

Orestovia and the origin of vascular plants

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LETHAIA



Krassilov, Valentin 1981 10 01: *Orestovia* and the origin of vascular plants. *Lethaia*, Vol. 14, pp. 235–250. Oslo. ISSN 0024-1164.

The enigmatic *Orestovia* from the Lower Devonian of Siberia has a vascular cylinder of spiral and annular tracheids, external and internal cuticles in the cortex, and stomata. Abundant spores are occasionally preserved between the cortex cuticles. The 'reticulate structures' are thyrrothecia of a hemisphaeriacean fungus. Spores of several types are found sticking to the cuticle. *Orestovia* can be conceived as a transitional form between the alga-like *Protosalvinia* and the sporangiate vascular plants. The origin of land plants is discussed.

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Numerous recent studies have somewhat narrowed but not filled the gap between the higher plants and their putative algal ancestors. A group of enigmatic alga-like plants, such as *Spongiophyton*, *Protosalvinia* and *Orestovia*, showing some adaptations to terrestrial life (cuticle, resistant spores) are crucial in this respect. They are currently considered as brown algae (Banks 1975), algae of unknown affinities (Niklas & Phillips 1976) or taxonomically isolated thalloid non-vascular terrestrial plants (Chaloner *et al.* 1974; Gray & Boucot 1977; Chaloner & Sheerin 1979). They also have bearing on the problem of the isomorphic alternation of generations in rhyniophytes postulated by Merker (1959), Pant (1962) and Lemoigne (1970). *Orestovia* is, I believe, the most abundant of the enigmatic Devonian 'thalloid' plants. Compressed stems of *Orestovia* form coal beds extending over 100 km along the Barzas River (Kuznetsk basin, Western Siberia). The peculiar Barzas cuticular coals (paper-coals or mat-coals) are assigned to the Early–Middle Devonian. Plant compressions were first observed by Zalesky, who compared them with the brown alga *Himantalia*. Kryshovovich (1933) suggested their psilophyalean affinity. Ergolskaya (1936) described the Barzas plants and named *Orestovia* after the geologist V. A. Orestov, as a by-product of her coal-petrographic studies. She observed stoma-like structures and, though sporangia were not found, provisionally assigned *Orestovia* to the psilophytes. Ananiev & Senkevitch (1962) held the same view. Ergolskaya had also discovered tracheid-like structures in the coal slides, but not within the intact compressions. Kräusel & Ven-

katachala (1966) re-examined *Orestovia* and supported its algal affinities. They included it together with the allied or possibly synonymous *Aculeophyton* in the Spongiophytaceae. Snigirevskaya (1971) studied *Orestovia* with SEM. She failed to observe stoma-like structures (which are externally inconspicuous, see below) and concluded that *Orestovia* was obviously not a higher land plant. Niklas & Chaloner (1976) included *Orestovia* in a group of 'thalloid Devonian plants' together with *Protosalvinia*, *Spongiophyton* and *Parkia*. In their opinion the absence of certain aromatic aldehydes, associated with lignin-like polymers, in all four genera confirms that these plants were non-vascular, thereby supporting the conclusions of Kräusel & Venkatachala as against those of Ergolskaya and Ananiev.

Orestovia devonica Ergolskaya

Material and methods. – I worked with a piece of Barzas coal measuring about 5 × 5 × 1 cm, consisting of several hundred tightly pressed *Orestovia* stems. Most compressions are about 10 mm wide, flat, and densely tuberculate on both sides (Fig. 1). Little else can be seen under the dissecting microscope and, as a matter of fact, with SEM. I left the shoots in HNO₃ + KClO₃ for ten days. After this they yielded to KOH, at which time it was possible to cleave them lengthwise, exposing the longitudinally ribbed and pitted interior. The pits correspond to the surface tubercles. One must be careful with alkali not to destroy the inner tissues completely. When

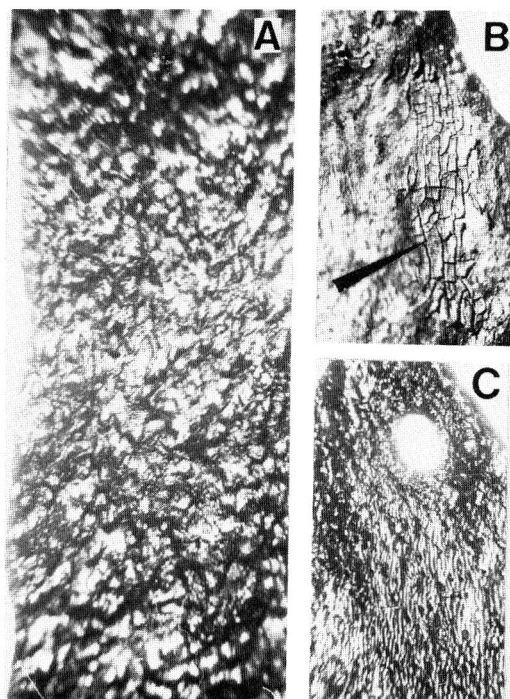


Fig. 1. Surface view (A) and split stems (B, C) showing conducting tissue broken into small blocks (B, arrow), a rounded perforation by a fungus and stomata seen as small dots (C), $\times 7$. BPI D1-1.

properly treated, the split shoots reveal strands of striated tissue, broken by cracks into small blocks (Fig. 1). These strands proved to be a vascular tissue. Other features revealed by splitting are stomata with the guard-cell thickenings conspicuous at low magnification and the hemispherical bulges leaving circular scars when destroyed (Fig. 1). The compressions were then further macerated to yield cuticles. The slides are in the repository of the Institute of Biology and Pedology (BPI) under numbers D1-1 to D1-80.

Stem. – Tubercles, stomata and other structures occur on both sides of compressions with equal frequencies, suggesting erect radially symmetrical stems (one can expect anisolateral distribution of various organs in prostrate stems or thalli). Transverse sections show a narrow slit between the two halves of the compressions, indicative of a central hollow. A thin vascular cylinder is sheathed by the inner cuticle of the cortex. The stems were easily compressed because of the lack of mechanically resistant tissue.

Conducting elements. – The vascular tissue consists of very long, tracheid-like tubes. End-walls were not observed in any of the numerous isolated tube fragments, some of them about 1 mm long. The side-wall thickenings are mostly spiral, less commonly annular and occasionally reticulate (Figs. 2, 3). Some tubes show a fine reticulate pattern, often combined with the spiral thickenings. A peculiar feature of the conducting tubes is that many of them have a rigid pivotal rod which can also be spirally twisted (Figs. 2D, 3D). The rods may consist of a resinous (?) infilling of the tubes, functioning as mechanical fibres. It can be seen from the split tracheids that the secondary walls have protrusions into the lumen corresponding to the thickenings (Figs. 2, 3).

Cuticles of the cortex. – Both the exterior and the interior of the cortex are cutinized, and there is also a middle layer of cuticle. A compression

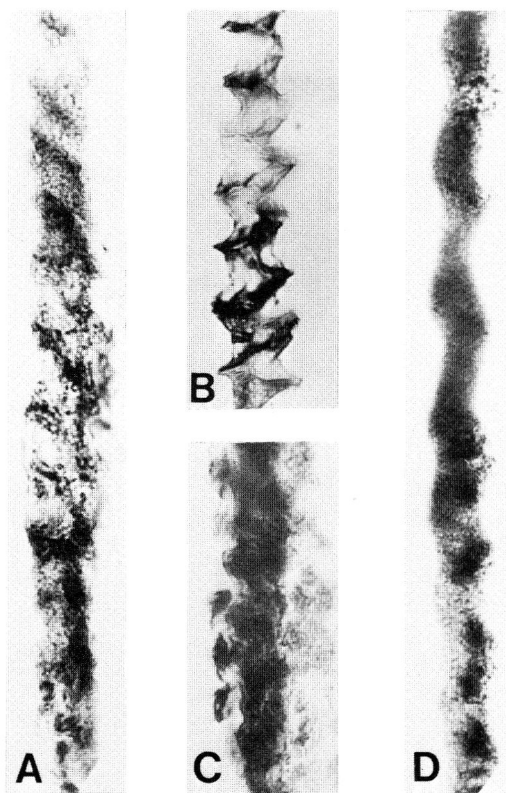


Fig. 2. Tracheids with spiral thickenings, one of them (C) split, showing secondary wall protrusions into the lumen. The lumen is filled with a dark substance which can be isolated as a spirally twisted rod (D), $\times 500$. BPI D1-18.

