

## Spore morphology in the moss genus *Pterygoneurum* Jur. (Pottiaceae)

by

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With 43 figures

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**Abstract:** This study presents a critical and detailed investigation of spore morphology in the moss genus *Pterygoneurum* (Pottiaceae) using LM, SEM, and TEM. Spores of this genus have not been studied previously. This paper treats all species worldwide. There are several distinguishable spore types within the genus. A group consisting of *P. ovatum*, *P. medium*, *P. compactum*, and *P. sampaianum* is characterized by spores with simple, branched or tooth-like processes. The ranges of variability in the shape and distribution of the surface processes and in spore morphology overlap for all species. This group could reflect interspecific and interpopulational gene flow. *P. subsessile* is distinctive in its large spores and multi-stalked processes, often separated by psilate areas. It could represent a transition towards cleistocarpous genera of the Pottiaceae such as *Acaulon* and *Phascum*. *P. californicum* is characterized by spores with granula-like processes separated by broad psilate areas; it shows some morphological convergence with the former species. Spores of *P. macleanum* and *P. kemsleyi* show a basal layer of granula and, overlying this, irregularly arranged larger processes. Spores of *P. lamellatum* and *P. arcticum* are densely covered with granular processes sometimes connected in short ridges. This spore type is reminiscent of that of *Crossidium*, which, together with other shared features, lends support to the view that *Pterygoneurum* could have evolved from ancestors of *Crossidium*.

### Introduction

The immense potential of palynology in plant taxonomy has dramatically increased with the application of electron microscopy. However, most investigation has been directed towards higher plant pollen (Skvarla et al. 1988, Harley & Ferguson 1990), while moss spores have received not so much attention. This is partially due to their generally small size and apparent uniformity of surface characters as seen with light microscopy, but also because spore ornamentation is often difficult to correlate with macroscopic characters (Saito & Hirohama 1974, Sorsa 1976). Such genera as *Bruchia* (McClymont 1955, Rushing 1985) and *Encalypta* (Horton 1982, 1983) are exceptional in that spore characteristics have proven to be of taxonomic value at the generic as well as the specific level. Not surprisingly, they have become models for the application of spore morphology in bryophyte systematics. Many gaps remain

in our knowledge of spore morphology in mosses, although it is known that several major discontinuities do occur (Boros et al. 1993).

Spore morphology has been of limited value in the taxonomy of *Pterygoneurum* (e.g. Limpricht 1890, Smith 1978, Catcheside 1980, Crum & Anderson 1981, Zander 1993). In closely related genera such as *Acaulon* (Stone 1989), *Phascum* (Carrión et al. 1990, Guerra et al. 1991), *Tortula* (Lewinsky 1974, Guerra et al. 1992), *Crossidium* (Cano et al. 1993), and *Pottia* (Carrión et al. 1993), however, it has been useful in resolving taxonomic problems. It is also a potential source of information about the evolutionary processes which may lead to the definition of biological or taxonomic boundaries.

From the beginning of a palynological investigation, it is essential to be alert to a variety of circumstances which could affect conclusions. For instance, it is usual to find spores in different stages of maturation, that is to say, with more or less elaborated sporoderm. As a consequence, it is possible that all the generic variation in spore morphology might be represented by a single species. It therefore follows that spores must be taken solely from mature sporophytes but, even so, treatment prior to examination could influence conclusions, the perine, for example, often being disrupted by KOH and methods of acetolysis. Despite having taken adequate precautions, it is still possible to find a distribution of sculpturing patterns which does not appear to correlate with taxonomic criteria. This was noticed in the *Pottia starckeana* aggregate (Carrión et al. 1993), but there the phenomenon was apparently a consequence of introgressive hybridization between species.

This paper reports the first, worldwide, treatment of spore morphology in the pot-tiaceous genus *Pterygoneurum* Jur. using light (LM), scanning electron (SEM), and transmission electron microscopy (TEM). The genus *Pterygoneurum* is characterized by a bulbiform habit, leaves with lamellae on the ventral surface of the costa and the stegocarpous capsule. It includes terricolous, basiphilous, and principally autoicous species with a circum-Tethyan distribution. Other problematic taxa such as *P. smardeanum* Vanek and *P. koslovii* Laz. are cleistocarpous and are therefore removed from the genus (Guerra et al. 1994).

#### Material and methods

Spores used in this study were obtained solely from mature sporophytes of field collections and dried herbarium specimens, that are listed in the Appendix. The samples were divided into three parts for LM, SEM, and TEM. For LM, the spores were shaken in distilled water and mounted in glycerol jelly. In order to avoid perine disruption, no treatments such as KOH or acetolysis were employed (Carrión et al. 1993). Spores to be used for SEM were critical point dried using 100% acetone and CO<sub>2</sub> as the transition fluid. The specimens were sputter coated (ca. 250 Å thickness) with gold and viewed with a Jeol JSM 6100 microscope at an accelerating voltage of 15 to 25 kv. For TEM, the material was fixed in 3% buffered glutaraldehyde for 2 hours, rinsed several times in 0,1 M Na-cacodylate buffer, and post-fixed in 2% OsO<sub>4</sub>. After dehydration to 100% ethanol, the material was infiltrated in Spurr's mixture and polymerized. Ultrathin sections were prepared using a diamond knife on a Reichert Jung Ultramicrotome, post-stained with uranyl acetate and lead citrate, and examined in a Zeiss EM 109 Turbo TEM operated at 80 kv.

### General observations

The spores of *Pterygoneurum* vary from subcircular or elliptical to plano-convex in equatorial view and from circular, subcircular, or elliptical to subtriangular in polar view (Figs. 1-18). The collections examined show a wide range of spore sizes (10-57  $\mu\text{m}$  in their equatorial diameter). As in other Pottiaceae, polarity is not always apparent at LM. Nevertheless, some spores show a leptoma-like area, slightly concave in the centre of the proximal face (Figs. 6, 8, 10). According to Erdtman's terminology, they would be katalept. In any case, polarity is well-defined ultrastructurally by differential thickness in the wall layers (Figs. 24-25).

