Aspects of Permian palaeobotany and palynology. XVIII. On the morphology and ultrastructure of *Potonieisporites novicus* (prepollen of Late Carboniferous/Early Permian Walchiaceae)

RUUD J. POORT and HARRY VELD*

Laboratory of Palaeobotany and Palynology, Utrecht University, Budapestlaan 4, 3584 CD Utrecht, The.Netherlands

SUMMARY

The type species of the palynological form-genus *Potonieisporites*, *P. novicus*, can be considered to represent Late Carboniferous/Early Permian conifers, assignable to the Walchiaceae of the Euramerican floral province. Morphological and ultrastructural analysis of the species falsifies earlier concepts of a monosaccate organization and the presence of a distal germinal area. The species is characterized by a monosaccoid sexine expansion, completely filled with an alveolate infrastructure. A proximal aperture is distinct, but there is no evidence of distal specializations indicative of the outgrowth of a haustorial pollen tube; the species thus qualifies as prepollen. These characters are included in an emended diagnosis for the species. A restricted concept of an exclusively walchiaceous status for the form-genus *Potonieisporites* can not yet be proposed, mainly because of the lack of conclusive evidence on the botanical affinity and the morphological/ultrastructural organization of similar pollen from the Gondwana floral province.

Key-words: Carboniferous, fossil conifers, Permian, pollen morphology, prepollen, Walchiaceae.

INTRODUCTION

The detailed study of the genus *Ortiseia* and the re-evaluation of the genera *Walchia* and *Ernestiodendron* by Clement-Westerhof (1984, 1988), in combination with the establishment of the genus *Otovicia* (Kerp *et al.* 1990), has contributed to the development of a natural concept of the Late Palaeozoic conifer family of the Walchiaceae (Göppert) Schimper (=Lebachiaceae Florin; Utrechtiaceae Mapes & Rothwell). One of the intriguing elements in this concept is the suggestion that the Walchiaceae were characterized by zoidogamy. On the basis of detailed cuticular analysis (Clement-Westerhof 1984) and fluorescence microscopy (Kerp *et al.* 1990), it was deduced that walchiaceous ovules are likely to possess pollen/archechonial chambers. Moreover, it was emphasized that walchiaceous pollen could qualify as *prepollen*, i.e. microspores of extinct zoidogamous seed plants that had not yet developed the capacity to produce a

distal haustorial pollen tube like in extant cycads and *Ginkgo* (for a review of the prepollen concept, see Poort *et al.* 1996). Light microscopic and scanning electron microscopic studies of *in situ* pollen from polliniferous organs clearly demonstrated the presence of a proximal aperture, indicative of proximal release of free antherozoids. No evidence was found as to the additional presence of distal specializations resembling a functional aperture for the outgrowth of a haustorial pollen tube.

In contrast to permineralized material, the recognition of a pollen/archegonial chamber in compressed fossil ovules frequently remains subjective. On the other hand, in many cases pollen morphological characters may provide convincing evidence of zoidogamy. In Late Palaeozoic gymnosperm categories, other than conifers, ultrastructural analysis has confirmed the presence of prepollen among pteridosperms (Lyginopteridales, Medullosales; e.g. Millay *et al.* 1978) and some Cordaitales (e.g. Millay & Taylor 1974). In order to verify the supposed prepollen condition of walchiaceous pollen, the present study therefore concentrates on the morphology and ultrastructure of *Potonieisporites novicus* Bhardwaj 1954; i.e. the palynological species to which dispersed pollen of the Late Carboniferous/Early Permian genera *Walchia*, *Ernestiodendron* and *Otovicia* can be assigned. The pollen of the Late Permian walchiaceous genus *Ortiseia*, corresponding to the palynological species *Nuskoisporites dulhuntyi* Potonié & Klaus 1954, is treated separately (Poort *et al.* 1997).