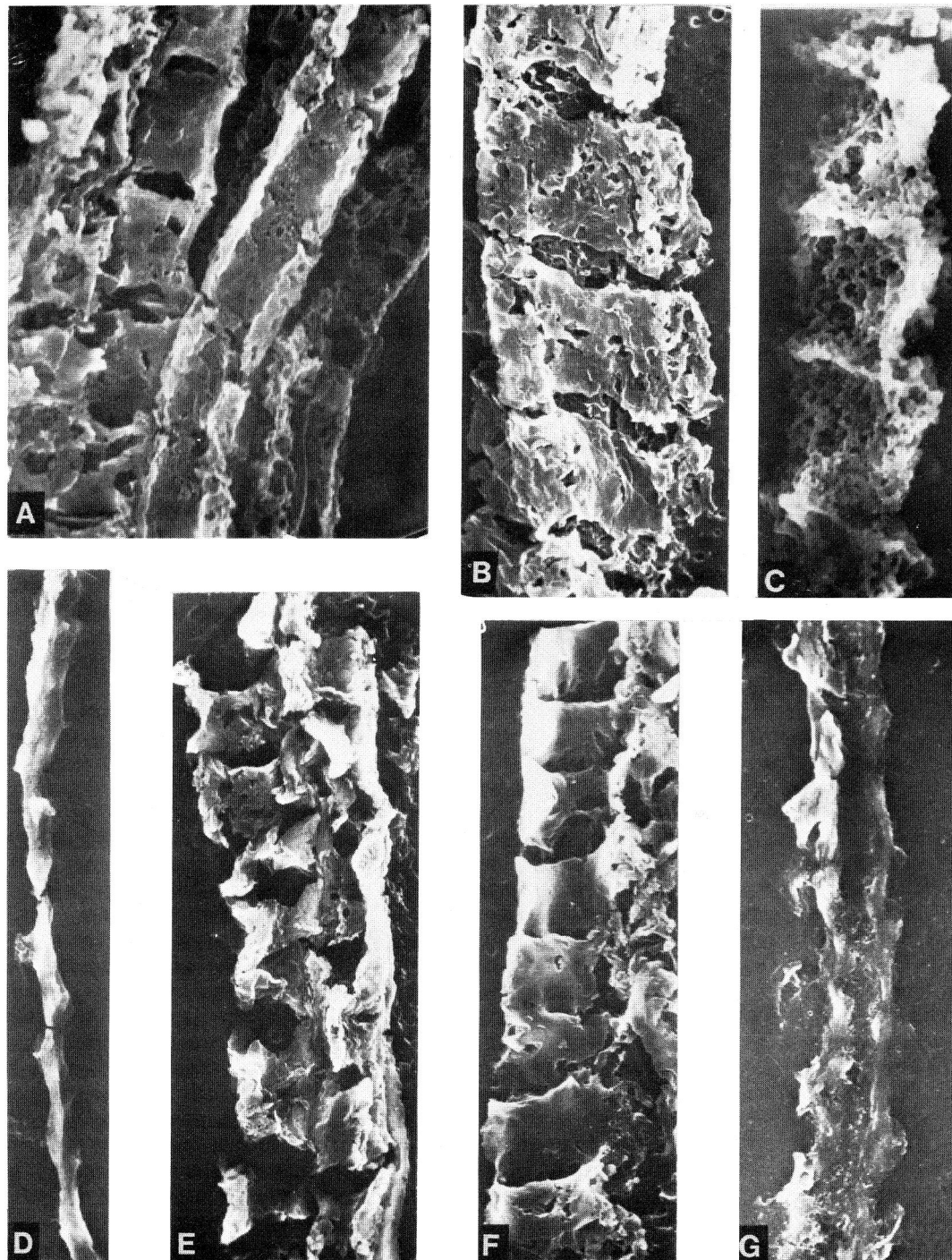


Fig. 3. Tracheids. SEM. □ A. Vascular strand, $\times 1200$. □ B. Spiral thickenings, $\times 2500$. □ C. Spiral thickenings, $\times 2000$. □ D. Isolated rod, $\times 1000$. □ E. Reticulate thickenings, $\times 2000$. □ F. Annular thickenings, $\times 2000$. □ G. Split tracheid, showing secondary wall protrusions into the lumen, $\times 2000$. BPI D1-21.

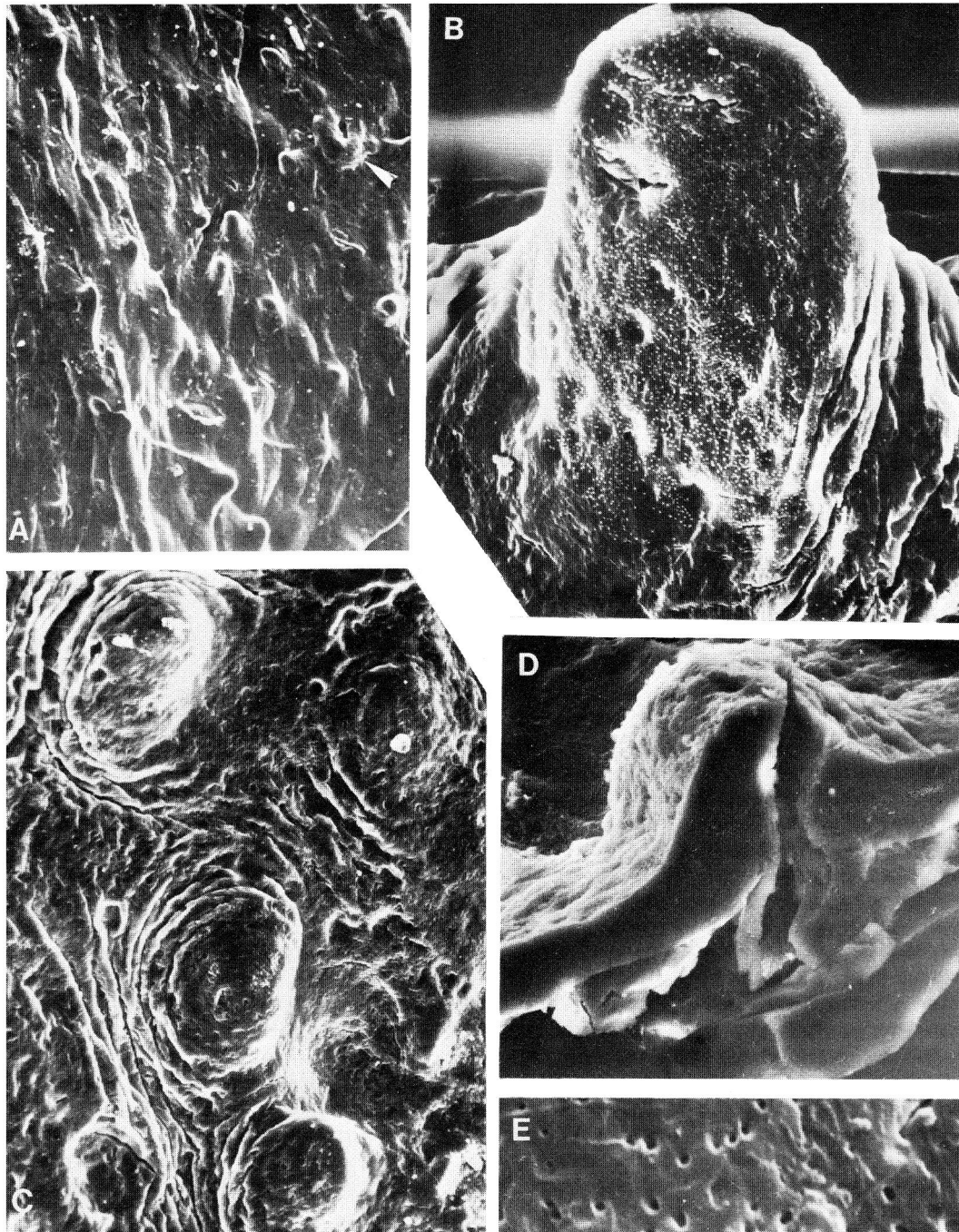


Fig. 4. Tubercles and pores, SEM. □ A. Conoidal tubercles and a stoma, surface view (arrow), $\times 75$. □ B. Prominent tubercle, $\times 600$. □ C. Hemispherical tubercles, $\times 250$. □ D. Section through tubercle, $\times 600$. □ E. Porous cuticle, $\times 600$. BPI D1-23, 24.