The mature sporoderm (Figs. 19-25) is composed of: (a) the innermost layer or intine, often more darkly staining in a basal part as seen in the TEM, thicker in the proximal (0.5-1.8  $\mu\text{m}$ ) than distal face (0.2-0.6  $\mu\text{m}$ ), of dense fibrillar appearance with medium to high electron-density; (b) the exine, thinner in the proximal (0.05-0.2  $\mu\text{m}$ ) than distal pole (0.2-0.6  $\mu\text{m}$ ), with low or medium electron density; (c) the irregular coating of perine, composed of uneven, very electron-dense material which provides the sculpturing pattern. Sometimes, there is also a separating layer between exine and intine, which is more conspicuous in the proximal wall.

The perine processes display great variability in size (from 0.08 up to 2.5  $\mu\text{m}$  in diameter, their length from 0.1 up to 2.2  $\mu\text{m}$ ). They are poorly defined geometrically both in shape and distribution, so that the conventional descriptive terminology of the exine surface in pollen grains is hardly applicable. This is often the case in perinate mosses where, apparently, the sporoderm is less distinctively patterned.

Processes are either completely disconnected (Figs. 19, 22, 23) or poorly separated from each other (Figs. 24, 25). Perine ornamentation elements are mainly verruca-, granula-, or gemma-like (more rarely baculiform). Their outline may be entire, somewhat branched or, less often, irregularly multi-stalked. In addition, very minute surface granulae or echinae may overlie the outermost processes.

### Particular observations

***Pterygoneurum ovatum* (Hedw.) Dix.**

Figs. 1, 2, 19, 26-29

Spore size: mean value 33.2  $\mu\text{m}$ , range 26-40  $\mu\text{m}$ . Perine variable. Processes simple, branched or tooth-like; regularly spaced and sometimes in close proximity but only rarely confluent. The diameter of processes ranges from 0.3 up to 1.5  $\mu\text{m}$ , their height from 0.4 up to 1.8  $\mu\text{m}$ .

***Pterygoneurum medium* (Salm.) Broth.**

Figs. 3, 30, 31

Spore size: mean value 34.1  $\mu\text{m}$ , range 25-40  $\mu\text{m}$ . Perine made up of granula, verruca- or gemma-like, unbranched processes, densely arranged, from 0.3 up to 1.5  $\mu\text{m}$  in diameter, from 0.3 up to 1.6  $\mu\text{m}$  in height. The spore resembles some densely sculptured morphs of *P. ovatum*.

**Pterygoneurum compactum** Cano, Guerra & Ros

Figs. 4, 5, 32

Spore size: mean value 29.5  $\mu\text{m}$ , range 23-40  $\mu\text{m}$ . Leptoma-like area irregularly oval. Processes simple, branched or tooth-like, mostly granular to verrucose, regularly spaced or locally coalesced, but never so uniformly confluent as in *P. medium* or the most perinous morphs of *P. ovatum*. Processes range from 0.2 up to 1.4  $\mu\text{m}$  in diameter, from 0.2 up to 1.4  $\mu\text{m}$  in height.

**Pterygoneurum sampaianum** (Mach.) Mach.

Figs. 6, 7, 33

Spore size: mean value 43  $\mu\text{m}$ , range 30-55  $\mu\text{m}$ . Processes irregularly branched, granula- or verruca-like, showing frequently localized coalescence, from 0.2 up to 1.5  $\mu\text{m}$  in diameter, from 0.3 up to 1.8  $\mu\text{m}$  in height.

**Pterygoneurum subsessile** (Brid.) Jur.

Figs. 8-10, 21-23, 34-35

Spore size: mean value 44.6  $\mu\text{m}$  range 33-57  $\mu\text{m}$ . Perine consists of multi-stalked processes, largely verrucose, rarely confluent, their distribution being characteristically irregular, thus leaving wide areas of psilate surface only interrupted by minute granula. The diameter of processes ranges from 0.6 up to 2.5  $\mu\text{m}$ , their height from 0.5 up to 2.2  $\mu\text{m}$ .

**Pterygoneurum californicum** Crum

Figs. 11-12, 36-37

Spore size: mean value 29.3  $\mu\text{m}$ , range 23-35  $\mu\text{m}$ . Processes from a very fine pattern and they do not appear clearly projected over the exine in LM. As seen with SEM, processes are mostly granula-like (as a rule not larger than 0.8  $\mu\text{m}$ ), and appear confluent in isolated areas, thus leaving much surface psilate.

**Pterygoneurum macleanum** Warnst.

Figs. 13, 20, 38-39

Spore size: mean value 34.3  $\mu\text{m}$ , range 29-43  $\mu\text{m}$ . Inner face of the sporoderm well defined in LM. Perine composed of a basal layer of granula (0.08-0.9  $\mu\text{m}$ ) and, overlying this, irregularly arranged larger processes (up to 2  $\mu\text{m}$ ).

