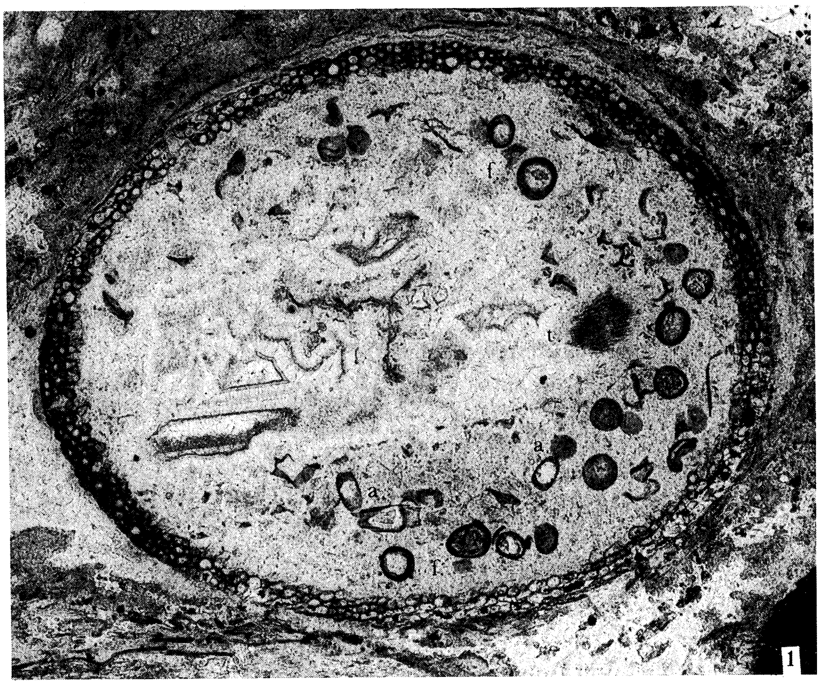
FIGURE 1. Hollow stem of *Rhynia* containing limb segments of trigonotarbid arachnids (a.), fungal spores (f.) and displaced plant tissue (t.) (magn. × 14). Hunterian Museum, Kidston Collection 2431.

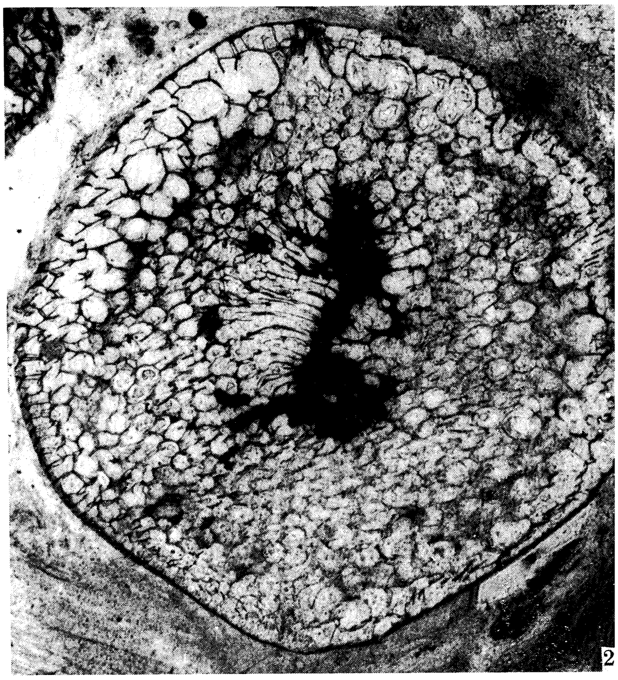
FIGURE 2. *Rhynia* stem necrosis, showing local hypertrophy and breakdown of outer cortex, and damaged and plugged vascular area bordered by hypertrophied cortex (magn. × 39), Kidston 2427. Original of Kidston & Lang (1921*a*), figure 16.

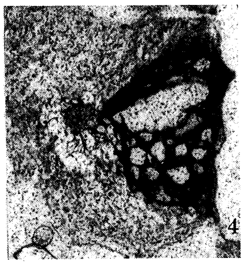
FIGURES 3 AND 5. *Rhynia* stems, showing necrotic cavities still roofed over by epidermis, neighbouring cortical cell hypertrophy and damaged and plugged vascular area (magn. × 39, 25) Kidston 2390, 2414. Figure 3, original of Kidston & Lang (1921*a*), figure 12.