MATERIALS AND METHODS

The preservation of *Potonieisporites* found *in situ* in polliniferous organs of *Otovicia*, as well as dispersed pollen in the embedding sediment (Kerp *et al.* 1990), proved to be unsuitable for combined light microscopic and electron microscopic (SEM, TEM) analysis. Morphological and ultrastructural observations have therefore been carried out on well-preserved dispersed material from the Late Carboniferous (Gzhelian) Rotliegend deposits exposed near Weiden (Oberpfalz, Germany; see Veld & Kerp 1992). Specimens of *P. novicus* were obtained through standard palynological techniques, using HCl (25%), HF (40%) and $ZnCl_2$. Light-microscopic slides were made in glycerine jelly. Material selected for scanning electron microscopy (SEM) was run through an alcohol series, mounted on stubs and sputter-coated with a thin layer of gold. These samples were studied with a Cambridge Stereoscan scanning electron microscope. Material for transmission electron microscopy (TEM) was prestained with a solution of osmium-tetroxid (1%) and uranylacetate (2%) in distilled water for 1 hour. After dehydration through a series of methanol and acetone, specimens were embedded in a solution of Araldit M (51 weight %), HY 964 (47 weight %) and DMP 30 (2 weight %). Sections were cut with a Dupont diamond knife on a Reichert ultramicrotome Om U 2, mounted on one-hole grids and post-stained with lead citrate (a solution of 4 weight % $Pb(NO_3)_2$, 5·3 weight % natrium-citrate and 90·7 weight % distilled water) for 5 min. The obtained samples were studied with a Philips 201 EM transmission electron microscope.

The applied descriptive terminology follows the *Glossary of Pollen and Spore Terminology* (Punt *et al.* 1994), unless otherwise stated.

THE PALYNOLOGICAL FORM-GENUS *POTONIEISPORITES*

The palynological form-genus *Potonieisporites* was established by Bhardwaj (1954) to include relatively large monosaccate pollen, characterized by an elliptical equatorial

outline and a monolete proximal aperture; the type species is *P. novicus* Bhardwaj 1954. Subsequently, Bharadwaj (1964a) recognized that the Late Carboniferous dispersed pollen from Europe on which *Potonieisporites* had been based, could well be compared with *in situ* pollen from polliniferous organs that are presently attributed to the Late Carboniferous/Early Permian genera *Walchia*, *Ernestiodendron* and *Otovicia* of the Walchiaceae (Kerp *et al.* 1990). To accommodate for the observed natural variability, Bharadwaj (1964b) provided an emended diagnosis for *Potonieisporites*, denoting variation in outline (elliptical to circular) and shape of the proximal aperture (straight or roof-shaped). Much emphasis was given to folding patterns in compressed specimens, notably on the frequent presence of two distal crescent-shaped folds perpendicular to the long axis.

   Although correlation with individual genera is not possible, the type species of *Potonieisporites* can be confidently assigned to the Walchiaceae. Throughout the world, however, *Potonieisporites* has become a popular taxon for classifying Late Carboniferous/Permian monosaccate pollen other than. *P. novicus*, either as separate species or without further identification at a species level. In order to minimize the risk of correlating similar but not identical pollen with the Walchiaceae, it is essential to formulate a new emended diagnosis for the type species, in harmony with contemporary pollen morphology, that may also serve as a more restricted concept for the form-genus.

MORPHOLOGICAL AND ULTRASTRUCTURAL ANALYSIS OF *POTONIEISPORITES NOVICUS*

Overall shape and size

In polar compression, the studied forms are elliptical to (sub)circular in outline (Fig. 1a–f; Fig. 2a–c,e), confirming the concept of Bharadwaj (1964b); elliptical forms are dominant. No illustrative material was found to further elucidate the lateral compressional aspect. The measured size varies from 116 to 138 μm in length, and 100 to 123 μm in width.

Structure of nexine

The nexine constitutes a central body characterized by an elliptical to (sub)circular outline in polar view (Fig. 1a–f). TEM sections indicate that the nexine is built up of two layers (Fig. 4b–e). In TEM descriptive terminology for the organization of pollen walls, the inner layer represents the endexine, whereas the outer layer corresponds to the foot layer of the ectexine. As a result of fossilization the inner layer is sometimes dissolved (Fig. 4a).

Structure of sexine

TEM sections indicate that the nexine is completely enveloped by the sexine, to which it is fused (Fig. 3a–c). The proximal and distal sexine, as well as the (sub)equatorial sexine expansion (see below) is clearly tectate; the infratectal layer is alveolate with compartments of varying shape and size (Fig. 3a–c, Fig. 4a–h). In light microscopy, the alveolate infrastructure appears as an infrapunctate, infrareticulate or infrarugulate pattern. SEM images may show elongated and radially orientated muri on the proximal surface of the (sub)equatorial sexine expansion (Fig. 2e); these muri may represent a

(a)

(b)

(c)

(d)

(e)

