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EXINE INTRASTRUCTURE OF *PRAECOLPATITES SINUOSUS* (BALME & HENNELLY) BHARADWAJ & SRIVASTAVA, 1969, AND *MARSUPIPOLLENITES TRIRADIATUS* BALME & HENNELLY, 1956

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ABSTRACT

Transmission electron micrograph studies of pollen grains *Praecolpatites sinuosus* (Balme & Hennelly) and *Marsupipollenites triradiatus* Balme & Hennelly, from the Permian of eastern Australia, show that these species have a two-layered exine. In each species, the inner layer (intexine) is laminated, suggesting that they belong to the gymnosperms; the outer layer (exoexine) is structured by small, irregularly shaped intraexinal cavities, and is described as incipient-alveolate. Their exinal structure is closely comparable with that of pollen of certain extant, primitive angiosperms (Magnoliaceae) reported by Walker.

Key-words — Exine intrastructure, *Praecolpatites*, *Marsupipollenites*, Palynology, Permian (Australia).

सारांश

प्रीकॉल्पेटाइटिस साइनुओसस (बाम व हेनली) भारद्वाज एवं श्रीवास्तव, 1969 तथा मार्सूपीपॉलिनाइटिस ट्राइ-रेडिएटस बाम एवं हेनली, 1956 के बाह्यचोल की अंत:संरचना – सी० बी० फ़ोस्टर एवं पी० ऍल० प्राइस

पूर्वी ऑस्ट्रेलिया के पर्मियन से प्रीकॉल्पेटाइटिस साइनुओसस (बाम व हेनली) तथा मार्सूपीपॉलिनाइटिस ट्राइ-रेडिएटस बाम एवं हेनली के परागकणों का पारगमन इलेक्ट्रान लघुचित्रीय अध्ययन प्रदर्शित करता है कि इन जातियों में दो पर्तों वाला बाह्यचोल होता है। प्रत्येक जाति में अन्दर वाली पर्त (इन्टेक्साइन) स्तरित है जो यह प्रस्तावित करती है कि ये अनावृतबीजीयों से संबन्धित हैं; बाहरी पर्त (एक्सोएक्साइन) छोटी, अनियमित आकार वाली अंत:बाह्यचोल गुहाओं से निर्मित है तथा आभासी-कणिकामय की तरह वर्णित की गई है।

INTRODUCTION

PRAECOLPATITES SINUOSUS (Balme & Hennelly) Bharadwaj & Srivastava, 1969 and *Marsupipollenites triradiatus* Balme & Hennelly, 1956 are well known as *Sporae dispersae* from Permian sequences of Antarctica, Australia, India, Pakistan, and South Africa (Balme, 1970; Anderson, 1977; Foster, 1979). Their stratigraphic and geographic distribution throughout these parts of Gondwanaland makes them potential index forms for local and inter-regional correlations. Preliminary work already indicates that correlation based on the first appearance of *P. sinuosus* is feasible between sequences in India and Australia (Foster, 1975). Locally, the oldest occurrence of *P. sinuosus* has been used to define the base of a miospore (interval) zone designated as " upper stage 4 " by Paten (1969); the zone has been recognized in Early Permian sequences throughout Australia (Kemp *et al.*, 1977). After its initial appearance, *P. sinuosus* is a persistent component of palynofloras from younger stage 5 assemblages. The biostratigraphic potential of *M. triradiatus* has yet to be exploited. In Australia it first appears in periglacial sediments (stages

2 & 3 of Evans, 1969) and continues throughout the younger Permian succession. In contrast to their well documented occurrences, the precise natural affinities of these taxa remain unknown.

The morphology and structure of the exine of *P. sinuosus* and *M. triradiatus* are of considerable interest, as both species have been described as possessing an infrastructured, columellate (tectate-perforate) exine; characters which are considered diagnostic of angiosperm pollen (Van Campo, 1971; Walker & Doyle, 1975; Doyle, Van Campo & Lugardon, 1975; Walker & Skvarla, 1975; Walker, 1976). In their original description of *P. sinuosus*, Balme & Hennelly (1956) described the exine as " about 2 μm thick, smooth or faintly granulate ". All subsequent authors, however, have considered that the exine is structured. Bharadwaj and co-workers have variously described the exine of *P. sinuosus*, and of taxa which are considered as conspecific (Foster, 1979), as " infrapunctate " or " intrabaculate ", or " intramicroreticulate " (Bharadwaj, 1962; Bharadwaj & Salujha, 1964; Bharadwaj & Srivastava, 1969); Balme and Playford (1967) considered it was " finely columellate "; and Foster (1979) noted " exine two-layered, 2-3 μm thick; exoexine scabrate or with fine intrastructure. Intexine thin, dark in colour, not always perceptible " (also see Balme, 1970).