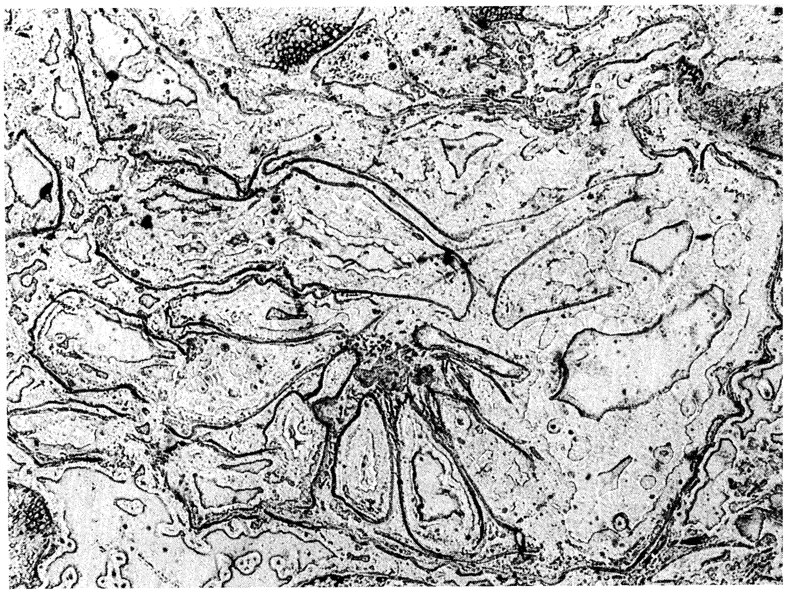
FIGURE 4. Stem fragment showing 'brecciated' tissue surrounded by opaque (?)gummosis (magn. × 29), Kidston 2428.

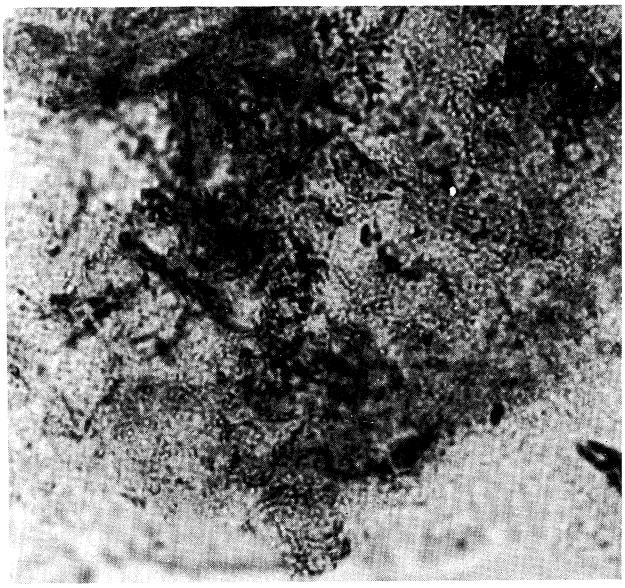
FIGURES 6–8. Trigonotarbid arachnid *Palaeocharinus* with a food mass (or regurgitate) held by chelicerae, between other limb bases. Hunterian Museum serial section A. 2451/25, prepared by A. G. Lyon. Figure 6: oblique transverse section of enrolled individual, carapace to right, opisthosoma above (magn. × 16); figure 7: detail of chelicerae (c.), limb bases, and food mass (magn. × 53); figure 8: detail of right side of food mass, showing possible cell outlines in general structureless organic mass (magn. × 260).











Figures 1–8. For description see opposite.

ships presumably existed elsewhere, and in earlier assemblages, which have not yet been detected. The interpretation of these observations is admittedly equivocal. Thus, hollow sporangia of *Rhynia* may contain trigonotarbid arachnids (Rolfe, in Kevan *et al.* 1975, p. 396, plate 56; Rolfe 1980, pp. 125–126) which have been taken as evidence that these presumably normally carnivorous arthropods may have been facultative herbivores, able to feed on the spores within those sporangia. This has considerable coevolutionary implications for the development of spore dissemination, culminating later in pollination by insects (Kevan *et al.* 1975; Scott *et al.* 1985). Such spore-feeding has been established for the Carboniferous from gut contents and bored spores (Scott & Taylor 1983; Taylor & Scott 1983; Scott *et al.* 1985), yet remains unproven for Rhynie (figures 6–8, plate 1). I prefer to regard the occurrence of such arthropods within Rhynie Chert stem 'straws' and practically sporeless sporangia (albeit with plant debris inside, and perhaps abscissed: Edwards 1980, pp. 184–185) as evidence that the arthropods actively sought out these refuges to conserve body moisture. It is also possible that the trigonotarbids consumed the contents of the sporangium before adopting it as a shelter (Chaloner & Macdonald 1980, p. 13). Such cryptozoic behaviour plays an important role in conserving water that would otherwise be lost by transpiration across their cuticles, since most arachnids lack the wax layer of other terrestrial arthropods (Little 1983, pp. 109–114). It may also explain the frequent occurrence of such trigonotarbids inside hollow stems (figure 1). Such sites must have been at a premium, even in the *Rhynia* thickets, in view of the absence of large-leaved plants to provide shade.