(f)
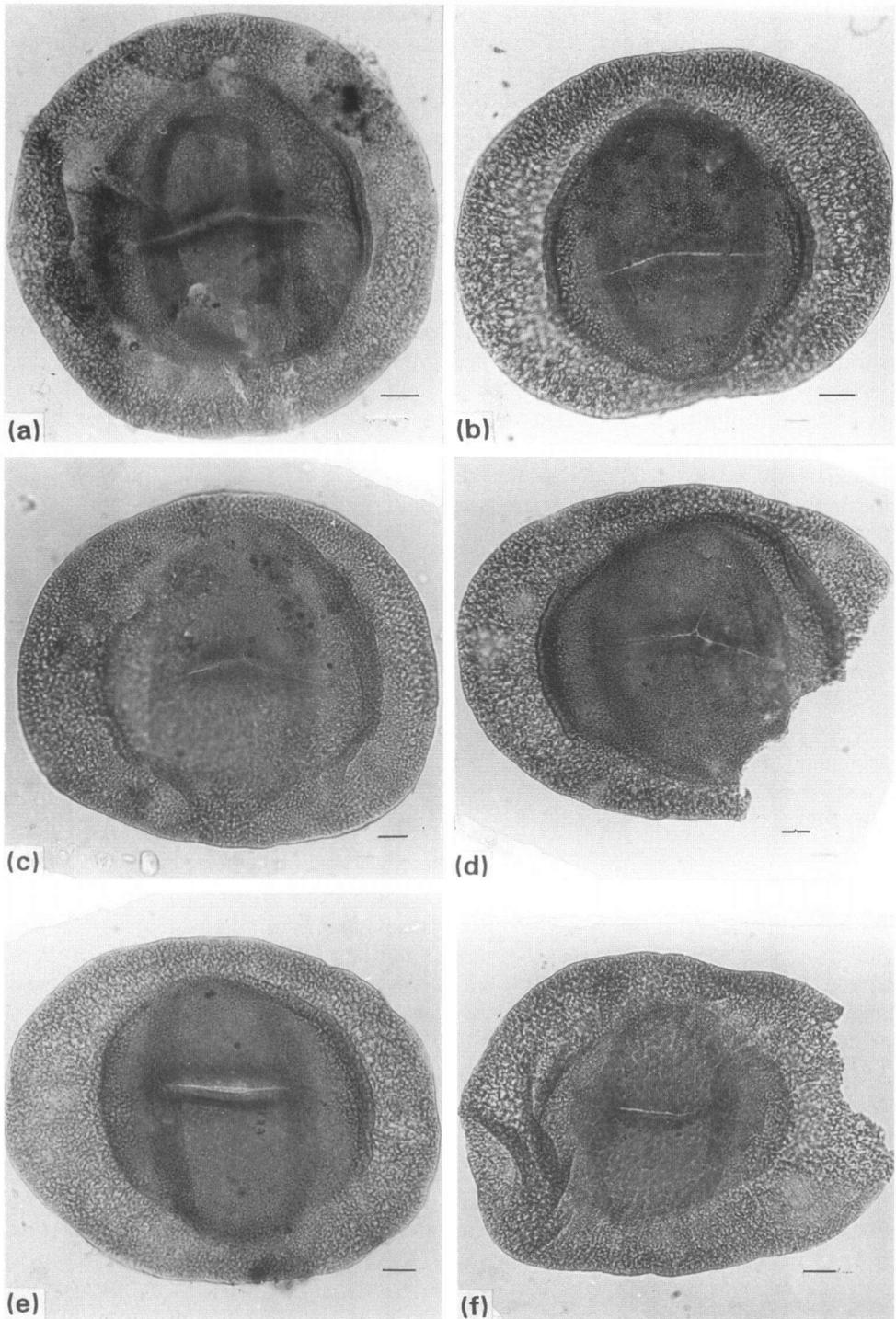
surface view of infratectal sexinal elements. Occasionally the distal sexine shows a gemmate to verrucate surface relief (Fig. 1f).