Similarly, Balme and Hennelly (1956) interpreted the exine of *M. triradiatus* as "about 2 μm thick on proximal face ornamented with flattened verrucae, granules, or fine indeterminate markings ". Subsequently, Balme and Playford (1967) considered that the species was " columellate, in the sense of Faegri and Iversen, (1964) ", a view supported by Pocock and Jansonius (1969). In the generic emendation of *Marsupipollenites*, Balme (1970) stated " exine columellate with small, closely spaced, rounded structural elements ". Foster (1979) concurred with Balme's structural interpretation, referring to the arrangement of infrasculptural elements in a closely allied species, *Marsupipollenites striatus* (Balme & Hennelly) Foster, 1975.

It should be emphasized that the above interpretations of exinal structure are based on studies using conventional transmitted light and scanning electron microscope (SEM) techniques, none of which unequivocally determine intrastructure. The purpose of this paper is to study the exinal structure of *P. sinuosus* and *M. triradiatus* using transmission electron microscopy (TEM) and relate the findings to earlier interpretations.

MATERIAL AND METHODS

P. sinuosus and *M. triradiatus* were originally described from the same locality, Fassifern Seam at 209·7 m (688 ft) in South Wallarah No. 5 borehole, Newcastle Coalfield, New South Wales (Balme & Hennelly, 1956, pp. 60-61). The assemblage from which they were described is assignable to palynological unit " upper stage 5 " of Paten (1969). Additional core material from the type locality was processed for use in this study, and topotypes were examined by conventional methods (Pl. 1, figs 1-8; Pl. 4, figs 13, 16). However, the overall yield of plant microfossils from the core material we processed was low, and because of the rarity of both species, it was not possible to select specimens for TEM study. The specimens sectioned came from the following localities.

P. sinuosus — Washed-cuttings from an unnamed Permian stratigraphic unit, intersected in Utah Development Co. boreholes OR13 at 196-198 m and OR7 at 182-1 84 m, Olive River Basin, Cape York Peninsula, Queensland. Palynostratigraphic unit, " upper stage 5 ".

M. triradiatus — Core samples from Blair Athol Coal Measures, intersected in Blair Athol No. 4 at 41·23 m; Blair Athol Basin, Central Queensland (Foster, 1975, 1979), Palynostratigraphic unit, " upper stage 4a ".

The methods of preparing specimens for TEM study have been given by Foster (1979). All electron-microscopy was carried out at the Electron Microscope Unit, University of Queensland.

OBSERVATIONS AND INTERPRETATIONS

Transmission electron micrographs of examples of both species show that the exine is two-layered, comprising an inner layer, which is referred to here as the intexine, and an outer layer, or exoexine (Pls 2-5). In both taxa, the intexine is laminated. The entire intexinal layer of

P. sinuosus is made up of laminae, although resolution of this feature is variable (cf. Pls 2, 3). For *M. triradiatus*, the laminae seem to be confined to the uppermost part of the layer, at its interface with the exoexine (Pl. 5, fig. 18c). According to Gullväg (1966), gymnosperm pollen characteristically possess an inner laminated layer (also see Van Campo, 1971; Walker, 1976) and on this basis it is suggested that both species studied belong to the gymnosperms. Walker (1976) noted that pollen of certain ranalean (angiosperm) families also have a laminated exinal layer, but pointed out that it is uncertain whether it is structurally analogous to the endexine (or intexine, as used in this paper) of the gymnosperms, as reported by Gullväg (also see discussion by Doyle *et al.*, 1975).