**Pterygoneurum kemsleyi** Willis

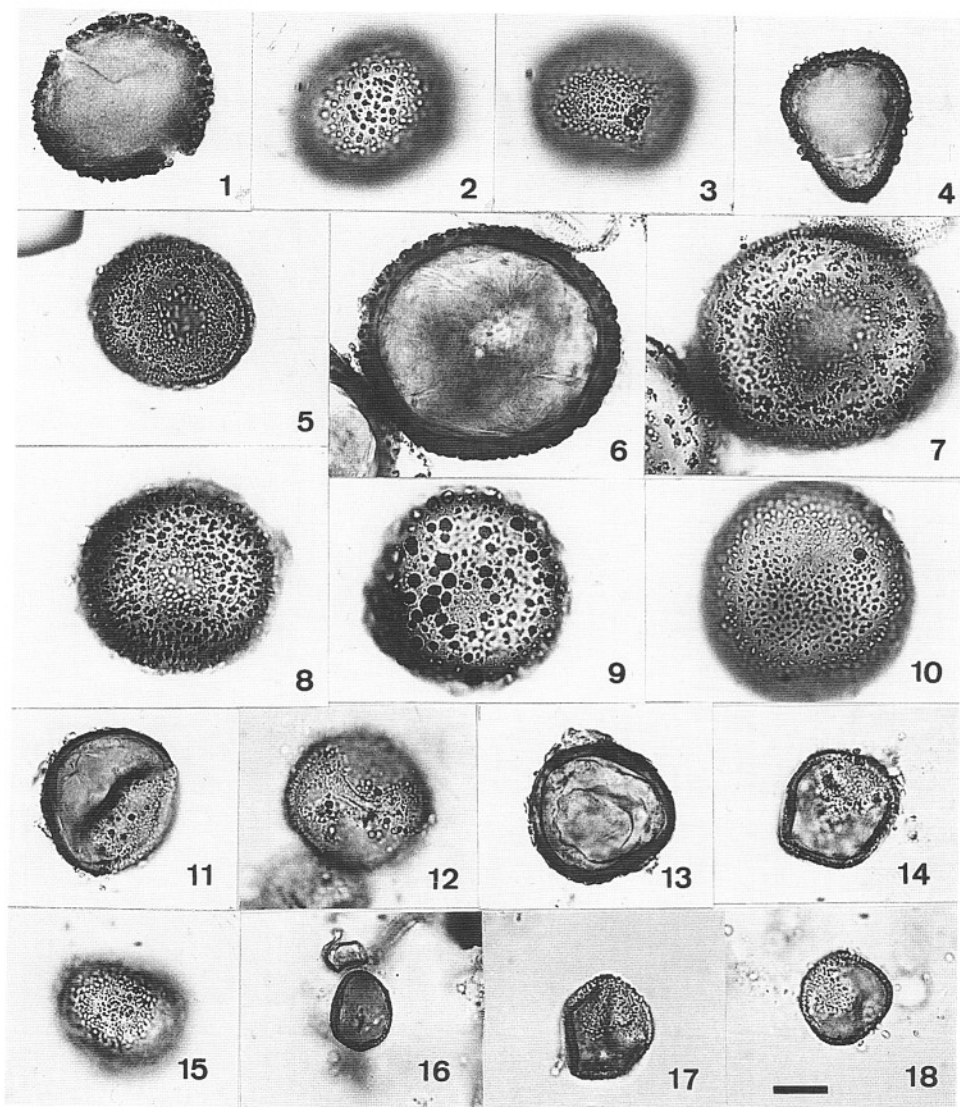
Figs. 14-15, 40

Spore size: mean value 31.2  $\mu\text{m}$ , range 26-41  $\mu\text{m}$ . SEM pattern identical to the preceding, with variable processes fairly incorporated over the basal layer of granular perine.

**Pterygoneurum lamellatum** (Lindb.) Jur.

Figs. 16-17, 24-25, 41-42

Spore size: mean value 19.6  $\mu\text{m}$ , range 10-30  $\mu\text{m}$ . Under SEM, the spore is densely ornamented with simple, granular processes (0.5-0.9  $\mu\text{m}$  in diam.) that sometimes connect to form short ridges (up to 2.5  $\mu\text{m}$  in their maximum dimension).

