

Systematic studies in the genus *Mohria* (Anemiaceae: Pteridophyta). III. Comparative sporangium and spore morphology

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ABSTRACT

The genera *Mohria* and *Anemia* (Anemiaceae: Pteridophyta) can be separated on both their sporangia and spores. In *Mohria* the capsule is globose with an apical annulus but in *Anemia* it is ovate-globose to cylindrical with a subapical annulus. The spores of both genera are radially symmetrical, tetrahedral and trilete with near parallel muri. The exinal sculpture in *Mohria* is cicatricose and in *Anemia* it can be canaliculate or cicatricose. In both genera the mural sets anastomose to form common muri that extend from near the distal pole to the equatorial radial region. The muri in *Mohria* are hollow and differ from those in *Anemia* which are solid or microporate. Supramural sculpturing in *Mohria* and *Anemia* is perinous. Spores of the other schizaealean ferns show no or little taxonomic affinities with *Mohria* and *Anemia*. In *Actinostachys* and *Schizaea* the spores are monolete and in *Lygodium* trilete but the exinal sculpture is smooth.

UITTREKSEL

Mohria en *Anemia* (Anemiaceae: Pteridophyta) kan onderskei word op grond van hul sporangiums en spore. By *Mohria* is die sporangiumkapsule bolronnd met 'n apikale annulus, maar by *Anemia* is dit eivormig-bolronnd tot silindries met 'n subapikale annulus. Die spore van albei genusse is radiaal simmetries, tetrahedraal en trileet met feitlik parallelle muri. By *Mohria* is die eksien gelitteken, maar by *Anemia* kan dit gelitteken of gekanaliseerd wees. Die muri-stelle by albei genusse verenig om gemeenskaplike muri te vorm wat vanaf die distale pool tot by die ekwatoriaal radiale gebied strek. By *Mohria* is die muri hol teenoor dié van *Anemia* wat solied of mikroporaat is. Supramurale skulptuur in *Mohria* en *Anemia* is perinies van aard. Spore van die ander *Schizaea*-agtige varings toon geen of min verwantskappe met dié van *Mohria* en *Anemia*. By *Actinostachys* en *Schizaea* is die spore monolities en by *Lygodium* is hulle trileties maar die eksien is glad.

INTRODUCTION

Mohria Swartz, together with *Anemia* Swartz, *Schizaea* J. Sm., *Actinostachys* Wall. and *Lygodium* Swartz are commonly placed in a single family, the Schizaeaceae (Engler & Prantl 1898–1902; Bower 1923; Christensen 1938; Copeland 1947; Tryon & Tryon 1982) because of their sporangium morphology. The subdivision of this assemblage into distinct families, the Anemiaceae (*Anemia* and *Mohria*), Lygodiaceae (*Lygodium*) and Schizaeaceae (*Actinostachys* and *Schizaea*) has recently gained wider acceptance (Nayar 1970; Bierhorst 1971; Löve *et al.* 1977; De la Sota & Morbelli 1987).

Although *Anemia* and *Mohria* are dissimilar in morphology they are evidently related in view of similarities in their plant anatomy (Prantl 1881; Bower 1918; Roux *et al.* 1992), trichomes (Mickel 1962; Roux *et al.* 1992), spores (trilete, tetrahedral, radially symmetrical with a cicatricose or canaliculate exinal sculpture) and chromosome numbers ($n = 38, 76$). *Anemia* is considered the out-group for *Mohria*.

The spore morphology of *Anemia* has been well documented (Mickel 1962; Hill 1977, 1979; Dettmann & Clifford 1991). Only recently, however, has their morphology been appraised in a systematic context (De la Sota & Morbelli 1987; Dettmann & Clifford 1991). Since an intensive study of *Mohria* has been lacking for some time, the spore morphology of merely two or three species has

been appraised in these studies. In a critical review of the genus, however, I found it to comprise seven species. The spore morphology of all the species recognised is investigated and their phylogenetic relationships evaluated.

MATERIAL AND METHODS

For SEM study untreated sporangia and spores were affixed to aluminium stubs using glue and sputter-coated with Au/Pd. Specimens were viewed in a Cambridge S200 SEM at 5 or 10 kV. Wax embedding was done using standard techniques. Sections 8–10 μm thick were serially sectioned with a rotary microtome and stained with safranin and fast green. Photography was done with a Zeiss 'Axoskop' fitted with a M35W camera. Ilford Pan F film was used for all photography.