The exoexine of both species is not columellate, but is nevertheless partly structured. In section, the solid nature of this layer is broken by discrete, irregularly shaped cavities, some of which open on the exterior of the grain and form fine surface punctations (Pl. 3, fig. 11d). The cavities are formed at more or less the same level within the respective exoexinal layers of each species. In the studied examples, they are more numerous and smaller in *M. triradiatus* than in *P. sinuosus*. There is a striking similarity between the exoexinal intrastructure of these species and that of grains of certain extant, primitive angiosperms of the Magnoliaceae which possess a so-called "granular" atectate ektexine, as defined by Walker (1976, p. 257, pl. 13, fig. C). In this case the term "granular" refers to pollen which have small intraexinal cavities within an otherwise more or less homogeneous outer layer, and are non-columellate. It is here proposed that the exinal structure of such pollen be referred to as *incipient-alveolate*. The term incipient indicates that the alveolae of these grains are widely and apparently randomly spaced, and irregularly interconnected. Their arrangement contrasts markedly with the regularly interconnected, honeycomb-like complex of alveolae evident in sacci of: pollen grains of extant Pinaceous and Podocarpaceous conifers, protosaccate grains of Palaeozoic-Early Mesozoic gymnosperms (see Doyle *et al.*, 1975; Foster, 1979); and of certain Carboniferous pteridosperm pollen (see Audran & Masure, 1977; Taylor, 1980). The term granular (used in a very broad sense by Walker), is not applicable to describe these grains, as they lack any clearly differentiated internal exinal granular structure (cf. examples figured by Van Campo & Lugardon, 1973; Walker, 1976). The exoexine of the incipient-alveolate grains seems (at magnifications of X 10,000-15,000) to be of more or less homogeneous composition.

The function of the intraexinal cavities is not yet known with certainty. Such structures may allow the grain to successfully undergo volume changes caused by hydration and dehydration, and ultimately "germinate" (Heslop-Harrison, 1976; Walker, 1976). It is notable that some of the cavities in *P. sinuosus* open on the outer surface of the grain (Pl. 3, fig. 11d) indicating that they may have been storage areas, similar to those in certain extant angiosperm pollen grains (for discussion see Heslop-Harrison, 1976). It is also possible they may have been exit points for pollen-wall proteins as discussed for some extant poplars by Knox, Willing and Ashford (1972).

According to the original diagnosis of *Praecolpatites* (Bharadwaj & Srivastava, 1969, p. 140), members of the genus possess not only a structured exine, but each grain commonly has five longitudinal furrows, four of which are bordered by exinal folds. This structural arrangement is confirmed by the present study, although three to six folds may be formed (Pls 2, 3). Within the longitudinal furrows, the exoexine is much thinner than the remainder of that layer and thereby forms tenuitates as suggested by Balme and Playford (1967). It should be noted that the intexinal layer remains of more or less constant thickness, even in the furrow areas. As Balme (1970) suggested, each tenuitas is a potential exit point for the pollen content. It also seems likely that each would allow the grain to undergo harmomegathid changes as a response to varying humidity.

M. triradiatus has also been described as having a distal furrow or sulcus (Balme & Hennelly, 1956; Balme, 1970) and the TEM sections show that the sulcus is delimited by an area of distinctly thinner exoexine over the distal face. There is no corresponding thinning of the intexine over this area (cf. Pocock & Jansonius, 1969).

The structure of the sulcal area is closely comparable with the cappula exine of extant gymnospermous grains (for example, of *Pinus*; see Ueno, 1958), and fossil grains (Foster, 1979). By analogy with these grains, it seems likely that the distal area of *M. triradiatus* provided an exit point for the pollen contents and that desiccation of the grain would be prevented by invagination of the thinner sulcal area when dehydration was imminent. Although the sulcus is probably a "germinal" area, SEM studies suggest that "germination" was also feasible through the small, trilete laesurae on the proximal face (Pl. 4, fig. 14).

The incipient-alveolate intrastructure of both species partly accounts for the columellate-like appearance of the grains, as observed using a conventional light microscope. However, surface features of the grains also contribute to this appearance. SEM studies show that the surface of grains of *P. sinuosus* are minutely granulate and pitted; for *M. triradiatus*, the grain surface is regularly to irregularly, minutely, "channelled" (also evident from TEM sections) and so appears in light microscopy as granulate to verrucate, as originally described by Balme and Hennelly (1956).

CONCLUSIONS

1. Grains of *Praecolpatites sinuosus* and *Marsupipollenites triradiatus* have two-layered exines which comprise an inner laminated intexine and an outer incipient-alveolate exoexine. The development of a laminated intexinal layer strongly suggests a gymnospermous origin for both species.

2. The term *incipient-alveolate* is introduced to describe otherwise more or less homogeneous exoexinal (ektexinal) layers in which widely and randomly spaced, and irregularly interconnected cavities (alveolae) are developed.

3. The columellate-like appearance of both species (as described in earlier papers), which is observed using a conventional light microscope, is attributable to the incipient-alveolate intrastructure and to surface features of the grains.