Monosaccoid expansion

TEM sections demonstrate that the sexine of the (sub)equatorial expansion is fused to the nexine and completely filled with an alveolate infrastructure (Fig. 3a–c; Fig. 4c,e). The volume of the infrastructural compartments is likely to have been affected by compression, but the limited thickness of the expansion suggests a relatively flattened differentiation. The expansion may be thickened towards its outer margin; light microscopically this thickening is reflected by a somewhat darker rim. A SEM image of the distal surface shows the distal inclination of the expansion (Fig. 2b). The expansion cannot be interpreted in terms of a monosaccate organization, implying partial separation of the sexine from the nexine. To denote an unseparated organization, Scheuring (1974) introduced the term proto(mono)saccate. This term is frequently applied in relation to pollen of other fossil gymnosperms despite its unsubstantiated connotation of an ancestor-descendant relationship between protosaccate and saccate organization. Meyen (1988) suggested the term quasisaccate. We prefer to use the neutral term (mono)saccoid to denote sexine expansions that are completely filled with alveolate infrastructure.
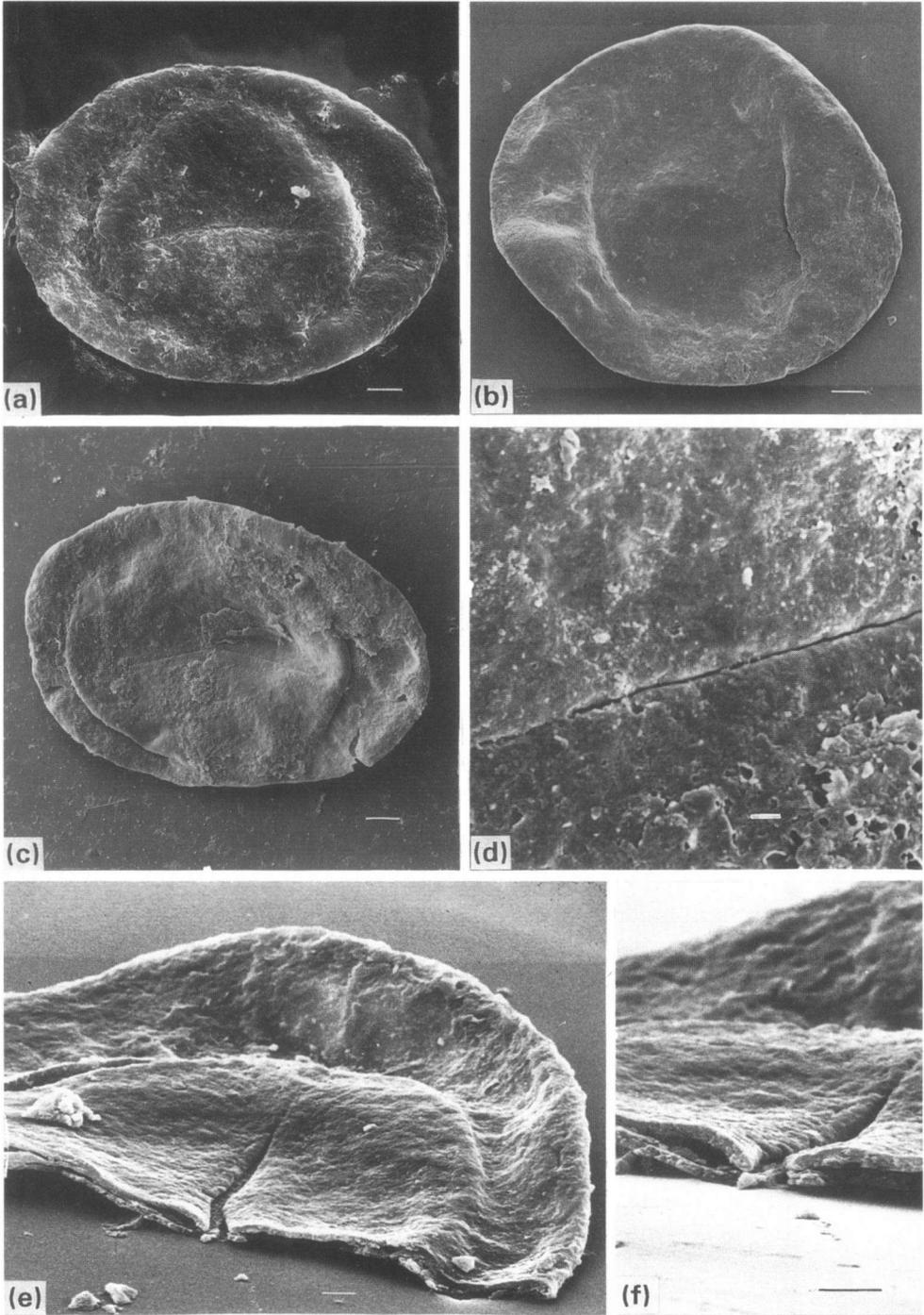
Proximal aperture

The shape of the longitudinally orientated proximal aperture is varied (Fig. 1a–f); the aperture can be a monolete mark (one laesura), a dilete mark (two laesurae), or a reduced trilete mark (three laesurae, one of which has a strongly reduced length). The length of the mark is variable (1/3 to almost the entire long axis of the central body). Open laesurae can be observed in both sexine and nexine (Fig. 2d,e,f; Fig. 4b,d,f). The TEM sections display prominent inward folding of sexine and nexine adjacent to the laesurae. This folding corresponds to the dark areas, earlier described as labra (Bharadwaj, 1964b), that can be light microscopically observed in compressed specimens (Fig. 1a–f).