Palaeopathology

Many specimens of *Rhynia* from the basal peat bed of the Rhynie Chert sequence (Tasch 1957, p. 7) show pathological features (figures 2–5). Extensive necrosis around stem cavities and punctures is accompanied by hypertrophy of neighbouring cells and the formation of opaque tissue, presumably by gummosis, as well as callus (Kidston & Lang 1921*a*, *b*). Such features were originally ascribed to prolonged action of local volcanic conditions, but Kevan *et al.* (1975) and Scott *et al.* (1984) attributed them to physical injury by arthropods or other metazoans, probing to the phloem to feed off sap (Raven 1983). Kevan *et al.* (1975) were careful to emphasize that the evidence for such damage having been caused by animals was not clear-cut, and that fungal as well as other pathogenic origins were not ruled out. As Butler & Jones (1949, p. 207) point out, 'in galls... there is nothing new in the tissues or organs of reaction, but merely a disorganization or an intensification or inhibition of normal processes of tissue and organ formation and differentiation...powers which plants can ordinarily make use of in dealing with such accidents or wounding or in meeting extremes of environmental or nutritional or growth modifying conditions'. Thus, all these options should be kept open until less equivocal evidence is available for the interpretation of these features. The extensive nature of much of the damage could also be interpreted as the result of nematode action (for example, Wallace 1973, pp. 13, 43, 45, 51–56, plate 4), with the host responding as the parasite invades, resistance being the rule and susceptibility the exception. Some of the holes, still roofed over by the thin epidermis (Kidston & Lang 1921*a*, figure 12, figures 3, 5 here), are reminiscent of the pocket galls created by living eriophyoid mites which not only provide protection for the brood, but supply food by extrasucculent cells (Jeppson *et al.* 1975, pp. 354, 365). Some of these associations may be truly parasitic (Conway-Morris 1981, p. 494).

Kidston & Lang (1921*a*) interpreted the hemispherical projections on *Rhynia* as a pathological response to injurious vapours, yet they also resemble the intumescences developed on plants suffering from excessive moisture (Butler & Jones 1949, p. 190). Some of these structures have subsequently been regarded as gametophytes (Lemoigne 1971), but not all of them can be so interpreted (Edwards 1980, p. 185). One wonders if they could represent sites of attack by arthropods, or other organisms, which have subsequently been plugged by hypertrophy of the outer cortex.

Fungi occur as parasites of Rhynie land plants, where they are accompanied by a springtail and mites. Extant members of these groups are known to be vectors of plant diseases: animals favouring plant pathogens as food are more likely to spread them than control them (Kevan *et al.* 1975, pp. 398, 407, 411). The existence of fungal hyphae-packed coprolites in the Silurian (Sherwood-Pike & Gray 1985) proves that fungivory was established by then. Mites also occur in the Gilboa assemblage, which is of interest since faecal pellets of extant mites may contain viable fungal conidia and microsclerotia (Beute & Benson 1979, p. 493; Kevan *et al.* 1975, p. 404).

Camouflage and defence budgets

It may be significant that no camouflage or mimicry has yet been documented in Devonian terrestrial arthropods, although it has been for Carboniferous forms (Rolfe 1980, p. 137; Scott & Taylor 1983; Taylor & Scott 1983).

Subtler indirect interactions may also have been present, which are unlikely to be detectable from fossils. Although 'the amounts of mass, energy and nutrients in and flowing through some extant arthropods are much smaller than for plants and microbes, arthropods have a strong indirect influence over plant productivity and nutrient cycling processes' (Seastedt & Crossley 1984, p. 157). The energy costs of producing anti-herbivore or anti-detritivore defences, even though these may not be used, may be very large (Feeny 1975). Since at least the Devonian, therefore, arthropods have interacted with plants and microbes to influence the present ecosystem.