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EXPLANATION OF PLATES

All figures are from unretouched negatives and prints. Print magnifications are given for each example. Photographic negatives from TEM and SEM studies are housed at the Electron Microscope Unit, University of Queensland or at Mines Administration Pty Limited (MINAD), Brisbane. Those in the MINAD repository are marked with an asterisk (*). Specimens used in light microscope studies are housed either in the Department of Geology and Mineralogy, University of Queensland (registered numbers prefixed with Y), or at MINAD (registered numbers prefixed P). Co-ordinates for Y. numbered specimens are from a Leitz Ortholux Microscope, housed at the University of Queensland; those for M × 2188, P. numbered specimens are from a Zeiss photomicroscope no. 67449 housed at MINAD.

PLATE 1

1-8. *Praecolpatites sinuosus* (Balme & Hennelly) Bharadwaj & Srivastava, 1969. Topotype material from Newcastle Coal Measures, Sydney Basin, N.S.W.; South Wallarah borehole D.D.H. 5 at 209·7 m.

1. Median focus (X 1,000); prep. P. 3929/1, 13·1 97·2; (a) phase contrast, (b) plain transmitted light.
2. Median focus (× 750); prep. P. 3929/1S, 12·3 103·6.
3. Median focus (× 750); prep. P. 3929/3S, 11·8 103·1.
4. Median focus (× 1,000); prep. P. 3929/1, 2·4 96·5; (a) phase contrast, (b) plain transmitted light.
5. Median focus (× 1,000); prep. P. 3929/1, 30·7 93·7.
6. SEM (× 750), neg. no. AOH 13*; prep. P. 3929/16/2.
7. SEM (× 750), neg. no. AOH 14*; prep. P. 3929/16/3.
8. SEM (× 750), neg. no. AOH 11*; prep. P. 3929/16/5; showing cross-section of grain.

PLATE 2

9-10. *Praecolpatites sinuosus* (Balme & Hennelly) Bharadwaj & Srivastava, 1969.

9a. Actual specimen sectioned (× 1,000); from OR7 (Olive River Basin), cuttings 182-184 m. Approximate position of sections (b) and (c) shown respectively by two arrows and one arrow.

9b. TEM (× 4,000) neg. nos 5786, 5787; showing dark laminated intexinal layer and clearly developed cavities in exoexinal layer.

9c. TEM (× 4,000) neg. nos 5892, 5893; showing increased number of exinal folds, arrows indi-

cate tenuitae (thin exoexine) developed in fold areas.

9d. TEM (× 6,000) neg. no. 5877; detail of extreme RH fold area of (b) and (c), arrow indicates thin (lighter) exoexine in fold.

10. TEM (× 10,000) neg. no. 5890; detail of weakly laminated, (darker) intexine (i), shown in (b).

Plate 3

11. *Praecolpatities sinuosus* (Balme & Hennelly) Bharadwaj & Srivastava, 1969.

11a. Actual specimen sectioned (× 1,000); from OR13 (Olive River Basin), cuttings 196-198 m. Approximate position of section (b) indicated by arrows.

11b. TEM (× 4,000) neg. no. 5793; irregular cavities in exoexine clearly developed. Intexinal layer is poorly and irregularly preserved.

11c. TEM (× 15,000) neg. no. 5790; details of fine laminae (i).

11d. TEM (× 15,000) neg. no. 5791; detail of fold area showing laminated intexine (i) and narrow channel of exoexinal cavity to outer surface of grain (arrowed).

Plate 4

12-17. *Marsupipollenites triradiatus* Balme & Hennelly 1956.

12a. TEM (× 1,500) neg. no. 5671; showing large area of sulcus (arrowed), note how the exoexine thins over this area. Specimen F130, from Blair Athol Coal Measures, B .A. No. 4 at 41·23 m.

12b. Actual specimen sectioned (× 750), arrows indicate approximate line shown in (a).

13. SEM (× 1,000) neg. no. MAH 34; distal aspect of unexpanded grain. Topotype specimen from Newcastle Coal Measures, Sydney Basin, N.S.W.; South Wallarah D.D.H. 5, 209·7 m; prep. P. 3929/MAH 25-34, 30·6 116·7, Y. 2838.

14a. SEM (× 4,428) neg. no. MAE 4; showing detail of proximal, trilete laesurae, and surface " chanelling ".

14b. SEM (× 880) neg. no. MAE 3; proximal aspect. Comparative specimen from Hebburn No. 2 Colliery, Greta Seam, Sydney Basin, N.S.W.; prep. P. 3937, specimen not recovered.

15. Median focus (× 750); same location as fig. 12, prep. F130/2, 33·0 108·9, Y. 2122.

16a. Proximal focus (× 1,000), phase contrast.