Distal aperture

TEM sections confirm the absence of a distal sexine-free area or sexine thinning (leptoma) that could be indicative of pollen tube formation. The distal sexine appears equally thick as the proximal sexine, or may be even thicker (Fig. 3a–c; Fig. 4a,b,d,f).

   In general, fossil gymnospermous pollen characterized by proximal apertures and absence of distal specializations indicative for the outgrowth of a pollen tube is known as prepollen. The prepollen concept is intimately linked with zoidogamy (see review by Poort *et al.* 1996). Renault (1896) coined the term *prépollinies* for the large pteridospermous and cordaitalean pollen, considered to be intermediate between pteridophytic spores and cycadophytic pollen. The term was revived and anglicized by Schopf (1938, 1948). The prepollen concept was elaborated by Chaloner (1970) and Jonker (1974,

Fig. 1. Photomicrographs of *Potonieisporites novicus*. (a) Specimen showing a circular outline, folding patterns and dilete organization of the proximal aperture. (b) Specimen showing an elliptical outline, folding patterns and dilete organization of the proximal aperture. (c) Specimen showing an elliptical outline, folding patterns and strongly reduced trilete organization of the proximal aperture. (d) Specimen showing an elliptical outline, folding patterns and reduced trilete organization of the proximal aperture. (e) Specimen showing an elliptical outline, folding patterns and monolete organization of the proximal aperture. (f) Specimen showing an elliptical outline, folding patterns and monolete organization of the proximal aperture, and distal surface ornamentation. All scale bars = 10 μm.

1977). As a result, prepollen is currently defined as 'the microspores of certain extinct seed plants characterized by proximal apertures and presumed proximal germination, rather than the distal, equatorial or other typical apertures of seed plant pollen grains' (Punt *et al.* 1994). Similar to a variety of pollen types of pteridosperms (Lyginopteridales, Medullosales; e.g. Millay *et al.* 1978) and Cordaitales (e.g. Millay & Taylor 1974), TEM sections thus confirm that *P. novicus* qualifies as prepollen.

Folds

Apart from random folding, two relatively consistent folding patterns may frequently be distinguished in compressed specimens: (1) folds occurring circum-equatorially in the central body, and (2) two distal lunar-shaped folds, perpendicular to the long axis, often interconnected by short longitudinal folds (Fig. 1a–f). TEM sections show the complex nature of the compression folds in the equatorial region of the nexine body (Fig. 4c,e). In contrast, the distal crescent-shaped folds are related to the sexine. They pronounce the distal onset of the monosaccoid expansion (Fig. 2b; Fig. 3a).

Emended diagnosis

Considering the above analysis, and noting the earlier information on *in situ* material (Bharadwaj 1964a), a new concept for *P. novicus* is summarized in the following emended diagnosis of the species.

Species: *Potonieisporites novicus* Bhardwaj 1954.
       Holotype: *Potonieisporites novicus* Bhardwaj 1954, Fig. 10.
       Original diagnosis: Bhardwaj 1954, p. 520.
       Earlier emendation: Bharadwaj 1964b, p. 83.
       Botanical affinity: Walchiaceae (Göppert) Schimper, emend. Kerp *et al.* 1990

Emended diagnosis: Large monosaccoid prepollen. Outline elliptical to (sub)circular in polar view; size variable, long axis between 100 and 200 µm. Nexine constituting a central body, with an elliptical to (sub)circular outline in polar view. Nexine completely enveloped by and fused to the sexine. Sexine with distinct tectum and alveolate infrastructure. Sexine (sub)equatorially forming a flattened and distally inclined monosaccoid expansion, completely composed of alveolate sexinous material. Monolete, dilete or reduced trilete mark present in proximal nexine and sexine; length of laesurae variable. Distal leptoma absent. Compressed specimens frequently with two characteristic crescent-shaped folds in the distal sexine, perpendicular to the long axis.

TOWARDS A RESTRICTED, WALCHIACEOUS CONCEPT OF THE FORM-GENUS *POTONIEISPORITES*

A natural classification of extinct conifers requires the recognition of natural genera, diagnosed on the basis of an analysis of both vegetative and reproductive organs.