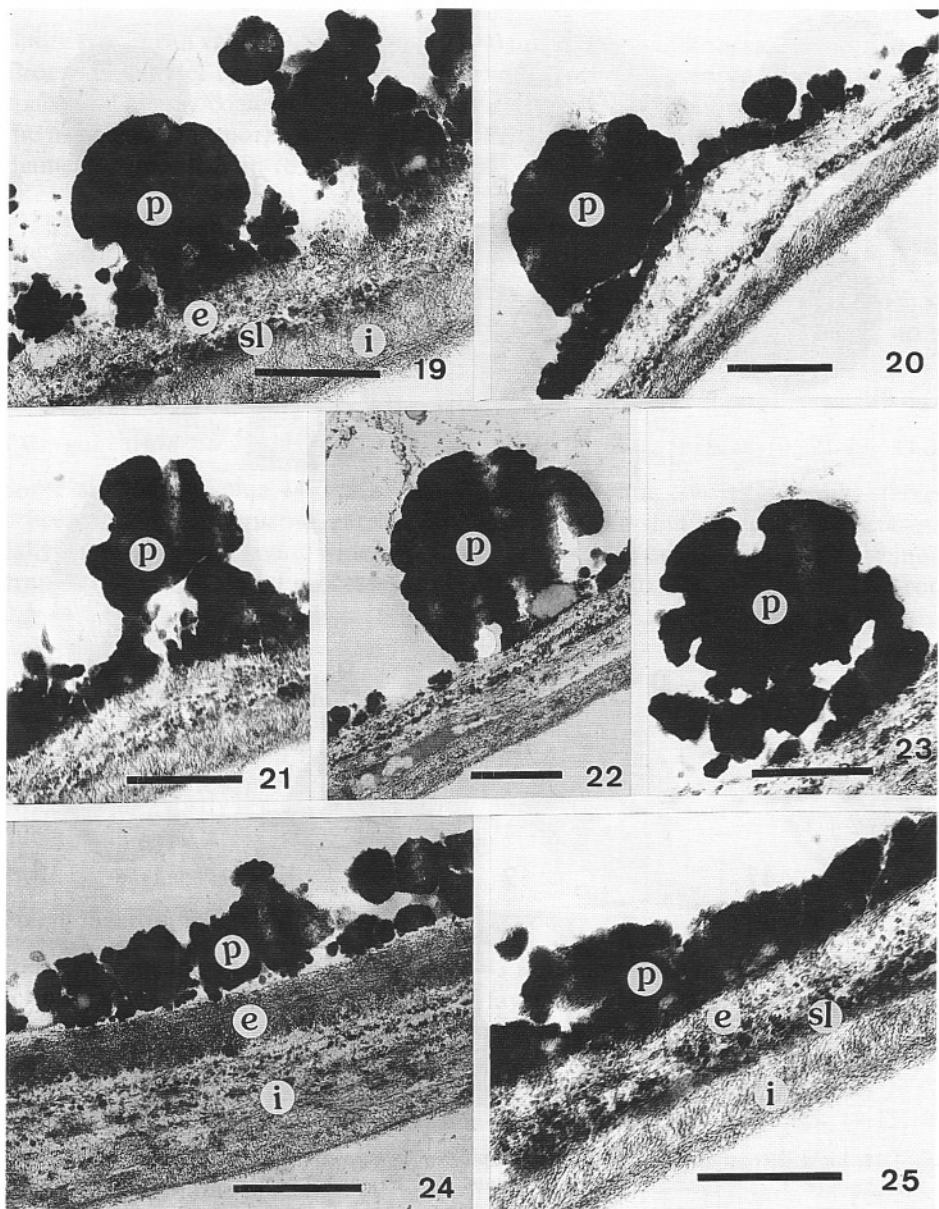


Figs. 1-18. Light micrographs of *Pterygoneurum* spores showing variability in size and ornamentation. 1, 2: *P. ovatum*. 3: *P. medium*. 4, 5: *P. compactum*. 6, 7: *P. sampaianum*. 8, 9, 10: *P. subsessile*. 11, 12: *P. californicum*. 13: *P. macleanum*. 14, 15: *P. kemsleyi*. 16, 17: *P. lamellatum*. 18: *P. arcticum*. Note sporoderm thickness in 4, 6 and 13. Bar = 10  $\mu$ m.

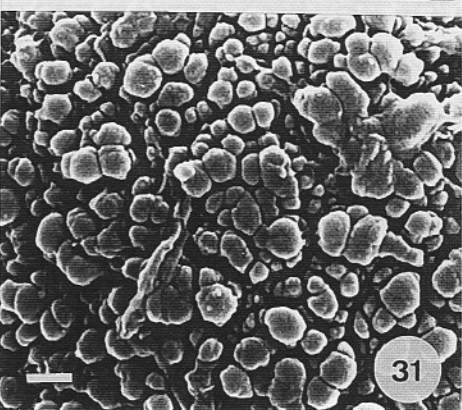
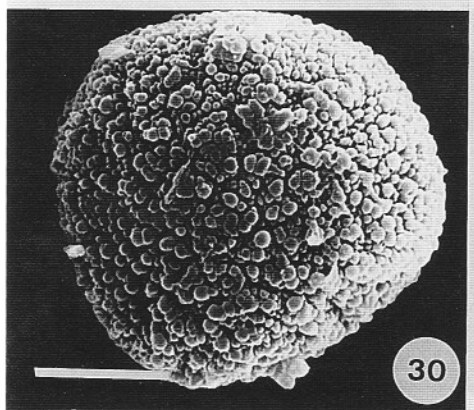
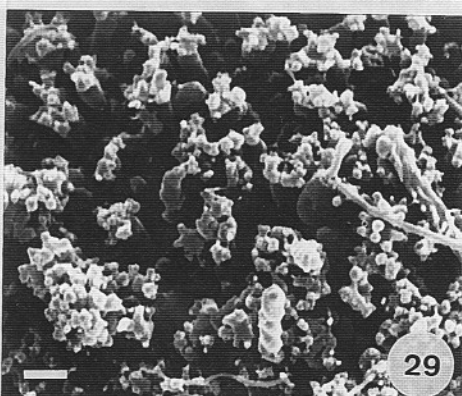
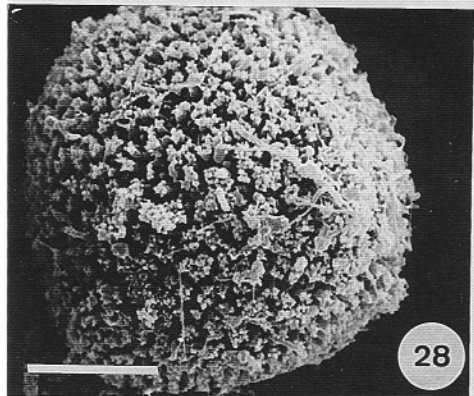
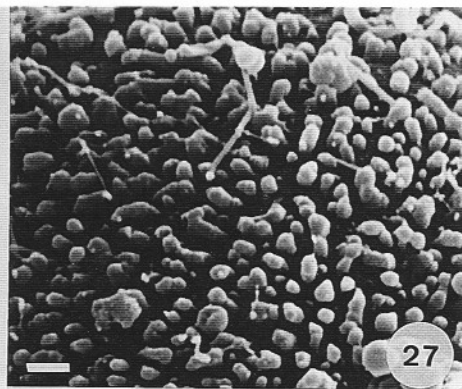
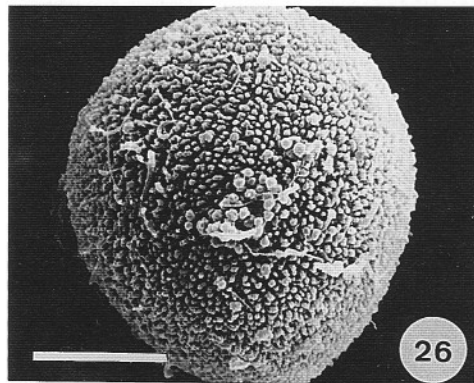
### *Pterygoneurum arcticum* Steere