16b. Proximal focus (× 1,000), plain transmitted light; unexpanded grain, note surface sculpture.

16c. Median focus (× 1,000), plain transmitted light. Topotype specimen, same location as fig. 13.

17. Distal focus (× 750), unexpanded grain. Comparative specimen from Baralaba Coal Measures; N.S. 77 (Kianga), 238·6 m, prep. 346/4, 49·1 125·0, Y. 2837.

Plate 5

18. *Marsupipollenites triradiatus* Balme & Hennelly 1956.

18a. Actual specimen sectioned (× 750), arrows indicate approximate position of (b).

18b. TEM (× 4,000), neg. nos 5677, 5678; showing small cavities developed in the exoexinal layer (lighter colour); only a relatively small section of the sulcus (arrowed) has been sectioned (cf. Pl. 4, fig. 12a); note how the exoexine is much thinner over the sulcus area.

18c. TEM (× 10,000) neg. nos 5672, 5673; detail of part of sulcus area (s); arrows show laminated interface between intexine (i) and exoexine. Through compression, the intexine in each hemisphere of the grain is in contact [RH in fig. 18(b)], the white bar indicates the line of contact.

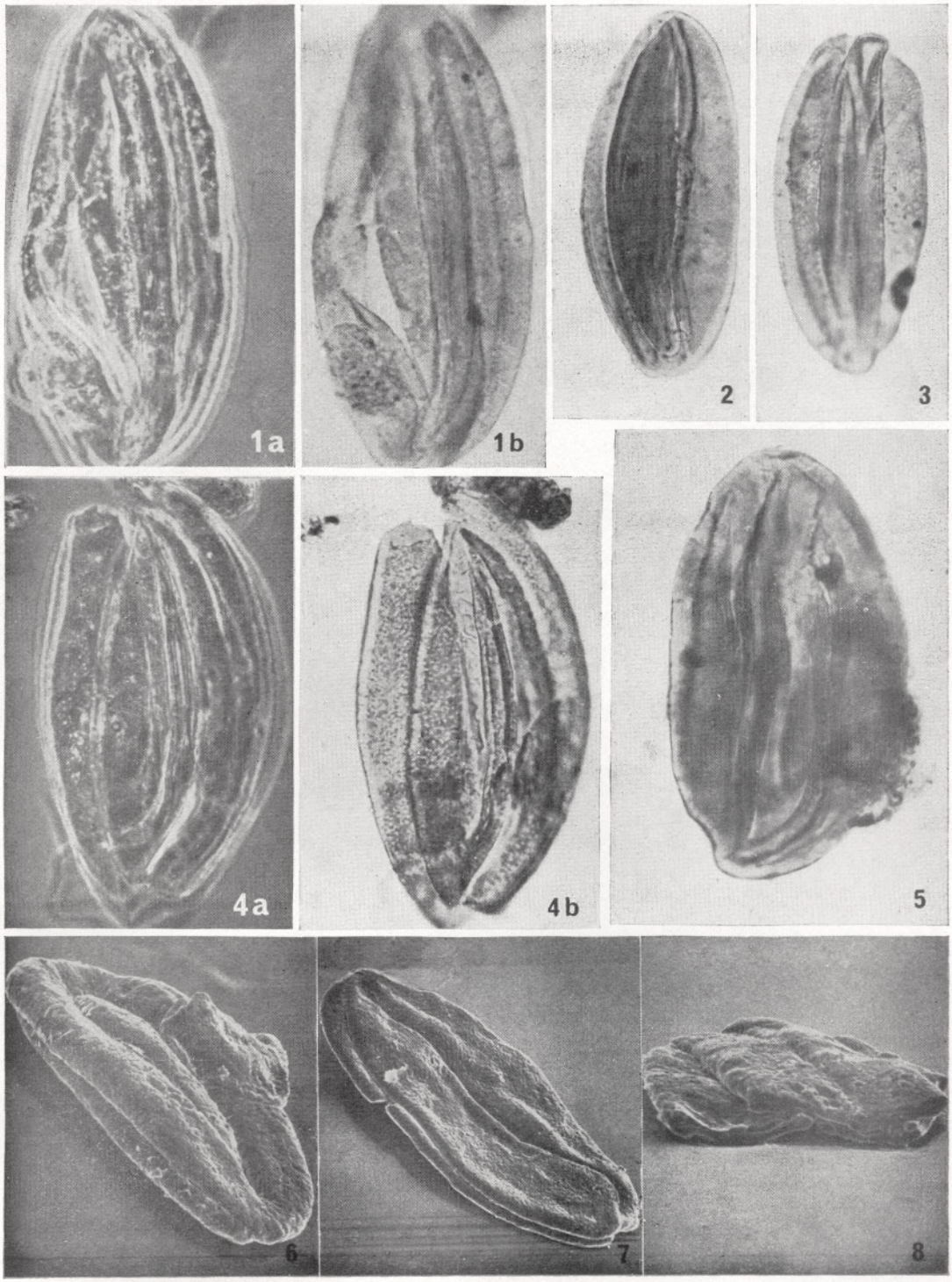
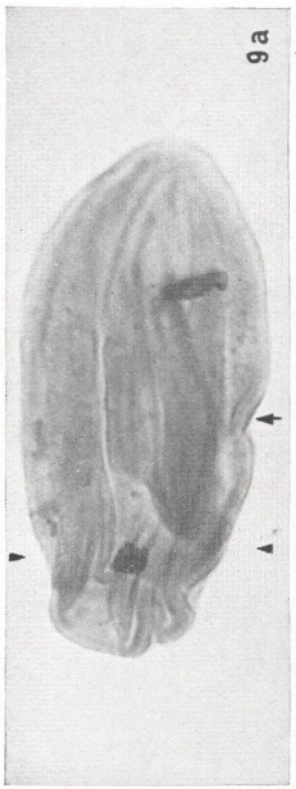
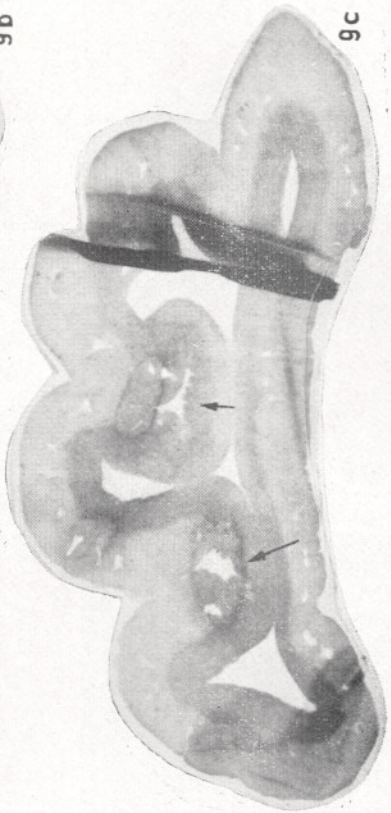