Fig. 2. SEM images of *Potonieisporites novicus*. (a) Proximal face of specimen showing dilete aperture. Outline of central body accentuated by sexinal folding. Scale bar = 10 µm. (b) Distal face of specimen, showing distally inclined monosaccoid expansion accentuated by sexinal folding. Scale bar = 10 µm. (c) Proximal face of specimen showing dilete aperture; outline of central body accentuated by sexinal folding. Scale bar = 10 µm. (d) Detail of Fig. 2c; dilete aperture. Scale bar = 1 µm. (e) Broken specimen in proximal view, showing section of open laesura of dilete aperture, and radially orientated muri on the inner part of the monosaccoid expansion. Scale bar = 5 µm. (f) Detail of Fig. 3e. Inward folding of the exine adjacent to laesura. Scale bar = 5 µm.

Fig. 3. TEM sections of *Potonieiporites novicus*. (a) Section subparallel to long axis. In this specimen the inner layer of the nexine was dissolved during fossilization. Note alveolate infrastructure of sexine and folding of sexine (left). (b) Section subparallel to short axis. Note alveolate infrastructure of sexine and complex folding of nexine. (c) Section through same specimen as Fig. 3b; laesura of proximal aperture sectioned. Note absence of distal leptoma. All scale bars=5 μm.

Within the Walchiaceae, the genera *Walchia, Ernestiodendron, Ortiseia* and *Otovicia* have now attained a natural status (Clement-Westerhof 1984, 1988; Visscher *et al.* 1986; Kerp *et al.* 1990; Kerp & Clement-Westerhof 1991). If fossil conifer remains do not permit an interpretation in terms of a natural genus, however, they should necessarily be included in form-genera. These form-genera logically have a variable degree of artificiality, ranging from taxa comprising fragments which only supposedly belong to conifers, to well-defined taxa enabling attribution of included organs to a single natural family. Within the resulting medley of more or less clearly defined form-genera, a practical way of integrating taxonomic progress may be the progressive 'promotion' of genera by adding relevant information to the diagnosis, based on a re-evaluation of its type-species (Visscher *et al.* 1986). Some form-genera of individual organs may thus become definitive of their parent plant group at a family level. Such taxa correspond to the, unfortunately discarded, concept of the 'organ-genus' of pre-1978 editions of the *International Code of Botanical Nomenclature*, ICBN). For the Walchiaceae, the form-genera *Culmitzchia* (foliage with preserved epidermal structure), *Walchiostrobus* (ovuliferous organs) and *Walchianthus* (polliniferous organs) have been re-diagnosed to accommodate conifer remains, not (yet) assignable to natural genera but clearly showing walchiaceous affinities (Clement-Westerhof 1984; Visscher *et al.* 1986; Kerp & Clement-Westerhof 1991). This procedure implies that species of which a former inclusion in walchiaceous genera or form-genera could not be reconfirmed, ought to be transferred to 'lower' categories of coniferous form-genera, such as *Hermitia* and *Thuringiostrobus*, established for foliage and ovuliferous organs with insufficient characters for identification at a family level (Visscher *et al.* 1986; Kerp & Clement-Westerhof 1991).

The taxonomy of dispersed pollen of Late Carboniferous/Permian conifers relies on form-genera that cannot yet be correlated with families. However, interpretation of palynological assemblages increasingly demands insight in the botanical affinity of individual pollen types, at lowest possible taxonomic levels. Conversely, pollen, when studied according to modern pollen morphological methods, may provide useful complementary information to whole plant taxonomy, as well as insight in the reproductive biology of extinct conifer families.

The palynological species *P. novicus* can be correlated with the Walchiaceae as diagnosed by Kerp *et al.* (1990). The new concept for the species emphasizes its prepollen condition and its monosaccoid organization. The absence of a leptoma falsifies views of previous authors who suspected the presence of a distal germinal area in walchiaceous pollen (Florin 1938–1945; Pontonié 1962; Bharadwaj 1964a). Functional interpretation of the distinctive proximal aperture in terms of an opening for the release of antherozoids provides further evidence for zoidogamy among the Walchiaceae. Since *P. novicus* represents the type species of *Potonieisporites*, one might consider to promote the status of this palynological form-genus to that of a form-genus for prepollen of the Walchiaceae.