Specimens examined

M. caffrorum (L.) Desv., 3218 DC Clanwilliam, Roux 2008 (NBG); 3318 CD Cape Town, Roux 1260 (NBG).

M. lepigera (Bak.) Bak., 1832 DD Zimbabwe, Taylor 3279 (NBG); 1932 CD Zimbabwe, Phipps 281 (BOL); Madagascar, De la Bâthie 7894 (P).

M. marginalis (Sav.) J.P. Roux, Réunion, Commerson s.n. (P); 2155 BC Réunion, De Marne s.n. (NBG); 2828 DB Bethlehem, Roux 907 (NBG); 2829 CA Harrismith, Roux 1524 (NBG).

M. nudiuscula J.P. Roux, 2828 CB Bethlehem, Roux 947 (NBG).

M. rigida J.P. Roux, 2828 DB Bethlehem, Roux 1910 (NBG), Steiner s.n.

M. saxatilis J.P. Roux, 3219 AA Wuppertal, Roux 2012 (NBG).

M. vestita Bak., 2530 BA Lydenburg, Steiner s.n. (NBG).

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RESULTS AND DISCUSSION

Sporangial morphology

The sporangium morphology of the schizaealean ferns has been discussed by Goebel (1905). Prantl (1881) showed that sporangia of *Mohria* are derived from a single marginal protodermal cell, the position of which, as a result of continual adaxial growth, eventually becomes superficial. This has been confirmed by Bower (1918). *Mohria*, along with all the other schizaealean ferns, is generally considered as belonging to the leptosporangiates because of their single-layered capsule wall.

Goebel (1905) defined leptosporangia as originating from a single cell and having a one-layered capsule wall. Eusporangia, on the other hand, develop from several cells and have, at least in the primordium, a many-layered capsule wall. In *Mohria*, neighbouring cells contribute to the formation of the massive stalk. Therefore, in gross morphology the sporangium of *Mohria* is intermediate between the two types.

During the early development of the sporangium a tapetum cannot be distinguished. Later, however, it separates from the sporogenous tissue as a bicellular layer (Figure 1A & B). Cells of the outer tapetal layer are rectangular in transverse section and periclinal. The inner tapetal layer consists of much larger cells (Figure 1B). Relatively early in the development of the sporangium the tapetum disintegrates leaving only the proximal part of the outer tapetal layer intact.

In *Mohria* I found that the distal portion of the lamina curves around the sporangia in a protective manner. It does not differ morphologically or anatomically from the lamina tissue, and the sporangia are therefore exindusiate. Based on the grounds of outgroup comparison this feature is considered plesiomorphic. *Anemia* is also exindusiate. Sporangia in the schizaealean ferns are not borne in sori. In *Mohria* sporangia occur individually near each vein

ending, or one or two sporangia may be borne at the terminal vein dichotomy. Sporangia in *Mohria* thus have a proper vascularization. In *Anemia* the vascularization is rudimentary or vestigial.

Sporangia in *Mohria* are large, up to 670 μm in diameter, globose and are borne on a short, massive stalk. The annuli, which are situated distally, consist of a single row of radially arranged elongated cells with densely lignified walls. These indurated cells may number up to 22. The stomium is formed by a few smaller cells with less lignified walls which interrupt the ring of annulus cells. The sporangia dehisce vertically with the slit always facing away from the lamina margin.

The number of rhomboidal apical plate cells varies. In *M. saxatilis* the cells may number three but in the other taxa there may be as many as six. Bierhorst (1971) considers a low number of apical plate cells as derived. Spore output per sporangium, even from the same frond, is extremely inconsistent. Bower (1923) gave the estimated number of spores per sporangium as 128 but reported counts of 101 and 107. The number, however, appears to be more variable, as I have made counts ranging from 57 to ± 196 . Bower (1923) and Wagner (1974) associated a large spore output with the primitive state. In *Anemia* the sporangia are also short-stalked or sessile but with an ovate-globose to cylindrical capsule. Annuli are subapically positioned.

Schizaealean ferns are held together largely by the morphology of the sporangium with its group of radially arranged annulus cells which may be terminal or lateral. *Senftenbergia*, a Carboniferous genus with a similar sporangium structure, has long been suggested as an ancient element of the schizaealean ferns (Radforth 1939). More recently, however, Mickel (1974) suggested that it is a member of the coenopteridalean ferns. If this is true, the 'schizaeoid' sporangium type must therefore have evolved more than once and thus cannot be used as a character diagnostic of the Schizaeales. The 'schizaeoid' ferns therefore appear to be polyphyletic.