Conclusion

Recent major backward extensions in time of terrestrial arthropods prove that the terrestrial geological record is still poorly sampled. Compared with the picture derived from careful study of fossil plant fragments, that derived from early fossil arthropods is scrappy, and any current list of first occurrences is premature. The excellence of preservation of terrestrial arthropods at sites such as Rhynie and Gilboa, coupled with the recent success in extracting Cambrian aquatic microarthropods, suggests that many sites of early terrestrial invertebrates and their aquatic ancestors remain to be discovered. Hitherto, Devonian terrestrial invertebrates have been discovered largely as a byproduct of palaeobotanical research. What is now required to fill out the currently inadequate record is a programme of systematic exploration by acid extraction of arthropod cuticles from relevant pre-Middle Devonian facies. By analogy with later prolific terrestrial fossil assemblages such as Mazon Creek, greatest success should be achieved by concentrating on delta-plain facies.

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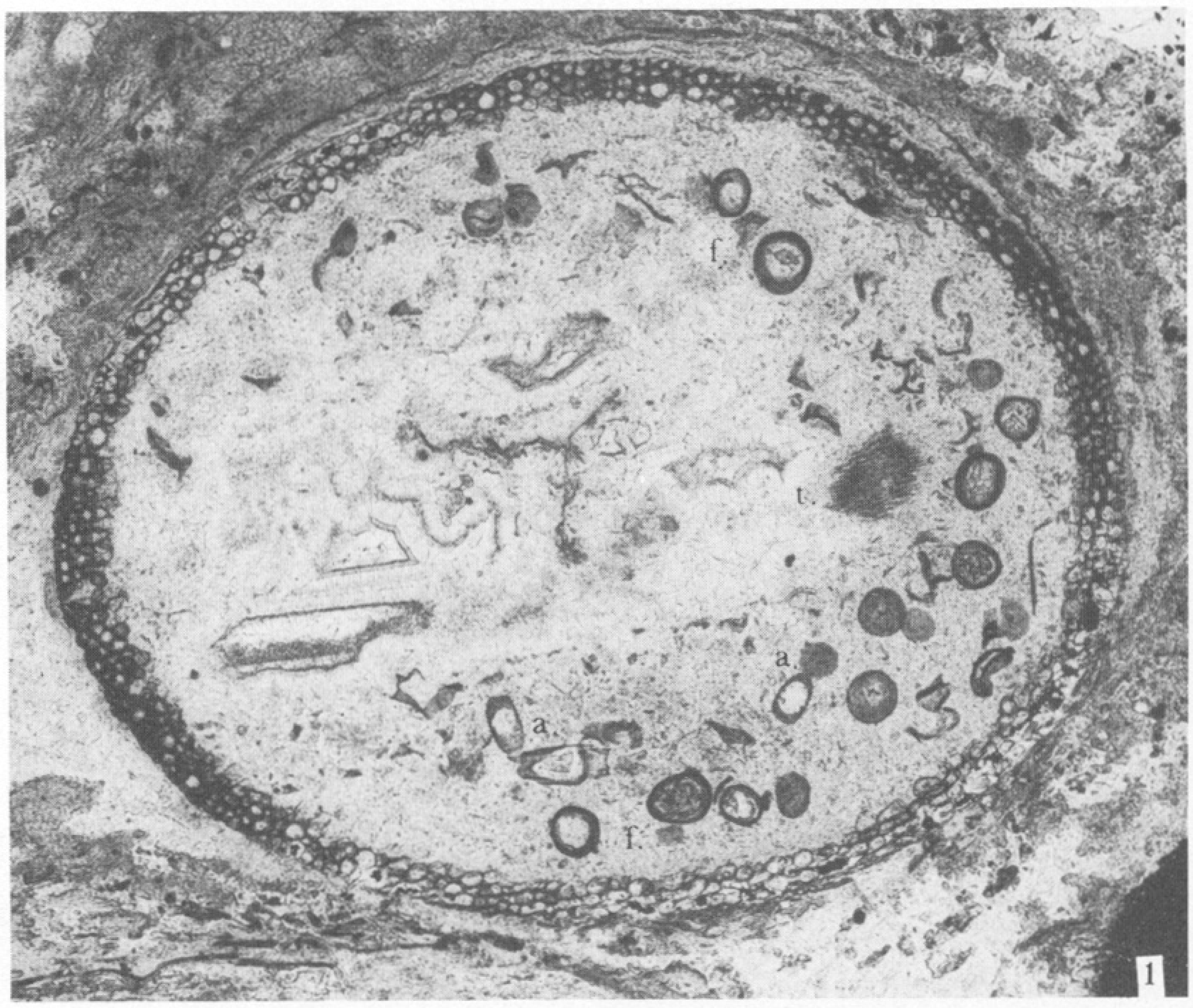