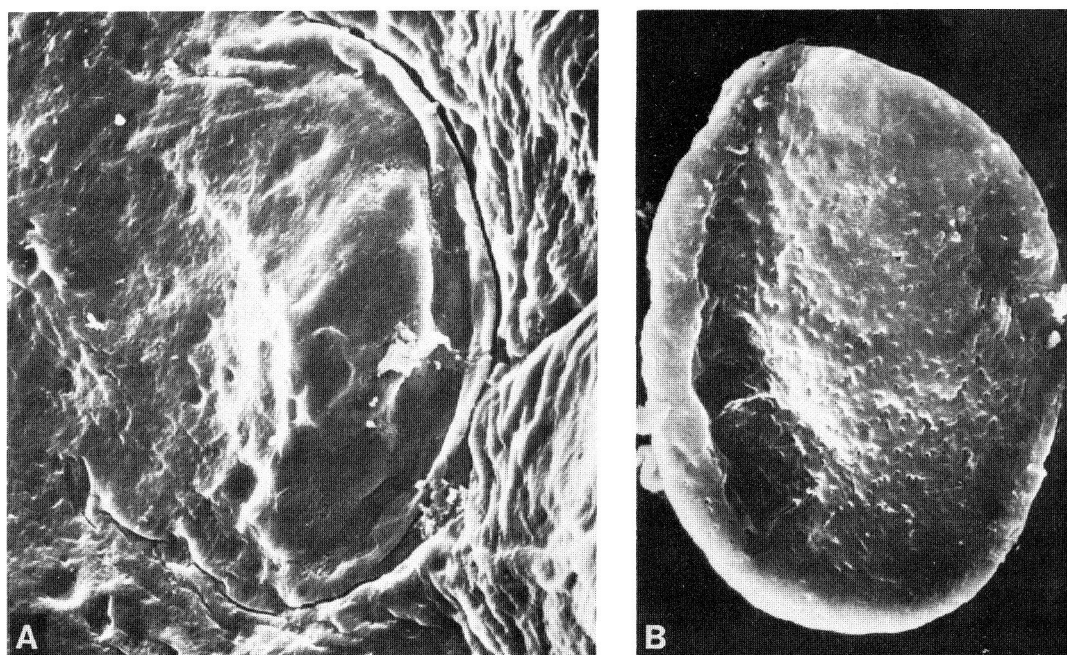


Fig. 5. Semi-detached (A) and smaller detached (B) gemma-like bodies, SEM, $\times 600$ and $\times 1200$. BPI D1–24.

yields altogether six cuticles. The outer and middle cuticles are fairly thick, smooth or show longitudinal rows of elongate rectanguloid, rhomboid or fusiform cells marked by ribs (Fig. 6C). The average cells are $105\text{--}150\text{ }\mu\text{m}$ long, $60\text{--}70\text{ }\mu\text{m}$ wide. Both cuticles are continuous over the tubercles, or one of them (the outer) is perforated by rounded holes. The inner cuticle is comparatively thin, smooth or scabrate, occasionally showing cells. All cuticles are minutely porous (Fig. 4).

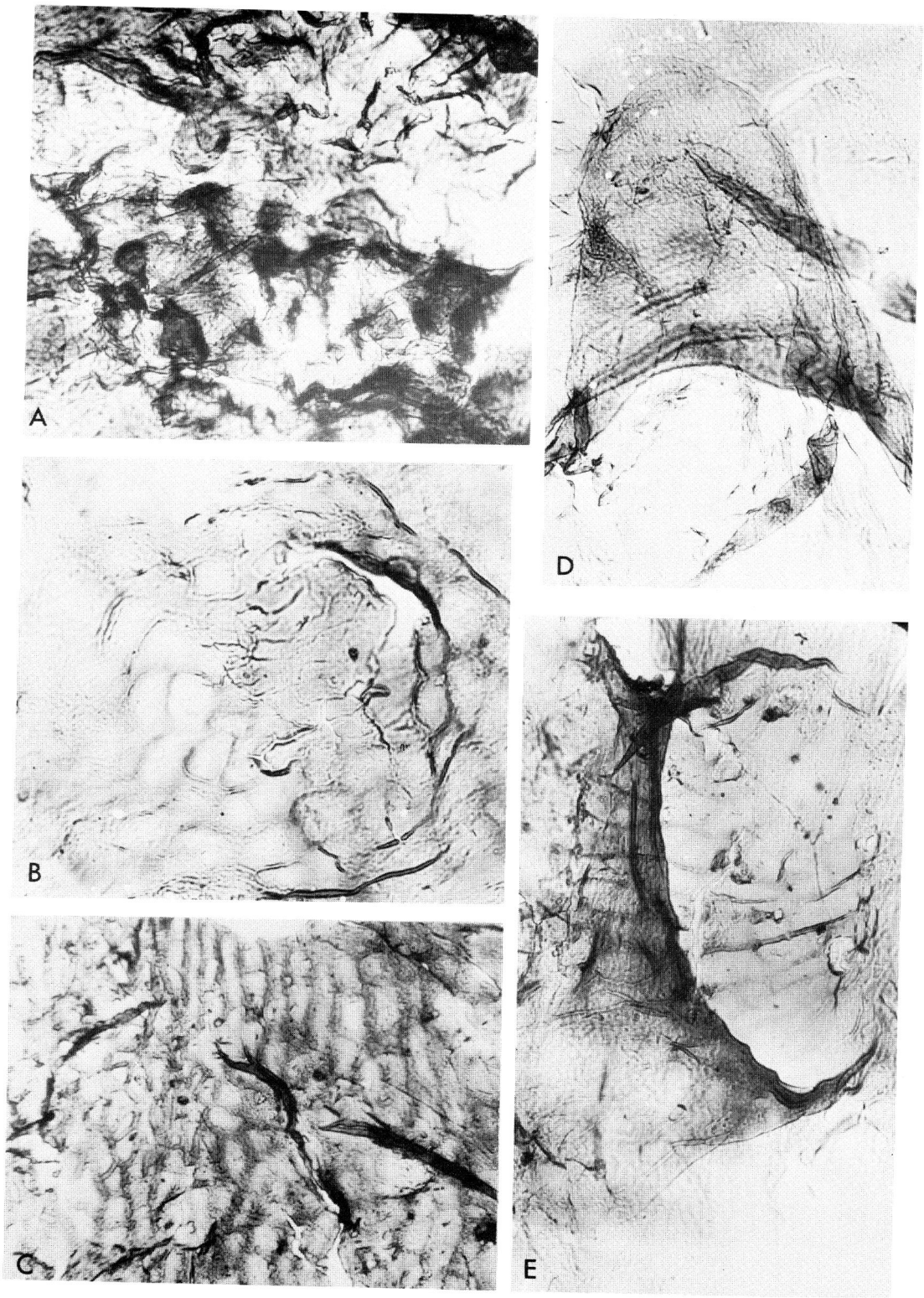
Tubercles. – The shape of the tubercles is variable: some of them are conoidal, even spiniform, others are dome-shaped, hemispherical, flattened, surrounded by concentric cuticle folds (Fig. 4). The mean diameter of the tubercles is $185\text{ }\mu\text{m}$. The central canal as seen in transverse section (Fig. 4D) suggests secretory function. However, the variability of the tubercles is still to be explained. Locally, the tubercles are substituted by crater-like pits (Fig. 6E). Some tubercles are sharply delimited as if going to be detached as gemmae. Gemma-like bodies were occasionally found among the tubercles (Fig. 5).

Stomata. – Stomatal apertures and sunken

guard-cell thickenings are prominent on the inner side of the cortex (Fig. 7). Their exterior expression is rather inconspicuous, but, fixing their position on the inner side, one can find a small, slightly elevated orifice among the tubercles (Fig. 4A, arrow). The orifice is elliptical, about $70 \times 64\text{ }\mu\text{m}$, bordered by a thick cuticular ridge. The whole structure, including the ridge, is about $143 \times 124\text{ }\mu\text{m}$. The stomata are longitudinally orientated, evenly spaced about 30 per cm^2 . The tubercles are often grouped in a ring at some distance from the orifice, as if inhibited by a morphogenetic factor around the stomata.