The Walchiaceae played a prominent role in the composition of Late Carboniferous and Early Permian meso- to xerophilous plant communities in the Euramerican floral province (e.g. Barthel 1976; Winston 1983; Haubold 1985). Because of the common stratigraphic co-occurrence of walchiaceous macrofossils and *Potonieisporites*, the innumerable and widespread records of *Potonieisporites* from Europe are likely to corroborate a restricted, walchiaceous, concept for the form-genus. This may also apply to North America. The palynological species *P. simplex* Wilson 1962 has been compared
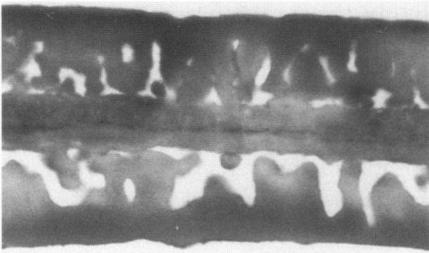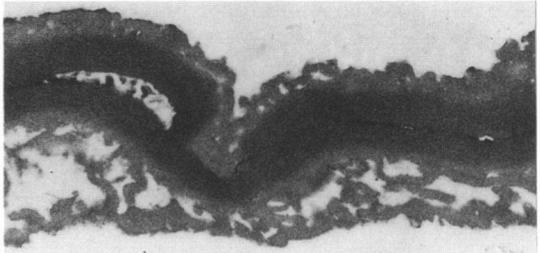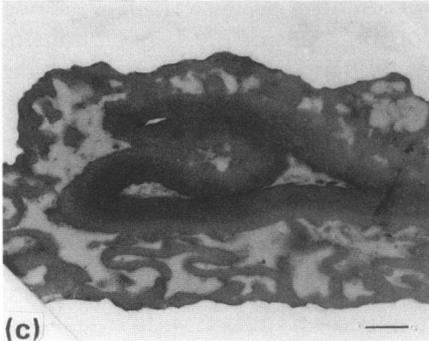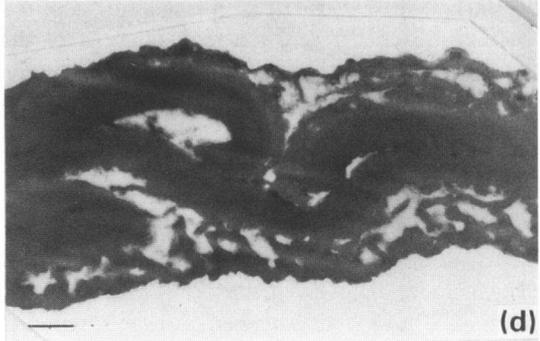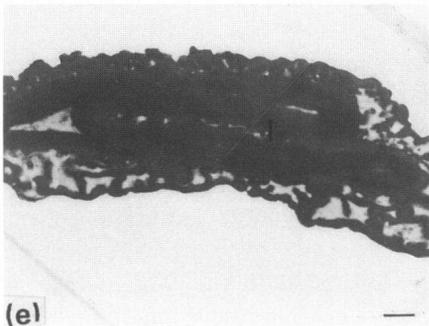
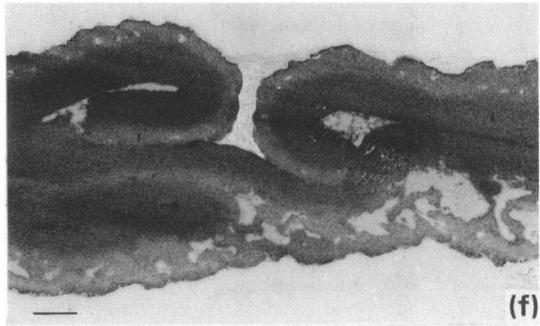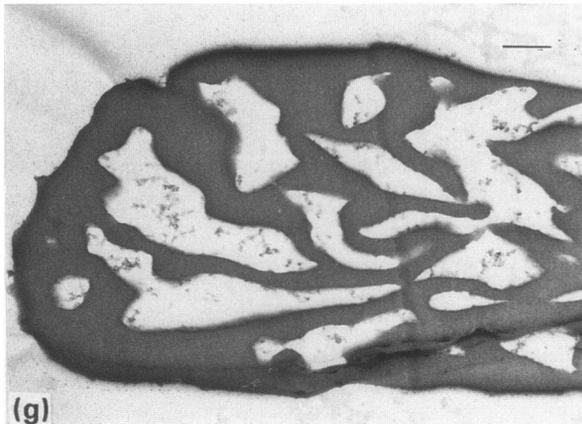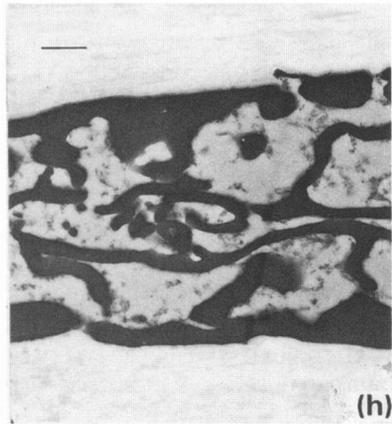with *Potonieisporites* found *in situ* in cones attributable to *Walchia garnettensis* (Florin) Clement-Westerhof 1984 from the Upper Carboniferous of Kansas (Winston 1984). Judging from the illustrations, the latter material could well correspond to *P. novicus*.