Figs. 18, 43

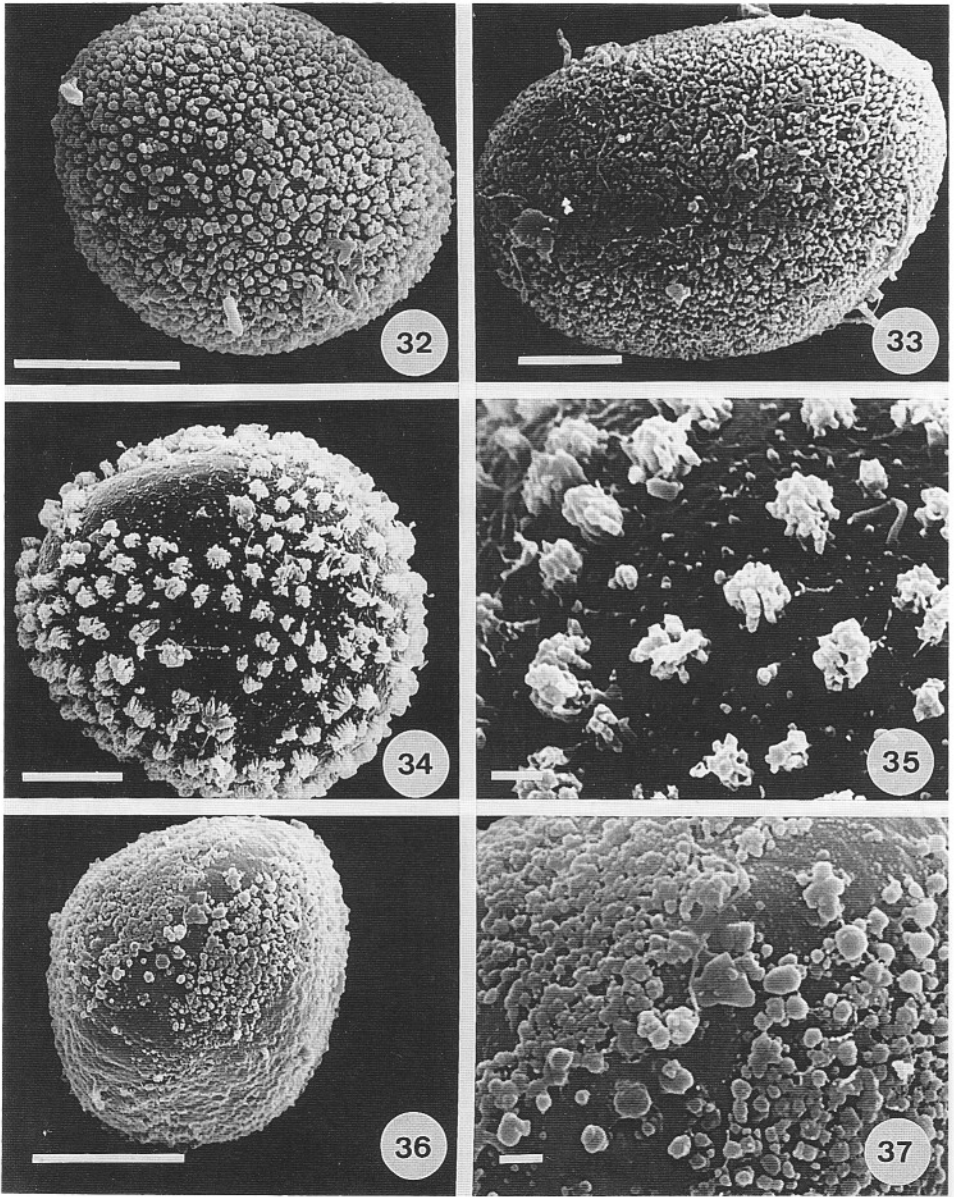
Spore size: mean value 22.6  $\mu$ m, range 13-34  $\mu$ m. Apart from the slightly larger size, the spores are similar to those of *P. lamellatum*.



Figs. 19-25. TEM micrographs of *Pterygoneurum* spores showing wall ultrastructure. 19: *P. ovatum*. 20: *P. macleanum*. 21, 22, 23: *P. sessile*. 24: *P. lamellatum*, proximal pole. 25: *P. lamellatum*, equatorial face. p = perine, e = exine, i = intine, sl = separating layer. Bar = 1  $\mu$ m.