PLATE 1





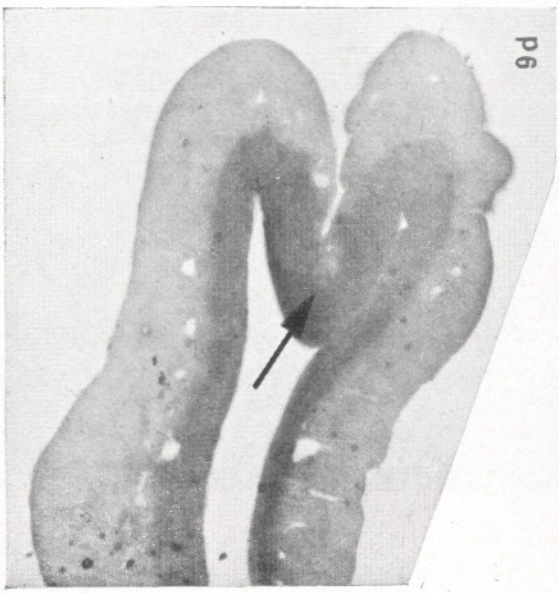


PLATE 2

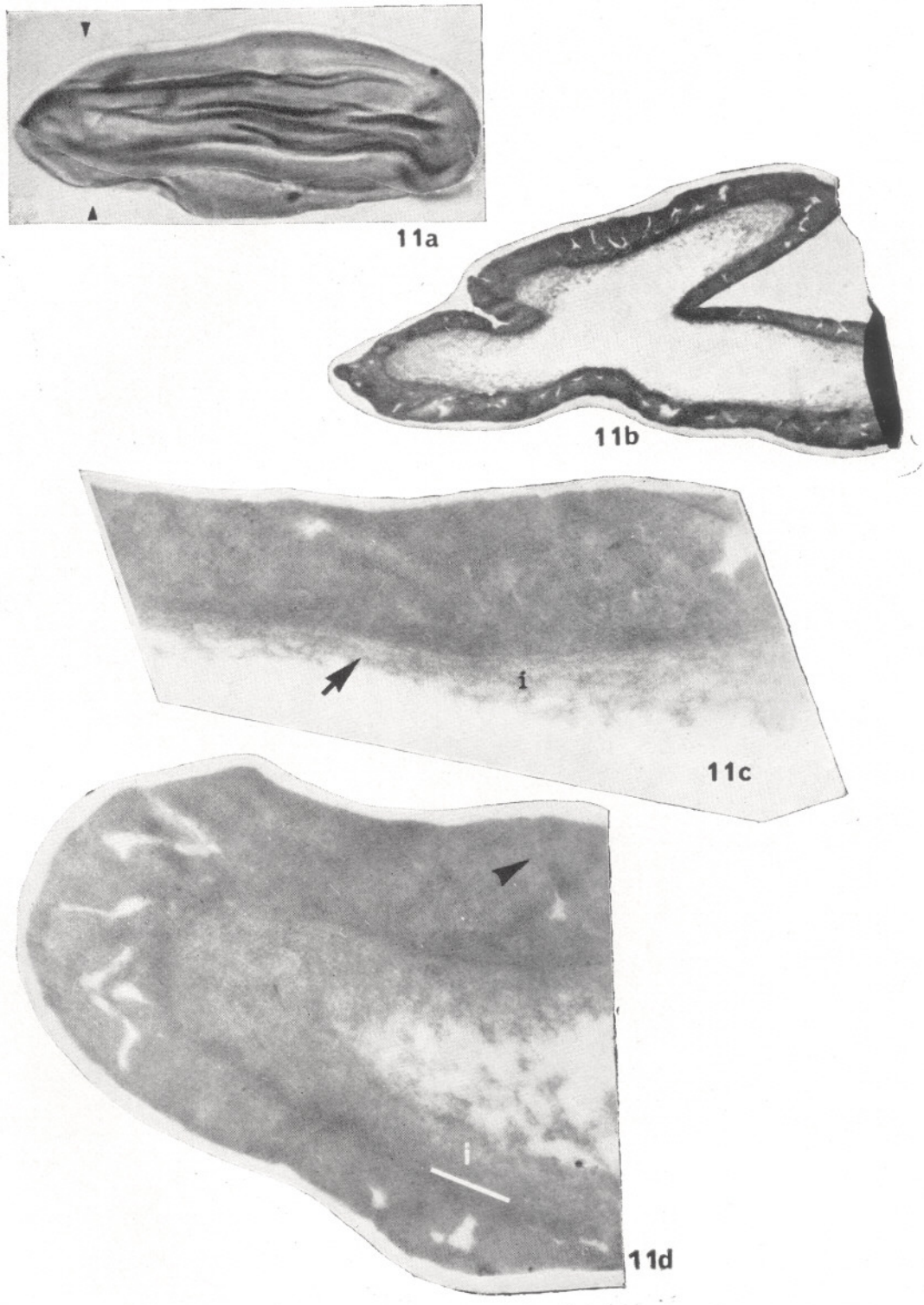
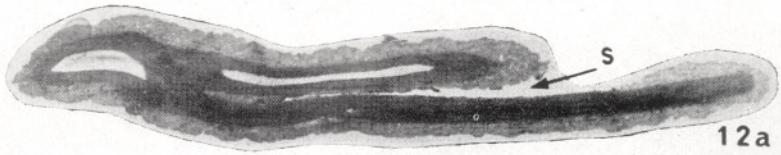
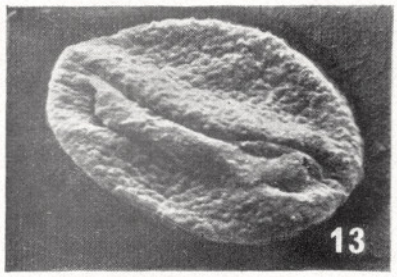
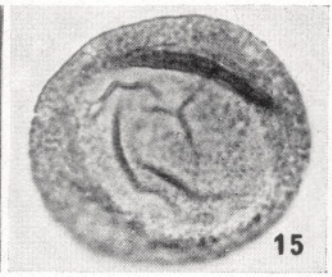
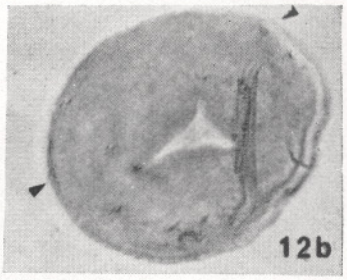