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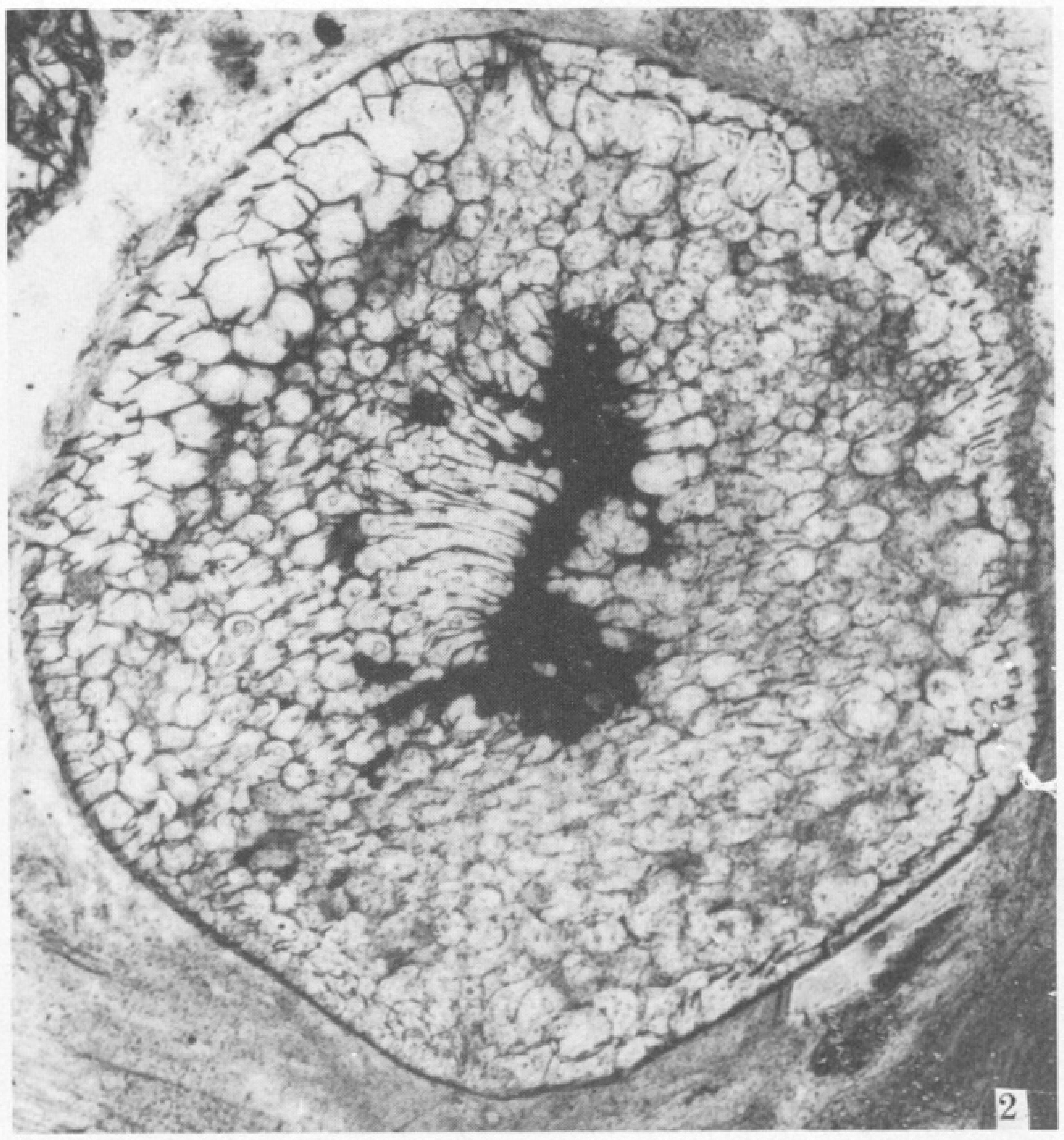