The guard-cell thickening, as seen from inside (Fig. 7), is bean-shaped, and slightly concave. The apertures are for the most part closed. The cuticle lining the aperture projects deep in the substomatal cavity (Fig. 8). Such stomata might function as hydathodes, as in many extant grasses.

Spores. – In a few specimens, abundant spores are found between the cortex cuticles (Fig. 9). Most of the spores are laterally compressed, showing *curvaturae perfectae* (Fig. 10) as in the spore-genus *Retusotriletes*. Better preserved spores are $150\text{--}190\text{ }\mu\text{m}$ in diameter, web round-



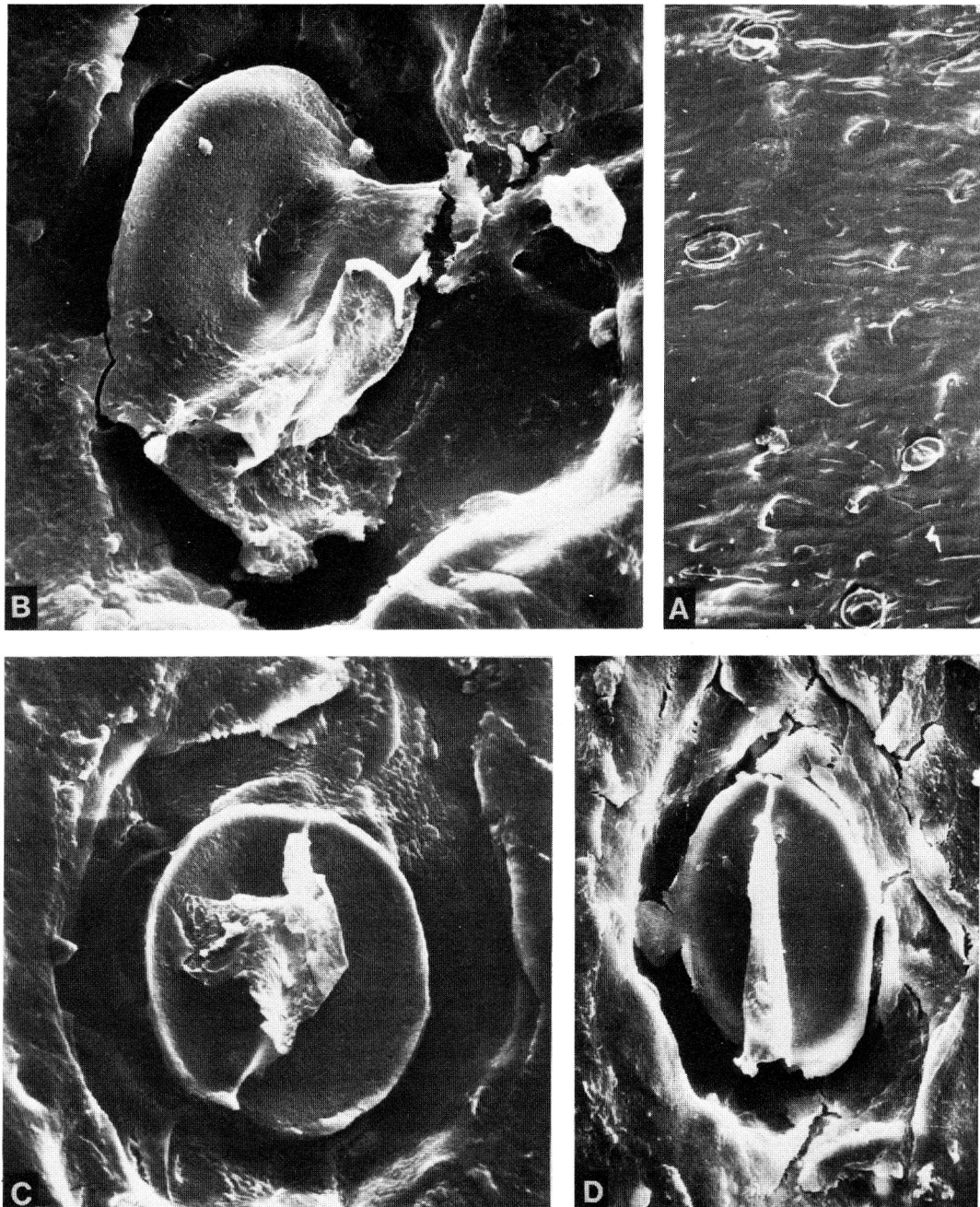


Fig. 7. Stomata, inside view, SEM. □ A. Topography of the cuticle with four longitudinal and oblique stomata and tubercles seen as pits, $\times 80$. □ B-D. Individual stomata showing guard-cell thickenings and the protrusions of a cuticle lining the aperture into the substomatal chamber. $\times 550$. BPI D1-30.

Fig. 6. Cuticular features. □ A, B. Incipient reticulate thyrithesia with dark hyphopodia. □ C. Outer cuticle showing rectangular cells. □ D. Conoidal tubercle. □ E. Collapsed craterlike tubercle, $\times 170$. BPI D1-11.

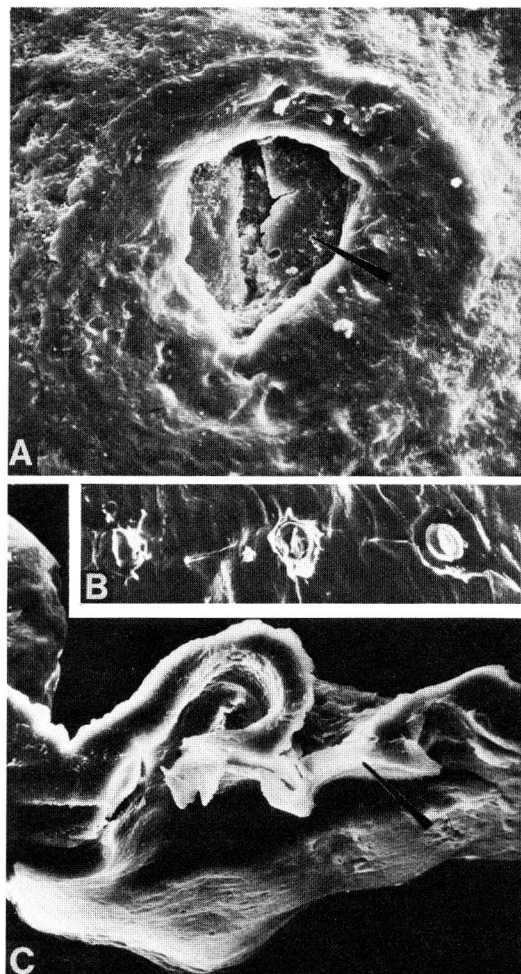


Fig. 8. Stomata, SEM. □ A. Outer view with a cuticular ridge, $\times 400$. □ B. A row of three nearly parallel stomata, $\times 70$. □ C. Transverse section of a stoma, showing guard cell thickenings (arrow) and the aperture lining cuticle protruding into the substomatal chamber, $\times 325$. BPI D1-25, 30, 31.

ed-triangular, aperture ridges reaching to the web, raised, almost straight. Contact faces smooth or scabrate, distal wall more or less conspicuously verrucate (Figs. 10, 11). The verrucae are seen in SEM only (compare Figs. 10 and 11C). A few specimens of the same size range show a central body sharply demarcated from a fringe (Fig. 11C).

Spores adhering to the stem cuticles, but not occurring within the cortex, are mostly about $75\ \mu\text{m}$ in diameter, with densely spinulate distal wall, often showing irregular pits in the exospore

(Fig. 11). A few spores are about $150\ \mu\text{m}$ in diameter, nearly hemispherical, proximally almost flat, with thick sinuous aperture ridges, distally showing long tapered processes which are often recurved and slightly expanded at the tips.