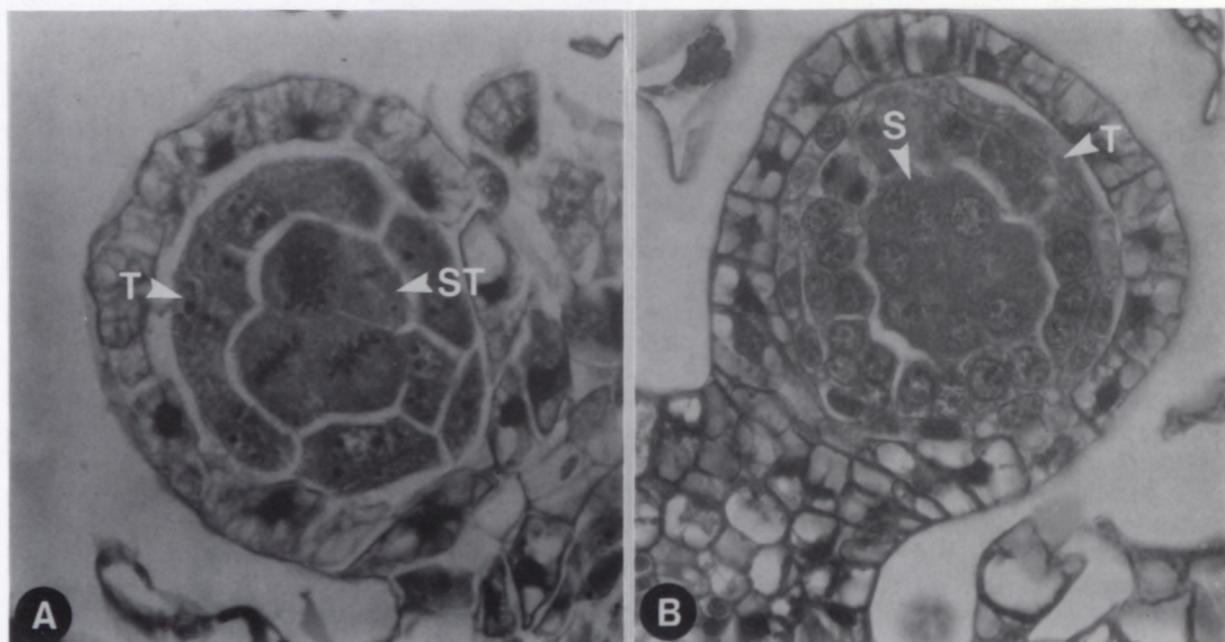


FIGURE 1.—Transverse sections of a sporangium of *Mohria caffrorum*. A, tapetal development and division of the sporogenous tissue, $\times 400$; B, mature tapetum and sporocytes before meiosis, Roux 2002 (NBG). S, sporocytes; T, tapetum; ST, sporogenous tissue.