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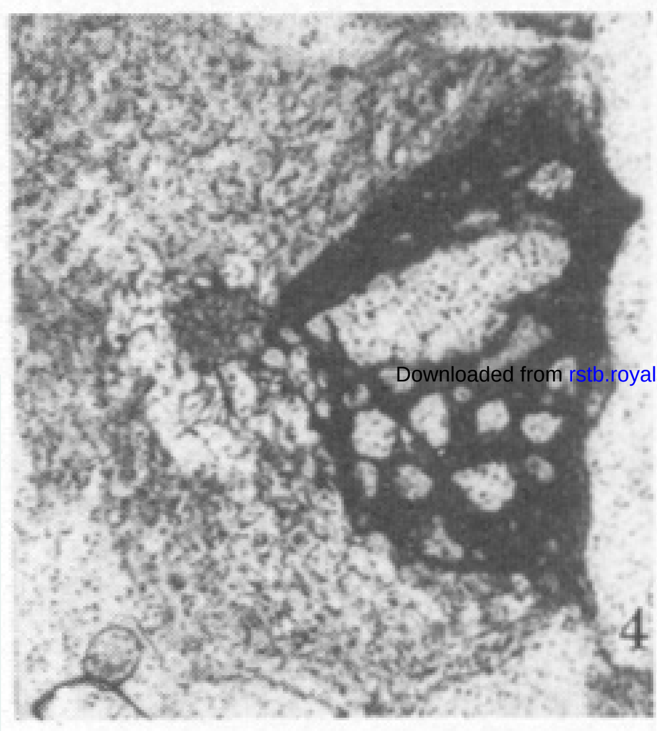

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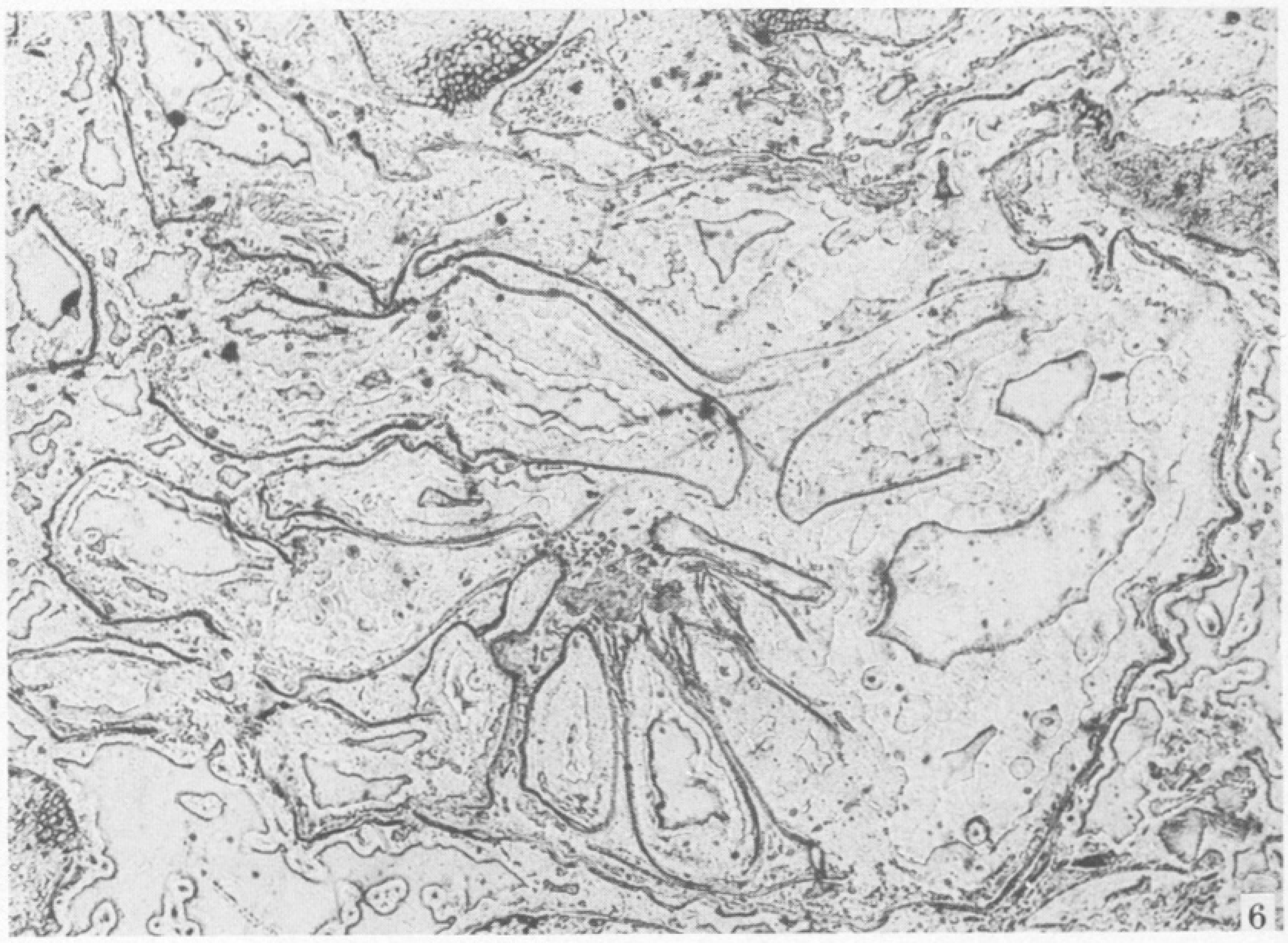