Fungi

Earlier workers have noticed 'reticulate structures' on the cuticle of *Orestovia* (Kräusel & Venkatachala 1966; Snigirevskaya 1971). Their nature has remained unknown. In the present material, several stages can be traced, from a few haustorial hyphae penetrating the stomata to the ripe ascostromata (Figs. 13–15). Intermediate stages are represented by the interwoven hyphae filling stomatal cavities (Fig. 13) and initial ascostromata of rounded or irregular form, nearly flat, $0.2\text{--}0.4\ \text{mm}$ across, with knob-like or clavate hyphopodia about $20\ \mu\text{m}$ thick (Fig. 14). The nearly ripe ascostromata shown in Fig. 15 are rounded-elliptical, up to $1\ \text{mm}$ in diameter, dimidiate, and inversed against the stem. Externally they show a slightly convex basal pseudo-parenchymatic layer of rounded-polygonal cells. When seen from the inside, they are more or less concave, exposing angular hypothecial cells with prominent hooked hyphae (Fig. 15B). In only one case there are several asci preserved as short clavate structures with rounded apices, about $25\text{--}30\ \mu\text{m}$ wide. Some filaments are seen between the asci, but I am not sure whether they are paraphyses or not.

There is no evidence of a true ostiole, the ripe ascostromata opening by a large hole in the central part (Fig. 13, top right). The holes are seen on the stem cuticles at low magnification (Fig. 1). Their edges are even or somewhat ragged. No traces of a free mycelium are distinguishable at the ripe ascostromata.

Inversed ascostromata (thyriothecia) suggest the order Hemisphaeriales in which they are dimidiate, fastened on the lower side of the hyphopodia or mycelial hyphae and turned upside down, that is, inverted against a host plant surface (Ryan 1926). The Hemisphaeriales comprise three families: the Trichopeltaceae with pycnotical ascostromata, the Microthyriaceae with radial thyriothecial structure and the Hemisphaeriaceae with non-radial reticulate thyriothecial membranes. The fungus on *Orestovia* can be referred to the latter family, which is

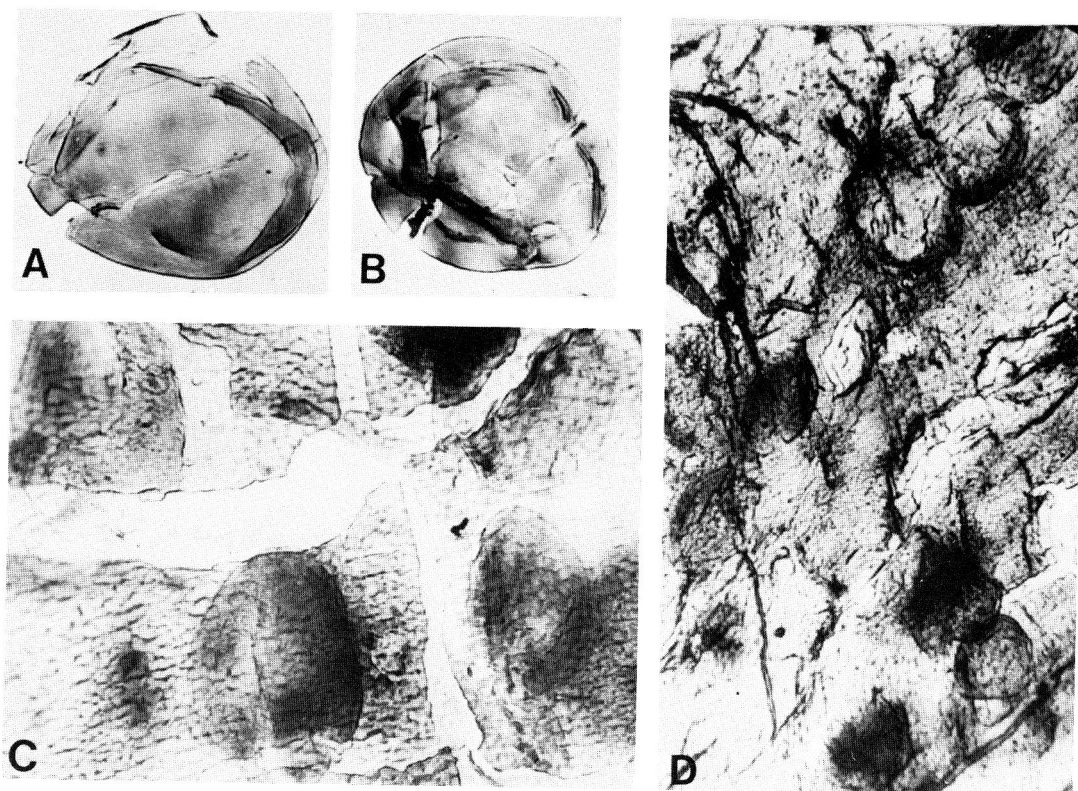


Fig. 9. Spores, between the cortex cuticles and extracted. □ A, B. $\times 70$. □ C, D. $\times 170$. BPI D1-12.

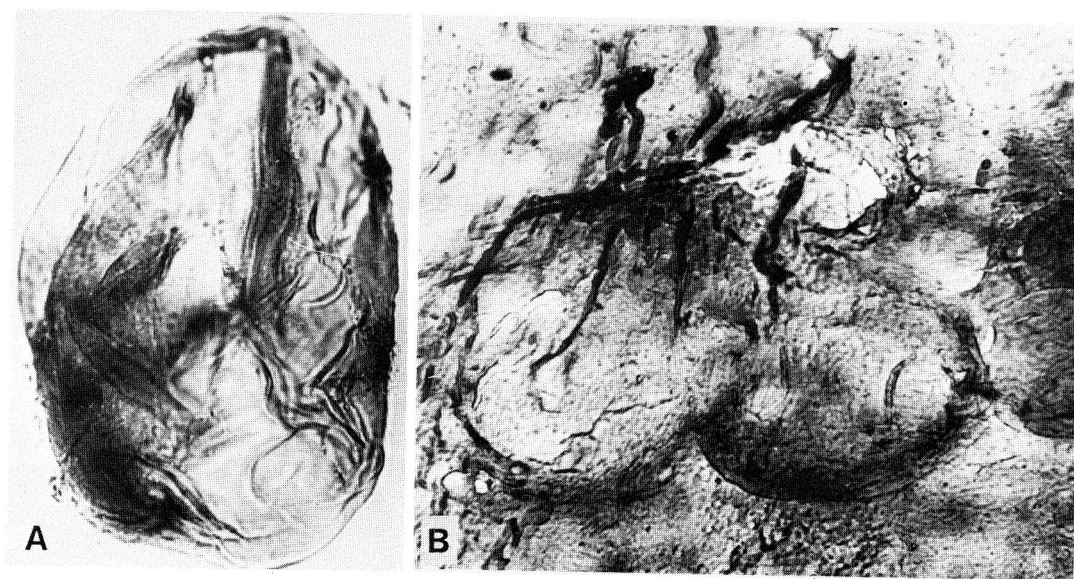
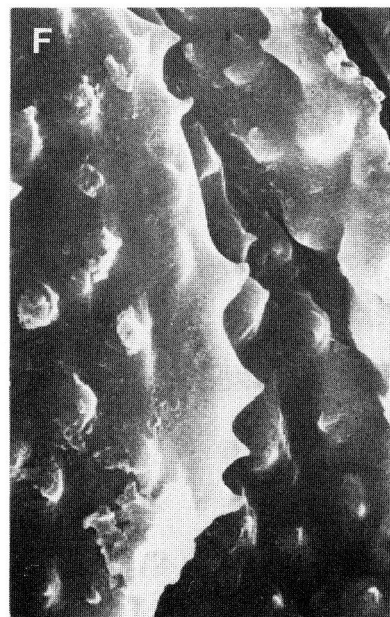
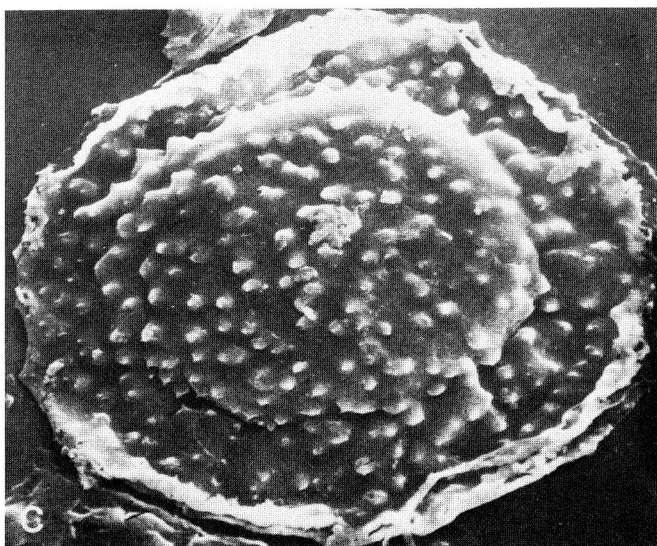
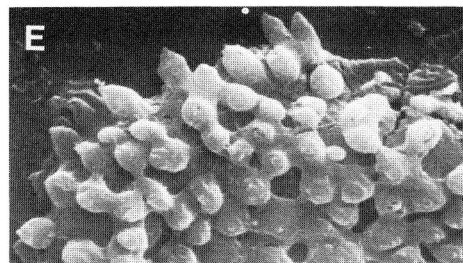
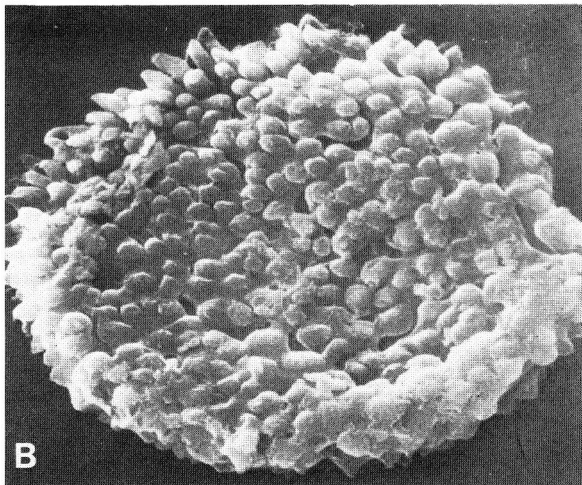
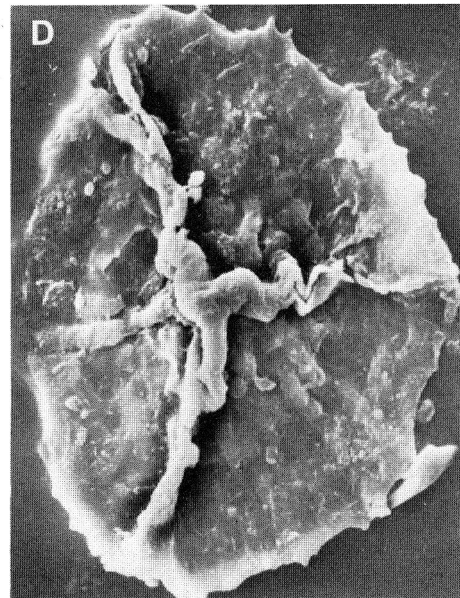
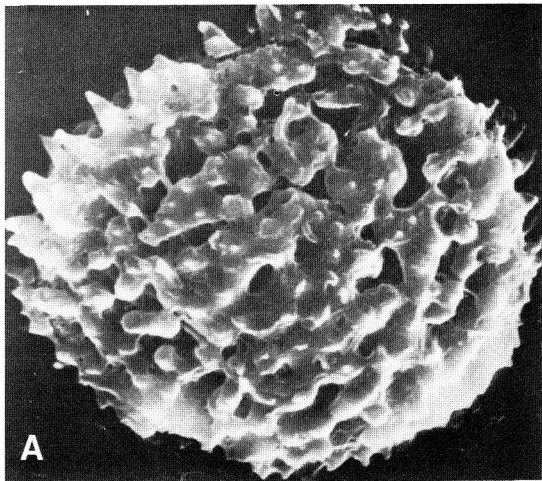