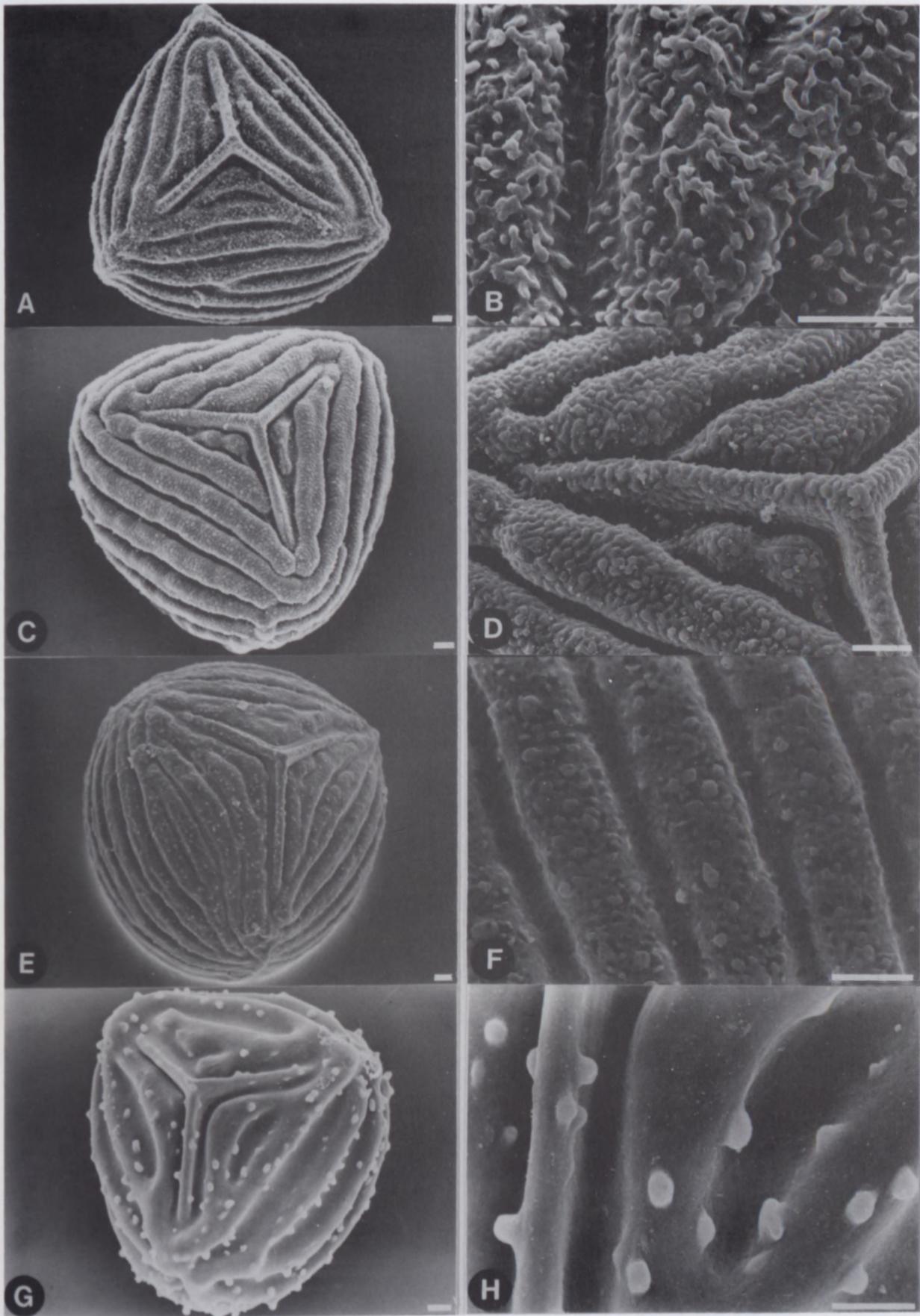


FIGURE 2.—Scanning electron micrographs of spore surfaces of *Mohria* species. A & B, *M. caffrorum*, Roux 2008 (NBG); C & D, *M. lepigera*, Taylor 3279 (NBG); E & F, *M. marginalis*, De Marne s.n. (NBG); G & H, *M. nudiuscula*, Roux 947 (NBG). Scale bar = 5 μ m.