In addition to genera of the Walchiaceae, *Potonieisporites* has also been related to *Emporia lockhardii* (Mapes & Rothwell 1984) Mapes & Rothwell 1991, a conifer species based on permineralized material, that has been applied to typify the Emporiaceae Mapes & Rothwell 1991. Despite similarities, this family is considered to differ from the Walchiaceae (Lebachiaceae Florin; Utrechtiaceae Mapes & Rothwell) because of the presence of stalked, rather than laterally attached ovules. Uncompressed pollen grains are classified as prepollen, a light microscopic section confirming the absence of a distal leptoma. In contrast to *P. novicus*, however, this section reveals a monosaccate rather than a monosaccoid organization. In a restricted concept for *Potonieisporites*, these forms should be excluded from the form-genus.

The major problem with respect to defining *Potonieisporites* as an exclusively walchiaceous form-genus is formed by extensive palaeobotanical and palynological information from the various parts of the Gondwana floral province. From these areas, Late Carboniferous/Permian plant megafossils that could qualify as Walchiaceae have never been reported. On the other hand, notably in India, but also in Australia, Africa and South America, species of *Potonieisporites* other than *P. novicus* are regularly applied in the classification of dispersed monosaccate pollen. Following the institution of *P. neglectus* Potonié & Lele 1961, some 25 species have been formally described from Gondwanaland. There are no realistic clues as to the botanical affinity of this material. At least part of the species show strong overall similarities with *P. novicus*; Potonié & Lele (1961) noticed the difficulties in separating *P. neglectus* from the type species. A detailed restudy of Gondwana forms is therefore required to detect whether or not their morphology and ultrastructure matches *P. novicus* in its present concept. Pending availability of such information, the probability of a walchiaceous affinity of the form-genus *Potonieisporites* remains restricted to records from the Euramerican floral province.

CONCLUDING REMARKS

The morphological and ultrastructural concept of *P. novicus* contrasts with the two principal pollen categories that are morphologically and functionally recognized in extant gymnosperms: (1) pollen with a distal aperture (leptoma) for the outgrowth of a pollen tube with an exclusively nutritive function; release of motile antherozoids not via preformed apertures but by wall decay (zoidogamy of cycadophytes, *Ginkgo*), and (2) pollen with a leptoma for the outgrowth of a pollen tube that also serves as a carrier for immotile cells or nuclei (siphonogamy of all other extant gymnosperm taxa). The morphological characters of *P. novicus* are shared with a variety of prepollen of

Fig. 4. TEM sections of *Potonieisporites novicus*. (a) Detail of Fig. 3a. Inner layer of nexine (endexine) absent. Sexine alveolate with well-developed tectum. (b) Detail of specimen of Fig. 3b,c. Inward folding of the nexine accentuates laesura. (c) Detail of Fig. 3b. Complex folding of two-layered subequatorial nexine. Alveolate infrastructure of sexine. (d) Detail of Fig. 3c. Inward folding of nexine increased in comparison to Fig. 4b. (e) Detail of Fig. 3b. Complex folding of subequatorial nexine. (f) Detail of specimen of Fig. 3b,c. Section through central part of specimen. Further increase of inward folding of nexine relative to Fig. 4b and Fig. 4d. (g) Detail of specimen with well preserved alveolate infrastructure of monosaccoid expansion. (h) Detail of specimen with well preserved alveolate infrastructure of monosaccoid expansion. Indications for a perforate nature of the tectum. All scale bars = 1 μm.

Late Palaeozoic zoidogamous pteridosperms (Lygenopteridales, Medullosales) and some Cordaitales. Apart from *P. novicus*, *Nuskoisporites dulhuntyi* (assignable to the walchiaceous conifer *Ortiseia*) also qualifies as prepollen (Poort *et al.* 1997). In reconstructions of the reproductive biology of pteridosperms and cordaitaleans, the prepollen condition has long since attracted wide attention (see Poort *et al.* 1996). It is not yet generally appreciated, however, that pollen of Late Palaeozoic conifer families could also qualify as prepollen. This may be due to the fact that concepts of reproductive biology of extinct conifers are usually based on comparisons with extant families. The presence of prepollen in the Walchiaceae challenges the existence of uniform siphonogamy in extinct conifers. Continuing ultrastructural studies of fossil pollen, both *in situ* and dispersed, may contribute to a more objective assessment of the temporal variation in reproductive strategies among conifers.

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