Fig. 10. □ A. Extracted spore, showing curvaturae, $\times 600$. □ B. Spores between the cuticles, $\times 170$. BPI D1-13.



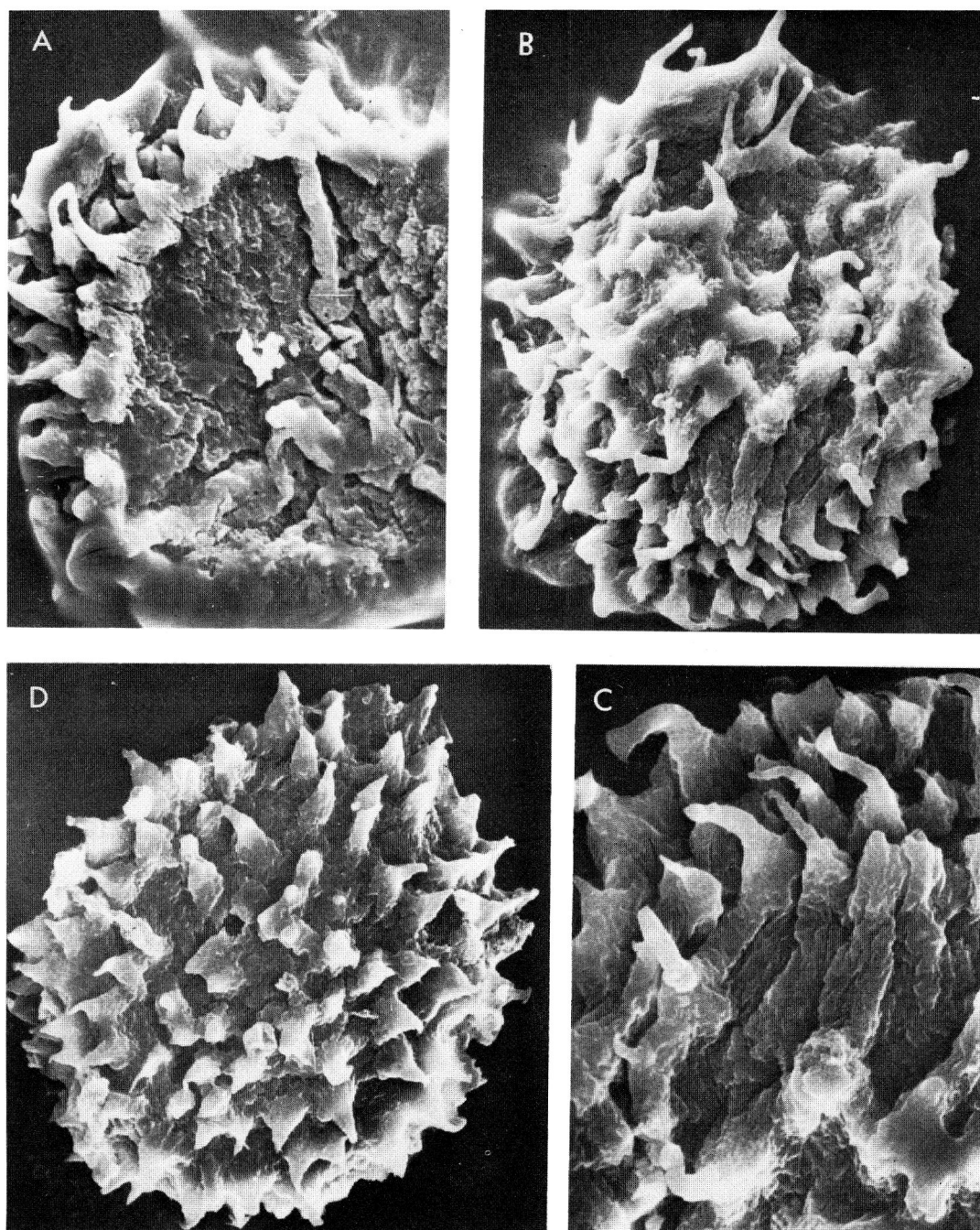


Fig. 12. Spores with long distal processes adhering to the stem surface, SEM. □ A, B. Proximal and distal aspects of the same spore, $\times 900$. □ C. Detail of B, showing processes, some of them with expanded tips, $\times 1600$. □ D. Another spore of the same type, $\times 900$. BPI D1-43.

Fig. 11. □ A, B, E. Spinulate spores adhering to the stem surface, distal aspect, showing lacunae in the outer exospore stratum, SEM, $\times 1600$ (A, B.) and $\times 2000$ (E). □ C, D. Spores extracted from between the cortex cuticles, distal and proximal aspects, SEM, $\times 900$. □ F. Part of C, $\times 2600$. BPI D1-42.