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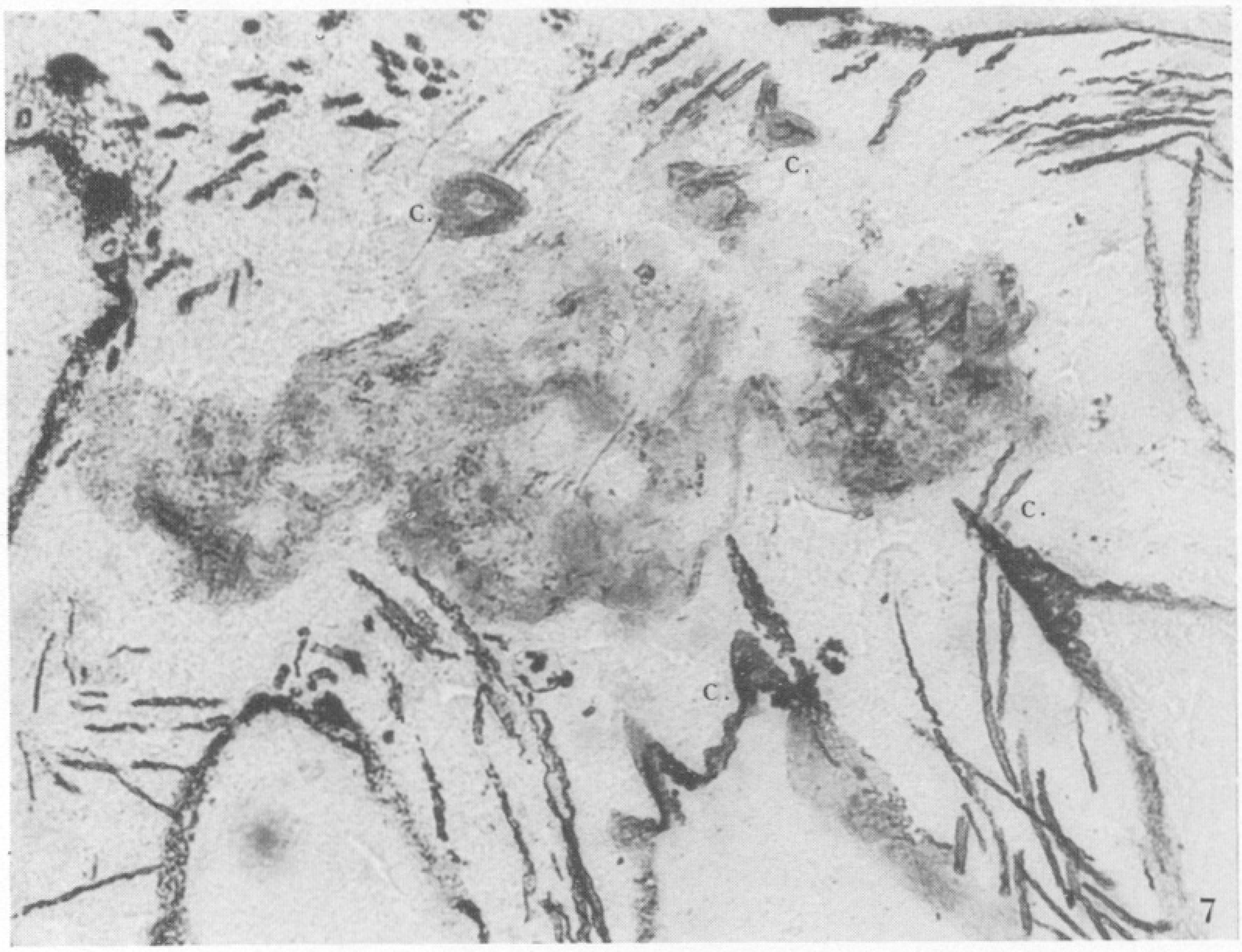