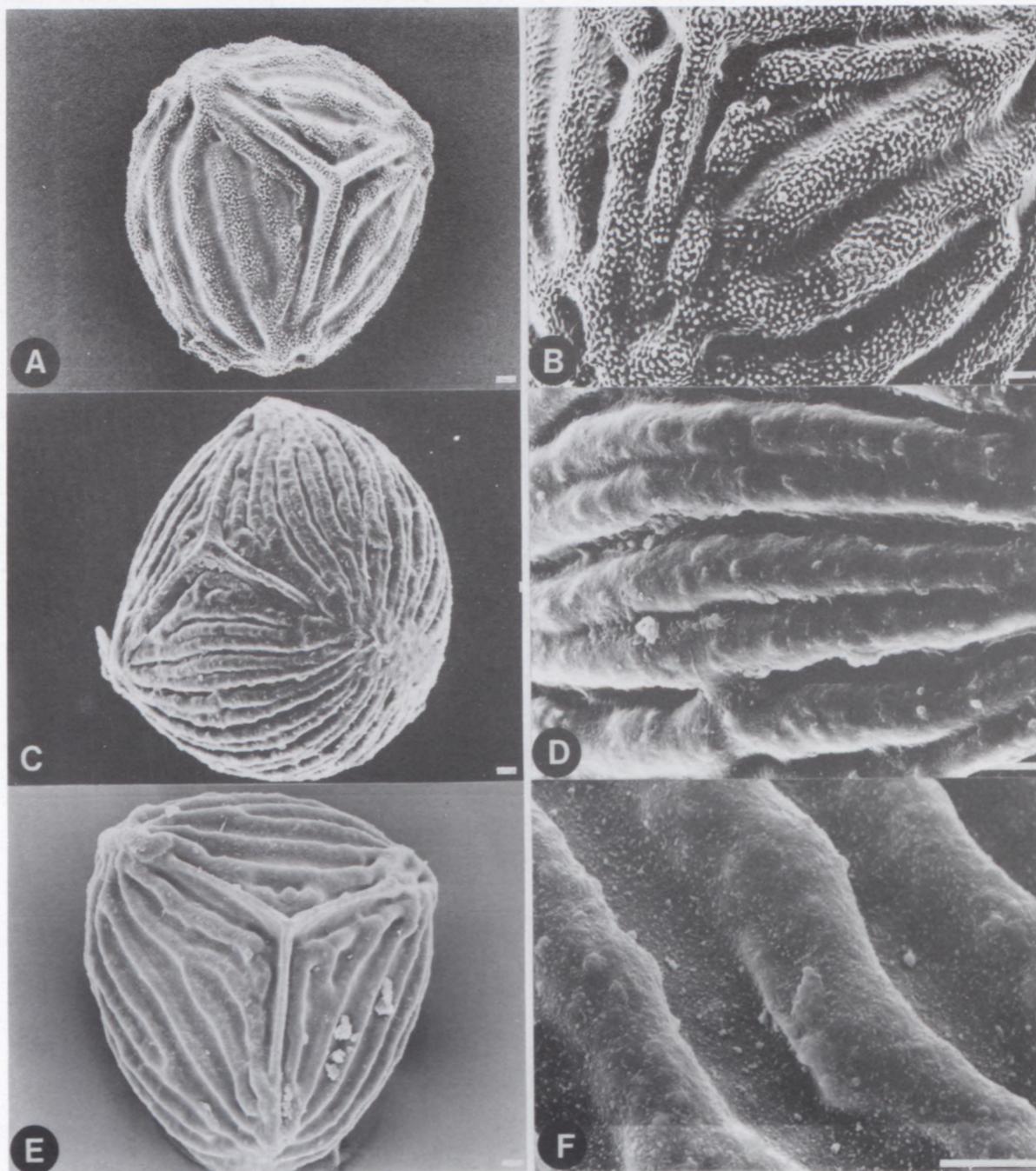


FIGURE 3.—Scanning electron micrographs of spore surfaces of *Mohria* species. A & B, *M. rigida*, Roux 1910 (NBG); C & D, *M. saxatilis*, Roux 2012 (NBG); E & F, *M. vestita*, Steiner s.n. (NBG). Scale bar = 5 μ m.

Spore morphology

A general overview of spore ornamentation in schizaealean ferns is provided by De la Sota & Morbelli (1987), whereas Dettmann & Clifford (1991) examined those of *Anemia*, *Mohria* and *Ceratopteris* Brongn.

Mohria spores are tetrahedral, trilete and radially symmetrical with a triangular to subtriangular amb 70–20 μ m in diameter. They possess a series of conspicuous parallel ridges or muri which are as broad or broader than the lumina or grooves. The muri are relatively straight and usually run parallel to the equatorial plane. In *M. lepigera* (Bak.) Bak. and *M. marginalis* (Sav.) J.P. Roux, however, they may often be somewhat spirally arranged. Muri of neighbouring series anastomose in the disto-equatorial radial regions which often coalesce with the laesura arms.

The laesura, like the proximal surface, is slightly elevated whereas the distal surface is broadly convex. Muri are formed by a thick cicatricose exine and are hollow (Erdtman 1957; Dettmann & Clifford 1991).

The supramural sculpture in *Mohria*, which is of perinous derivation, ranges from almost smooth in *M. vestita* Bak. (Figure 3E & F), reticulate-verruculate in *M. caffrorum* (Figure 2A & B) to colliculate in *M. marginalis* (Figure 2E & F) and *M. lepigera* (Figure 2C & D), verrucate in *M. nudiuscula* J.P. Roux (Figure 2G & H) and finely granulate in *M. rigida* J.P. Roux (Figure 3A & B). I have been unable to determine polarity of the fine sculpture.