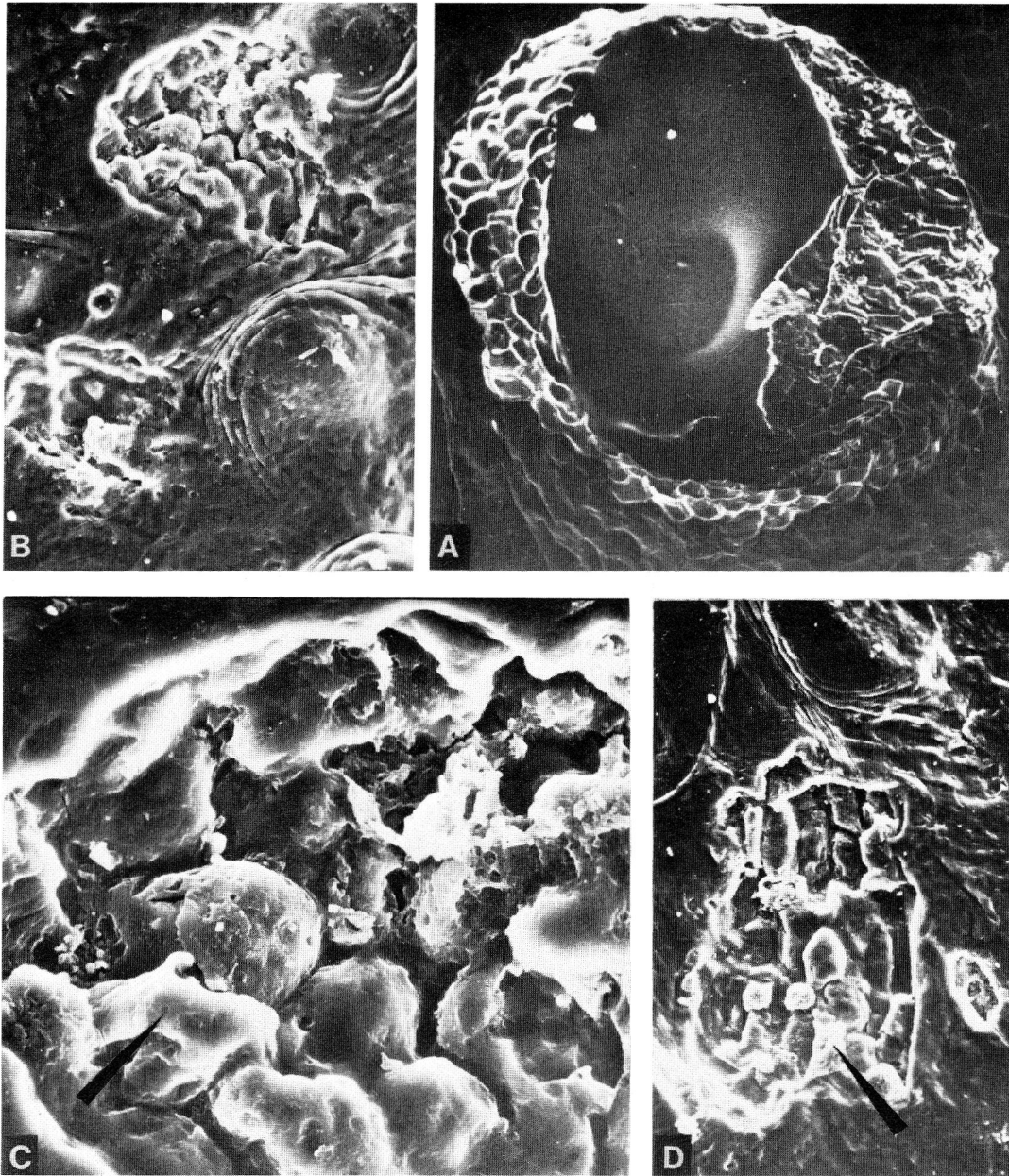


Fig. 13. □ A. Pore in the ripe thyriothecium, SEM, $\times 100$. □ B-D. Incipient ascostromata showing hyphopodia (arrows), SEM, $\times 300$ (B, D) and $\times 1000$ (C). BPI D1-74.

further subdivided in accordance with the presence or absence of free mycelium, epithecium and other characters (Stevens & Manter 1925). Among the four subfamilies, the Dictyopeltineae Theiss., which is the most common, is characterized by reticulate thyriothecial membrane with-

out free mycelium. The presence of paraphyses, the shape of pseudo-ostiole (rounded or stellate), and the number of ascospores are the most important generic characters. The Devonian fungus is hardly comparable with the extant Dictyopeltineae on generic level.

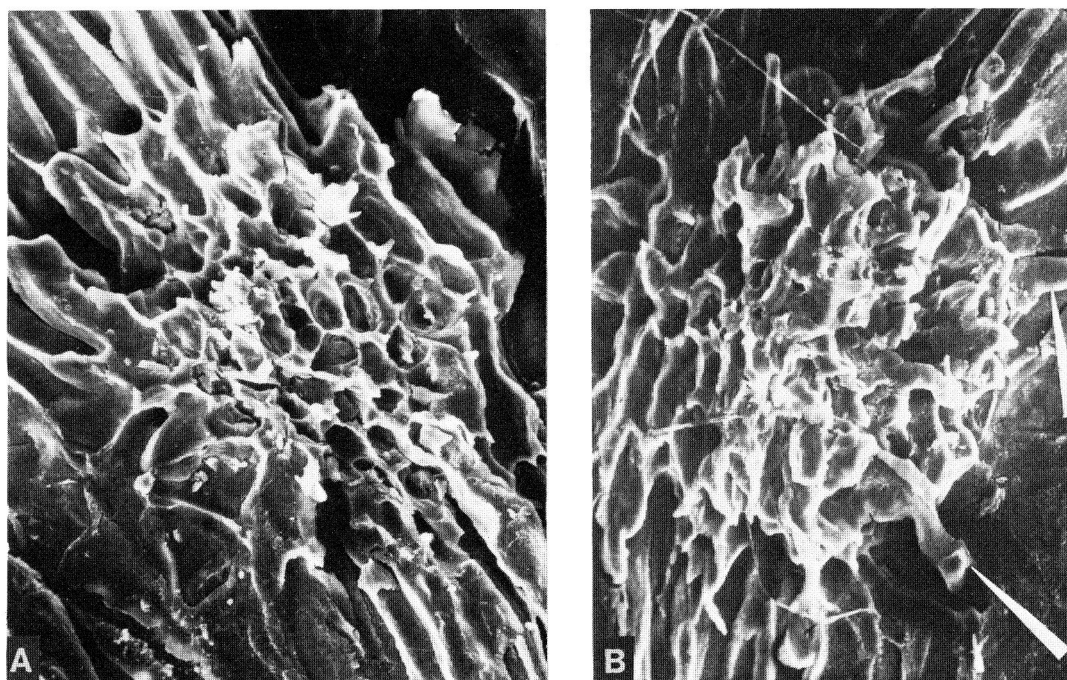


Fig. 14. Immature thyriothechia, inside view, showing hyphopodia (arrows), SEM, $\times 250$. BPI D1-74.

Discussion

Orestovia is not an alga but a vascular leafless plant with stomatiferous stems, growing abundantly in extensive peat-land. It is conceivable that *Orestovia* formed pure stands, while the plant producing smaller spinulate spores and spores with long distal processes grew in close proximity.

The extant hemisphaeriallean fungi are mostly ectoparasites on leaves of tropical plants. Those growing on *Orestovia* suggest a very early differentiation of the Ascomycetes which preceded the evolution of land plants.

I suggest that at least some of the stem tubercles of *Orestovia* produced gemmae comparable with the sporophytic gemmae of *Psilotum*; it is known that *Psilotum* propagates successfully by sporophytic and gametophytic gemmae (Holloway 1939). No sporangia were found in association with *Orestovia*, but unripe spores have been observed within the cortex, suggesting some kind of sporogenous tissue.

The discovery of vascular tissue in *Orestovia* casts some doubt on the current interpretation of other 'alga-like' Devonian plants such as *Pro-*

tosalvinia and *Spongiophyton* (see also Gray & Boucot 1977). The former genus had stout bilobed 'thalli' covered with a thick cuticle (Niklas & Phillips 1976). The sporogenous tissue was confined to the apical notch, as in some marchantialean liverworts. Spore tetrads were found under the cuticle. The spores are of the same type as in *Orestovia*. In both genera they are much larger than the conventional *Retusotriletes*, resembling megaspores in size and separation of the exospore (or its outer layers) from the central body. I believe that *Protosalvinia* and *Orestovia* are related (presumably through their pre-Devonian ancestors) and represent successive evolutionary stages in the direction of the sporangiate vascular plants. *Retusotriletes*-type spores were found in sporangia of *Psilophyton dawsonii* (Banks *et al.* 1975) and *Zosterophyllum cf. fertile* (Edwards 1969), which might retain some ancestral spore characters.