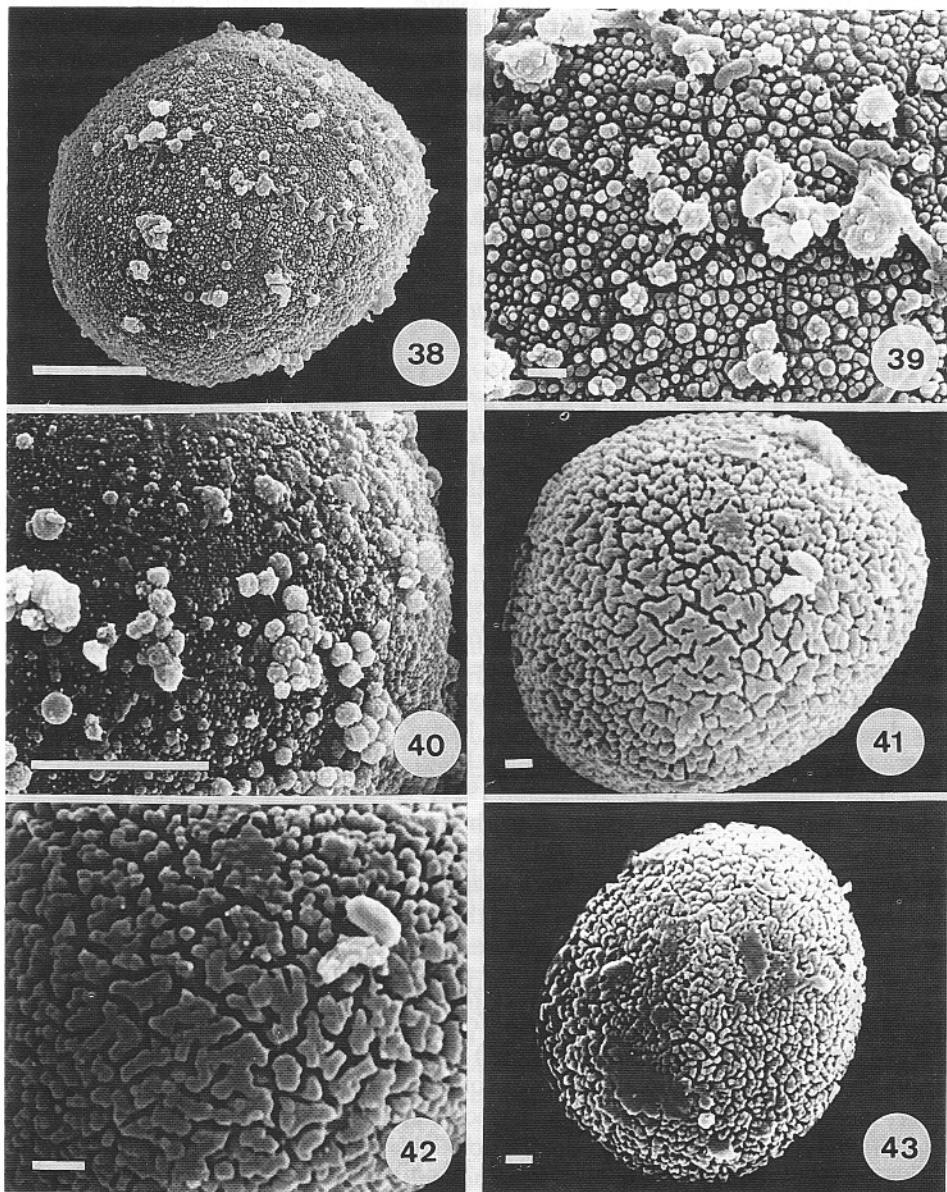


Figs. 26-31. SEM micrographs of *Pterygoneurum* spores. 26, 27: *P. ovatum*, processes simple. 28, 29: *P. ovatum*, processes branched. 30, 31: *P. medium*. Bars (26, 28, 30) = 10  $\mu\text{m}$ . Bars (27, 29, 31) = 1  $\mu\text{m}$ .



Figs. 32-37. SEM micrographs of *Pterygoneurum* spores. 32: *P. compactum*. 33: *P. sampaianum*. 34, 35: *P. sessile*. 36, 37: *P. californicum*. Bars (32, 33, 34, 36) = 10  $\mu\text{m}$ . Bars (35, 37) = 1  $\mu\text{m}$ .





Figs. 38-43. SEM micrographs of *Pterygoneurum* spores. 38, 39: *P. macleanum*. 40: *P. kemsleyi*. 41, 42: *P. lamellatum*. 43: *P. arcticum*. Bars (38, 40) = 10  $\mu\text{m}$ . Bars (39, 41, 42, 43) = 1  $\mu\text{m}$ .

## Discussion

*Pterygoneurum* does not have a well defined spore type and, moreover, similar patterns of ornamentation can be seen in other members of the Pottiaceae, as well as in mosses which are not taxonomically close. Spores like those of *P. ovatum* have been observed in several species of *Pottia*, *Funaria* (Boros et al. 1993), *Weissia*, and *Trichostomum* (Saito & Hirohama, 1974). Very similar sculpturing to that of the spores of *P. kemsleyi* and *P. macleianum* has been noticed in *Phascum cuynetii* (Carrión et al. 1990). The same is true for *Pterygoneurum californicum* and *Phascum curvicolle* (Carrión et al. 1990). Multi-stalked verruca as in *P. subsessile* have been described hitherto in *Weissia*, *Hymenostomum*, *Trichostomum*, and *Pseudosymblypharis* (Saito & Hirohama 1974). Microechinula overlying the processes have been reported from *Tortula* (Guerra et al. 1992). The SEM pattern of the spores of *P. lamellatum* is widely distributed in *Crossidium* (Cano et al. 1993). In addition, not altogether surprising in Pottiaceae, differences between species are sometimes more of degree than of kind and, therefore, spore morphology is considered to be one of the many characteristics necessary to describe each species of *Pterygoneurum* adequately but, in isolation, it is not always sufficient to distinguish species.

It is quite apparent from a survey of the literature that knowledge of spore morphology in *Pterygoneurum* has never progressed much beyond the times of Limpricht (1890). Detailed spore descriptions for *Pterygoneurum* are rarely included in floras and taxonomic reports. Observations generally have been rather superficial and have employed little discriminative terminology. Thus, for example, spores of *P. ovatum* are described as “feinwarzig” (Limpricht 1890), “verrucosas” (Casares 1932), densely granular (Scott et al. 1976; Catcheside 1980), papillose (Smith 1978), and densely and finely papillose (Crum & Anderson 1981). Nevertheless, there are several points of correlation with the results presented herein: (1) Spores of *P. lamellatum* appear to be the smallest, and those of *P. subsessile* the largest. (2) Spores of *P. ovatum* show marked variation both in size and surface sculpturing. (3) Spores of *P. sampai-anum* are less densely ornamented than those of *P. ovatum*. Spores of *P. kemsleyi* display mostly a finer pattern of sculpturing than those of *P. ovatum*.

Of the works which treat spores of bryophytes more fully, perhaps the atlas by Boros et al. (1993) is the best source of information. Unfortunately, it only provides an LM description of *P. pusillum* (Hedw.) Broth. (= *P. ovatum*), and a smaller mean spore size (27.9  $\mu\text{m}$ ) is quoted than was found in our work (33.2  $\mu\text{m}$ ). It is not, however, inconsistent because that is a character which varies enormously in some species of *Pterygoneurum*. In fact, descriptions of the spores of *P. ovatum* differ widely from author to author: 40-50  $\mu\text{m}$  (Catcheside 1980) - 22-33  $\mu\text{m}$  (Casares 1932, Crum & Anderson 1981).

Several general conclusions can be drawn from the results and they lend support to a wider discussion in the context of taxonomy, ecology and evolutionary processes.

Firstly, the spore sculpturing of *P. medium*, *P. compactum* and *P. sampai-anum* is included within the variability showed by *P. ovatum*. Processes are simple and densely arranged in *P. medium*, branched and locally coalesced in *P. sampai-anum*, and

simple or branched and not very coalesced in *P. compactum*; whereas they are simple or branched, regularly spaced or closely arranged in *P. ovatum*. In *P. medium*, the spore size is remarkably similar (mean 33.2  $\mu\text{m}$  in *P. ovatum*, 34.1  $\mu\text{m}$  in *P. medium*), while *P. compactum* (29.5  $\mu\text{m}$ ) and *P. sampaianum* (43  $\mu\text{m}$ ) display spores which are slightly smaller and larger, respectively. In comparison with *P. ovatum* and *P. medium*, the sporoderm outline is more frequently conspicuous in an LM optical section of *P. compactum* (Fig. 4) and, especially of *P. sampaianum* (Fig. 6).