Spore diameter ranges from 70–120 μ m with no distinction between taxa. Slight variations also occur

within a species. Spore diameter in the genus, however, averages $87.77 \mu\text{m}$ ($n = 85$, $SD = 9.16 \mu\text{m}$) with the largest percentage (31.76%) falling within the range 81–90 μm (Figure 4). Wagner (1974) suggested that spores exceeding 70 μm are derived.

Spore ornamentation provides evidence of the close relationship between *Mohria* and *Anemia*, especially subgenus *Coptophyllum*, as was suggested by Mickel (1962). De la Sota & Morbelli (1987), identified three spore types in *Mohria* based on the structure of the muri. My observations, however, showed only two types: spores with closely spaced muri and narrow lumina as in *M. lepigera* and *M. marginalis* (Figure 2C, D, E & F) and spores with broad muri and lumina as in *M. caffrorum* (L.) Desv., *M. nudiuscula*, *M. rigida* and *M. vestita* (Figures 2A, B, G & H; 3A, B, E & F). *M. saxatilis* J.P. Roux belongs to the latter type but here the muri are somewhat fossulate (Figure 3C & D).

CONCLUSIONS

Mohria and *Anemia* can be separated on features of both the sporangia and spores. Sporangium ontogeny in *Mohria* is not of the true leptosporangiate type but is rather intermediate between the developmental patterns of the leptosporangium and the eusporangium. The annulus of *Anemia* is subapical, whereas in *Mohria* it is distal and composed of a row of indurated trapezoid cells which intergrade proximally with a few small isodiametric apical plate cells. In *Mohria* the sporangium capsule is globose, whereas that of *Anemia* is ovate-globose to cylindrical. Mickel (1962) considered the globose sporangium of *Mohria* to be derived.

Mohria and *Anemia* have radially symmetrical, tetrahedral, trilete spores with the exine sculptured to form near-parallel muri overlain by a thin perine. The mural sets in both genera anastomose with each other to form three common muri that extend from near the distal pole to the equatorial region. In *Mohria* these muri often coalesce with the laesura. The cicatricose muri of *Mohria* are hollow. In *Anemia* the exinal sculpture may be canaliculate or cicatricose but the muri are solid or microporate. Hollow muri may therefore, on the principle of outgroup comparison, be considered derived. Only *M. nudiuscula* has spores with a supramural sculpture

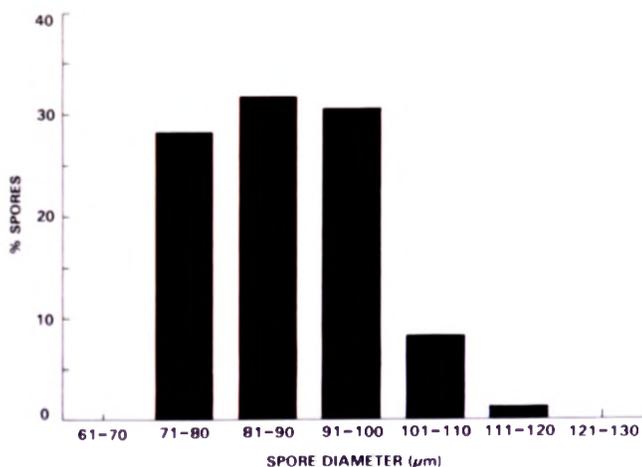


FIGURE 4.—Range of spore size in *Mohria*.

(Figure 2G & H). The perine of *Mohria* and *Anemia* subgenus *Coptophyllum* is thicker and more ornate than that found in the two other subgenera of *Anemia* (Dettmann & Clifford 1991).

Spores of the other extant schizaealean ferns show little or no morphological similarities to those of *Mohria* and *Anemia*. In *Actinostachys* and *Schizaea* the spores are monolete, whereas those of *Lygodium* are trilete with a smooth exinal sculpture.

Mohria and *Anemia* exhibit numerous plesiomorphic features with reference to the sporangium and spores. The sporangia are large, exindusiate, non-soriolate (monosporangiate), sessile or short-stalked and have neither a true eusporangiate or leptosporangiate development. Annuli consist of a ring of apically or subapically positioned end cells. The spore output per sporangium is large (> 64 spores per sporangium), and the spores are trilete and large (> 70 μm) in diameter. These features are significant in explaining evolutionary pathways within the pteridophytes and also indicate the phylogenetic position of the schizaealean ferns.

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