Palaeobotanical efforts to solve the problem of land plant ancestry were traditionally centred on the rhyniophytes, accidentally the most ancient European vascular plants. However, it is impossible to relate the rhyniophytes to any group of putative algal ancestors or to any of the more

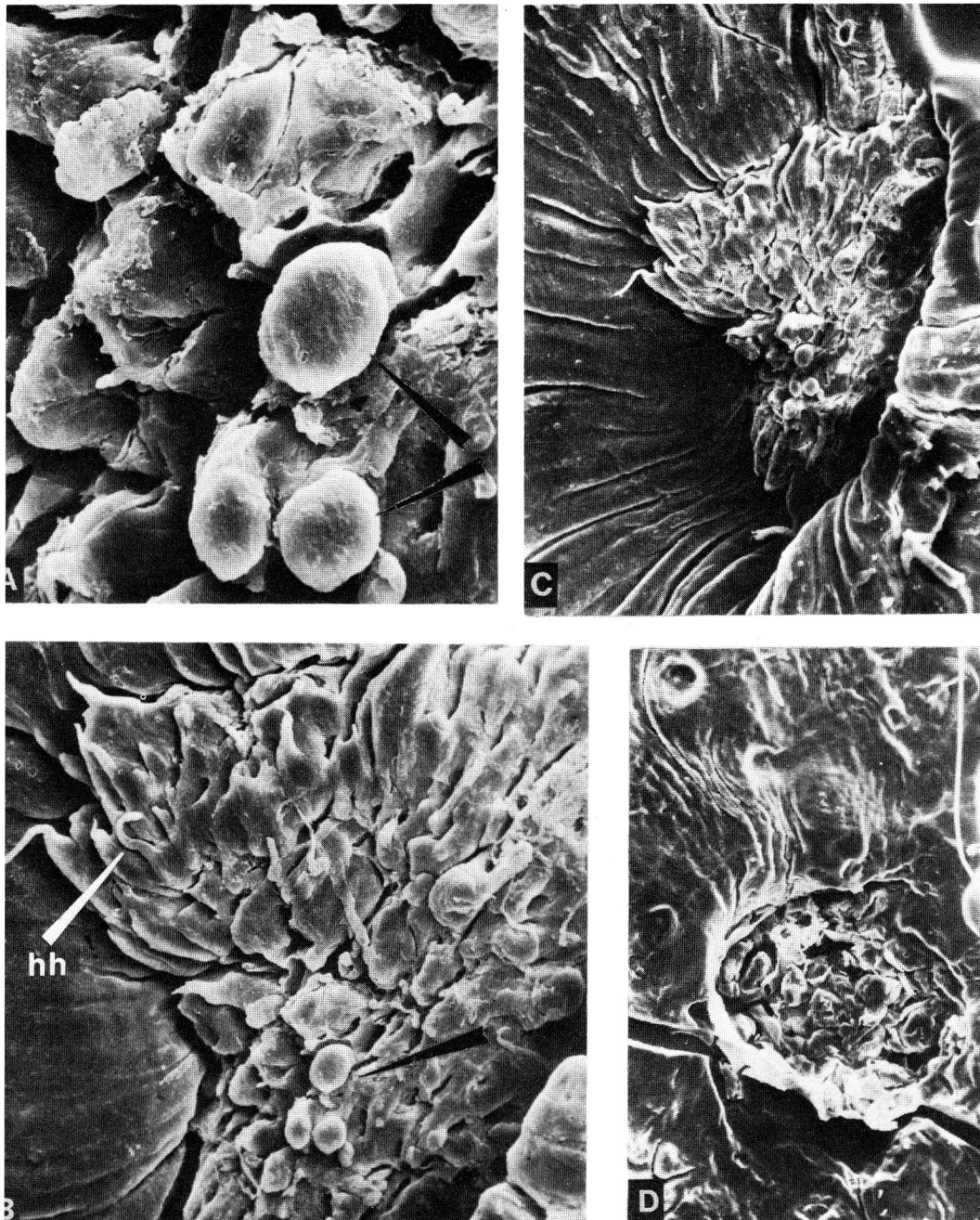


Fig. 15. □ A-C. Thyriothecium, inside view. SEM, general aspect (C, $\times 140$) and hypothecial cells (B, $\times 300$; A, $\times 1000$) with a few asci (arrows) and hooked hyphae (hh). □ D. Another thyriothecium, inside view, $\times 140$. BPI DI-75, 75a.

advanced land plants. The rhyniophytes were evidently a blind alley in early land plant evolution. On the other hand, *Orestovia*, though obviously not the earliest vascular plant, is more promising because it resembles the most advanced brown algae and can at the same time be related to the higher drepanophyceean evolutionary level.

In *Orestovia*, the evolution of vegetative parts was much ahead of the sporogenous tissue, still not forming sporangia. *Spongiophyton*, the cutinized thalli with pores on one side (Chaloner *et al.* 1974), resembled the liverwort *Spherocarpus* with archegonia at the bottom of involucres. This genus might represent a separate line of land plant evolution.

Various hypotheses on the origin of multicellular land plants and the alternation of generations have been advanced as mere deductions from the conditions discovered in various groups of extant algae. Principally, these hypotheses are: (1) Originating from some hypothetical highly differentiated 'Thalassophyta' (resembling the most advanced brown algae) by steadily progressing specialization of tissues for terrestrial life; (2) originating from some algae with homologous (isomorphous) alternation of generations, as in some green and brown algae; (3) intercalation of a diploid stage by postponement of the meiosis in the life cycle of some filamentous green algae; in this hypothesis bryophytes are considered intermediate between the algal ancestors and vascular plants – a view favoured by so many bryologists; and (4) a variant of (3) in which the ancestral group is conceived as highly evolved terrestrial algae (extinct terrestrial charophytes) and the alternation of generations as isomorphous.

Recently, Stebbins & Hill (1980) advanced the latter hypothesis. According to them, plants entered terrestrial life as unicellular, relatively undifferentiated forms. 'Given the probability that in the early Paleozoic many thousands of square kilometers were covered with millions or billions of cells belonging to soil inhabiting algae', these algae have more chance of evolving into higher plants than any aquatic plants. In stating this, they apparently overlooked the difficulty of producing, without higher plants, those thousands of square kilometres of soil needed for the soil inhabiting algae. They admitted the lack of fossil evidence as embarrassing, but 'entirely to be expected' and concluded that the origin of land plants 'will probably be always

a matter of conjecture'. If so, one is at liberty to conjecture anything, even the immensities of rich soil without plants.

When starting this work, I was a supporter of the isomorphous alternation hypothesis as ingeniously applied to rhyniophytes by Pant (1960), but then I chose to keep closer to the actual evidence. The comparison of some Rhynia specimens with the vascularized gametophytes of *Psilotum* is too strained, because the latter are covered with prominent antheridia never noticed in *Rhynia*, as well as the four-celled archegonium neck rosettes also conspicuous in surface view (the archegonium-like sections might have been simulated by hydathodes or stomata). The most primitive alga-like terrestrial plants, such as *Protosalvinia* and *Orestovia*, were sporophytes, less specialized for spore production than the sporophytes of liverworts.

Thus, as the evidence shows, the invasion of land was performed by plants with massive sporophytes resembling the most advanced brown algae. They reproduced by spores and presumably also by gemmae. Spores were produced by meiotic cell divisions in the morphologically unspecialized subepidermal tissue. The gametophytes might have been even more ephemeral than in most ferns, possibly semi-aquatic. Sporophytes soon acquired sporangia through terminalization of sporogenous tissue. After the development of soil, many soil-inhabiting algae and fungi entered land. Some of them because engaged in symbiosis with the gametophytes, as they are at present. From this symbiosis evolved the long-living gametophytes which could reproduce by gemmae, or with the aid of reduced sporophytes, eventually deprived of their photosynthetic functions, as in the bryophytes.

Further work on *Orestovia* and its allies may evoke more reliable evolutionary hypotheses.

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