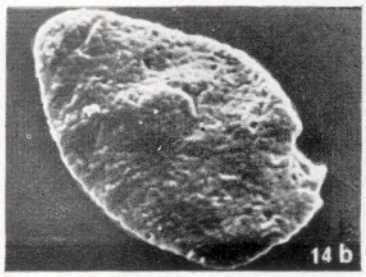
PLATE 3











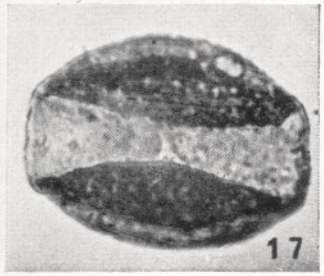


PLATE 4

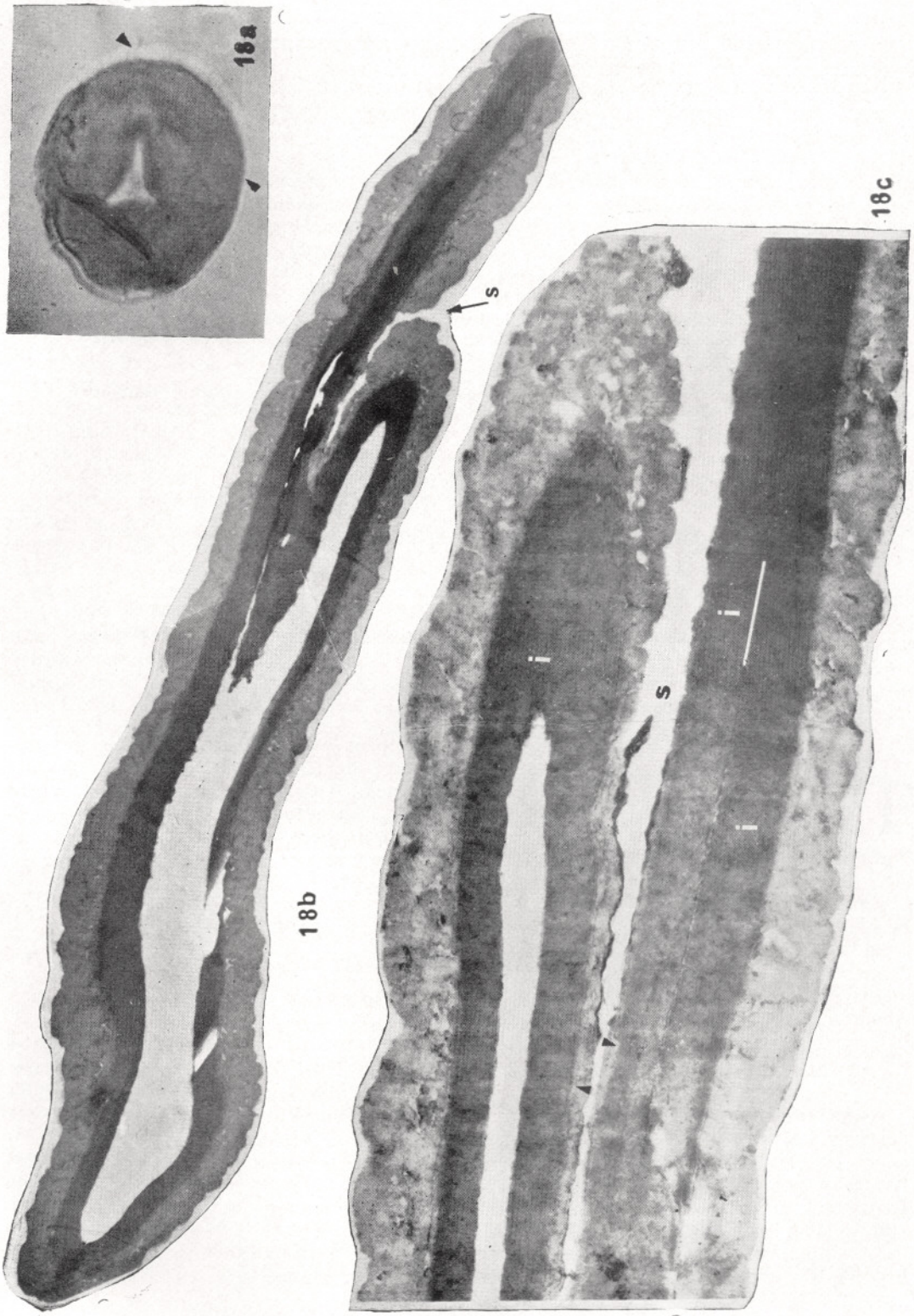


PLATE 5