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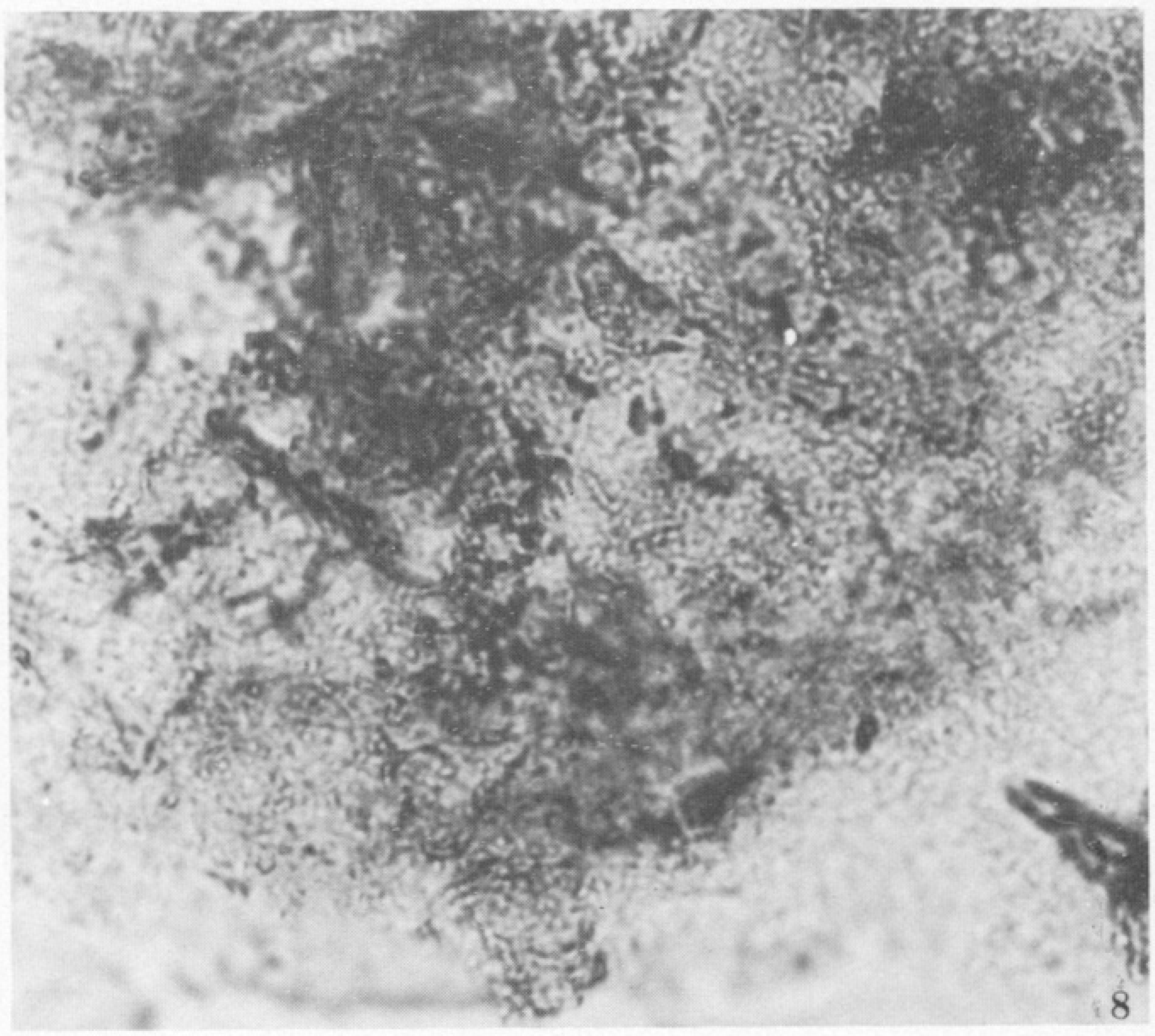

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FIGURES 1–8. For description see opposite.