A recent taxonomic revision of Spanish *Pterygoneurum* (Guerra et al. in press) suggests the synonymy of *P. medium* and *P. ovatum* as well as the morphological proximity of *P. ovatum*, *P. compactum*, and *P. sampaianum*, based on the common absence of a peristome, the vertical alignment of the operculum cells and the similar size and shape of the capsule.

Whether or not the critical characters (leaf and lamellae anatomy) considered to justify specific rank are indeed of sufficient weight is open to debate, given that a worldwide study of the systematics and biogeography of this genus is still needed. In autoicous species, the possibility that localized outbreeding and interpopulational gene flow may have taken place should not be immediately rejected because the species concerned grow in close proximity, and often even in the same cushion. Spore production would serve to increase the opportunity for hybridization by establishing new gametophytes in close proximity (Anderson 1980). Furthermore, there are often samples whose identification proves impossible as they show intermediate morphology. Therefore, introgressive hybridization represents a plausible hypothesis to explain the clearly overlapping variation in the spore morphology of these three species. It must be added that this group has always been associated with a certain amount of nomenclatural confusion, and this also contributes to the view that only one species might be involved.

Secondly, the spores of *P. subsessile*, with their multi-stalked processes and large size, are distinctive within the genus (Figs. 34, 35). This agrees with the traditional view that *P. subsessile* is a well-defined taxon (e.g. Crum & Anderson 1981). It is the only species possessing immersed capsules and could represent a transition of the genus towards cleistocarpy. It shares with cleistocarpous genera such as *Phascum* and *Acaulon* their large, highly sculptured spores (Catcheside 1980, Carrión et al. 1980, Casas & Sérgio 1990). Longton (1988) suggested that desert-dwelling bryophytes display a phylogenetic trend to increase in spore size. Evolutionarily, that tendency would parallel the sporophytic reduction typical of *P. subsessile*.

In a cladistic analysis of the pottiaceous genera, Zander (1993) has emphasized that the sporophytic contraction seen in the cleistocarpous Pottiaceae may be regarded as an evolutionary adaptation in accordance with environmental stress in arid biotopes. Certainly, the exerted capsules of the presumed ancestors could have suffered negative selection pressure because they lacked the physical protection and constant humidity which, during their development, is afforded by the perichaetial leaves. It must be remembered in this context that sporophytes are slow to mature. But beyond abiotic constraints, competition must also be high within the patches. Thence, the production of heavy spores would be positively selected in a Darwinian sense

if they were transported over such short distances as to germinate in the predictable environment of the cushion composed of the progenitors. In this context, predominance of inbreeding derived from the autoicous condition of most of the species involved would be selectively favoured. On the other hand, the existence of limited numbers of smaller spores, would make greater dispersal distances possible. This might be valid, not only for *P. subsessile*, but also for many other short-lived, xerophytic mosses. The case of *P. sampaianum* may be even more interesting, as some populations show two types of spores according to their size and wall thickness. Of course, proof of much of this would need rigorous experimental investigation. Nevertheless, the possibility that pioneering, terrestrial communities of subordinate ecological niches were regulated by a dynamic balance between both extrinsic and intrinsic abiotic and biotic stresses is substantiated by the fossil record of early land plants (Dimichele et al. 1987, Traverse 1988).

Thirdly, as for *P. subsessile*, the spores of *P. californicum* are well differentiated. Besides their small size, they are the least sculptured. Only type material has been available and, according to Guerra et al. (in press), it displays gametophytic morphological convergence with *P. subsessile*. SEM study of the spores of both species reveals very different processes, but with the common feature of wide, psilate areas (Fig. 37). A careful LM examination discounted the possibility that spores were immature, because they were brownish in colour and had a well-contrasted perine. However, it is true that *P. californicum* should be treated very cautiously until it is collected again and studied in more detail.

Fourthly, the spore sculpturing in *P. macleanum* and *P. kemsleyi* is identical and well differentiated from that of the remaining species. Spore size is also similar for the two species. The material examined shows considerable gametophytic similarity. Given that *P. macleanum* comes from South Africa and *P. kemsleyi* from Australia, we feel that a detailed comparative study considering our results together with foliar anatomy and sporophyte characters would be of major interest in the context of palaeobiogeographical discussion. It must be taken into account that *Pterygoneurum* must have evolved, in common with other closely related genera well-adapted to highly arid habitats, from ancestral populations living around the mid-continental warm sea existing in the Triassic since the first breakup of Pangaea (Frey & Kürschner 1988).

Fifthly, no consistent differences in ornamentation were observed between the spores of *P. lamellatum* and *P. arcticum*, although the available specimens of *P. arcticum* were found to have generally more scattered processes. The ranges of spore diameter for the two species overlap (10-30  $\mu\text{m}$  in *P. lamellatum*, 13-34  $\mu\text{m}$  in *P. arcticum*). This concurs with the taxonomic opinion of Corley et al. (1981) that *P. arcticum* is synonymous with *P. lamellatum*.

The spore ornamentation in *P. lamellatum* and *P. arcticum* is similar to that described for *Crossidium* and *Microcrossidium* (Cano et al. 1993). Moreover, the spore size of both species is relatively small for the genus *Pterygoneurum*, and approaches the range of *Crossidium* (9-32  $\mu\text{m}$ ). Hence, the spore morphology supports the traditional view that *Pterygoneurum* and *Crossidium* are taxonomically and phylogenetically related (Delgadillo 1975, Frey et al. 1990). Allegedly, the former would have been

evolved from ancestors of the latter through a peristome reduction and modification of the filaments into the ventral costal lamellae. In fact, we have observed immature leaves of *Pterygoneurum* which strongly resemble fully developed leaves of *Crossidium*. Hypothetically, one might therefore suggest some evolutionary alteration of ontogeny (e.g. terminal prolongation, sensu Takhtajan 1991) to explain such a character derivation. This relationship is reinforced by the work of Zander (1993), who regards the genera *Aloinella*, *Globulinella*, *Crossidium*, *Pterygoneurum* and *Stegonia* to be monophyletic. Special attention must be paid to this study because it is based on vegetative features, namely the absence of a stem hyalodermis and the presence of sheathing perichaetial leaves. It must be remembered that, in Pottiaceae, taxonomic interest has always centered on sporophyte characters.

Certainly, some of the generic treatments of Zander (1993) will be a matter for debate, but this study must be welcomed as it provides the first complete phylogenetic attempt in the Pottiaceae. It has also generated many hypotheses that can be tested in the future. Cladistic analysis can be a powerful tool for the study of character evolution, especially if the plants involved grow in stressful environments where morphological convergence can overshadow phyletic lines. Even when admitting disagreements of Cronquist (1988) over the cladistic interpretation of the paraphyletic groups, it is perhaps to be wondered whether, with the task of determining the course of evolution, we have not prompted too much speculation about the adaptive significance of certain characteristics.

In conclusion, the genus *Pterygoneurum* displays five interesting, and potentially important, trends in spore morphology. From a taxonomic point of view, these major trends support: (1) the synonymy of *P. ovatum* and *P. medium*, and the taxonomic affinities of *P. ovatum*, *P. compactum*, and *P. sampaiianum*, probably due to introgressive hybridization; (2) the distinctness of *P. subsessile*, (3) the gametophytic morphological convergence between *P. californicum* and *P. subsessile*; (4) the taxonomic closeness between the South African *P. macleianum* and the Australian *P. kemsleyi* species, and (5) the synonymy of *P. arcticum* with respect to *P. lamellatum*. Finally, while *P. subsessile* could represent the transition of the genus *Pterygoneurum* towards cleistocarpous genera such as *Phascum* and *Acaulon*, *P. lamellatum* suggests the existence of a shared ancestor with *Crossidium*. Hypothetically, the evolutionary trend symbolized by *Crossidium*-*Pterygoneurum*-*Acaulon* would involve peristome reduction, increase in spore size and progressively more heavy perines.

#### Appendix: selection of specimens studied

***Pterygoneurum ovatum*** (Hedw.) - USA: Nebraska, Lincoln County, SW of Brady, Kiener (NEB). USA: Vernal pools in Pixley Natural Area, about 5 miles east northeast of Pixley, Tulare County, California, Howell (CAS). ENGLAND: Blatchley, near Frome, N. Somerset, Watson (KEW). CANADA: British Columbia, Iron Mask Hill, Kamloops, MacFadden (LAM). SPAIN: Granada, Sierra Nevada, El Dornajo, Varo (GDAC).

***Pterygoneurum medium*** (Salm.) - IRAN: Karadj-Tal (Karadja-Kandevan-Pass), 1410 m, auf Kalkfelsen, Frey (K). AFGANISTAN: Afganistan, Aitchison (1884-85), n° 183 (Holotype, K).

***Pterygoneurum compactum*** Cano, Guerra & Ros - SPAIN: Lérida, Balaguer, Brugués et al. (BCB).

**Pterygoneurum sampaiianum** (Mach.) Mach. - PORTUGAL: Portimao, Sampaio (PO). SPAIN: Murcia, Lorca-Caravaca road, Ros (MUB). SPAIN: Murcia, Mazarrón, Ros (BCB). SPAIN: Navarra, Lerin, Barranco Salado, Heras (Herb. HERAS).

**Pterygoneurum subsessile** (Brid.) Jur. - GERMANY: Regensburg, Wegböschungen der Winzer Berger, Familler & Brückner (B). USA: Nebraska, Sioux Co., Agate Fossil Beds National Monument, Churchill (NEB). USA: 3 mi from Stone House on Bear Canyon, Tuscon, Arizona, Bradt (LAM). AUSTRIA: prope Vindobonam, Beck (BRIU). HUNGARY: prope Csepel, Förster (BRIU). SPAIN: Zaragoza, Chiprana, Lloret (BCB). CZECHOSLOVAKIA: Moravia, prope pagnum Pouzdrany, Müller (FI).

**Pterygoneurum californicum** Crum - USA: Alkali flats along Panama Lane 5 miles W of Highway 99 just south of Bakersfield, Kern Co., California, Koch (Holotype, MICH).

**Pterygoneurum macleanum** Warnst. - SOUTH AFRICA: Terra Capensis orientalis, in aperti circa Graaf Reynett, Maclea (Lectotype, BM). SOUTH AFRICA: Cape, 22 Km from Britstown at Smartt Syn. Dam, Karro Vedl, Magill (PRE).

**Pterygoneurum kemsleyi** Willis - AUSTRALIA: Western Australia, Feysville, 15 miles SE of Kalgoorlie, Kemsley (Holotype, WELT). AUSTRALIA: Victoria, Boundary Bend, Swan Hill, Stone (Herb. I.G. STONE).

**Pterygoneurum lamellatum** (Lindb.) Jur. - BELGIUM: Remincourt (pr. Liège), Cornet (LUND). FRANCE: Paris, à la Glacière, Jeanpert (GB). SPAIN. Murcia, Caravaca, Loma Ancha, Ros (MUB). USA: Arizona, Pima Co., Haring (LUND). CZECHOSLOVAKIA: Slovakia, Parkan, in terra loessica pagi Lubá, Pilous (H). AUSTRIA: Wien, Juratzka (BM). HUNGARY: Comit. Bács-Bodrog Hungariae meridionalis, Ad opp. Bácsstopolya, Koscsis (LUND).

**Pterygoneurum arcticum** Steere - CANADA: Franklin District, Bathurst Island, inland east of May Inlet, Blake (ALTA). USA: Alaska, Vicinity of Umiat, Colville River, Steere et al. (NY). USA: Alaska, near mouth of Ogotoenk Creek, southeast of Cape Thompson, Steere (NY).

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