Systematic studies in the genus *Mohria* (Pteridophyta: Anemiaceae). VI. Taxonomic review

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Keywords: Anemiaceae, Mohria, taxonomy

ABSTRACT

A taxonomic review of the genus *Mohria* Sw. is presented, including diagnostic features, distribution and variation. A key to the taxa in the genus is provided and each species described.

UITTREKSEL

'n Taksonomiese oorsig van die genus *Mohria* Sw., waaronder kenmerkende eienskappe, verspreiding en variasie word aangebied. 'n Sleutel tot die taksons in die genus word verskaf en elke spesie word beskryf.

INTRODUCTION

The genus *Mohria* Sw. is largely an African one, occurring from the Western Cape in South Africa, along the eastern mountain ranges as far north as Kenya. Although the genus has a largely eastern distribution, two species, *M. lepigera* (Baker) Baker and *M. vestita* Baker, also occur on the Bihe Plateau in southern Angola. *Mohria*, furthermore, occurs on Madagascar and Réunion Island.

Mohria was first described by Plukenet (1700) as *Filicula* geranii arvensis folio et facie aethiopica. It was not until 1771 that Linnaeus in his *Mantissa plantarum altera* described *Polypodium caffrorum* from a König collection. König, a pupil of Linnaeus, was on his way to Tranquebar (India) but spent a short period (April 1–28, 1768) at the Cape of Good Hope, where he collected on Lion's Head, Table Mountain, Devil's Peak, the flats towards Constantia and along the sea shores (Gunn & Codd 1981).

The younger Linnaeus, however, in his Supplementum plantarum (1781), transferred Polypodium caffrorum L. to the genus Adiantum L. P. caffrorum has since been transferred to genera such as Lonchitis L. by Bernhardi (1801) and Colina by Greene (1893). Before describing the genus Mohria in 1806, Olaf Swartz initially placed what is today known as Mohria caffrorum in the genus Osmunda L. (Swartz 1801). At the time of publication of the genus Mohria, M. thurifraga was the only species known.

The genus *Mohria* honours Daniel Matthias Mohr, German botanist and later professor of philosophy at the University of Kiel (Stafleu & Cowan 1981).

A review of the genus has never been undertaken, with the result that all the collections, till recently, have either been placed in *M. caffrorum* or *M. lepigera*. The review presented here is the result of studies on the morphology and anatomy of the rhizome and frond (Roux *et al.* 1992), vestiture morphology (Roux 1992a), sporangium and spore morphology (Roux 1992b) and karyology (Roux 1994).

TAXONOMIC REVIEW

Mohria *Sw.*, Synopsis filicum: 6, 159 (1806). Type: *M. thurifraga Sw.*, nom. superfl. [= *Polypodium caffrorum* L.; now *M. caffrorum* (L.) Desv.].

Terrestrial or lithophytic. Rhizome dictyostelic, prostrate or creeping, irregularly branched, scaled, often stoloniferous, stolons amphiphloic siphonosteles. Fronds polystichous, erect or spreading, closely spaced or crowded, homomorphic to dimorphic; vernation circinate or non-circinate. Stipe terete, firm, variously set with naviculate trichomes, hairs and/or scales, fertile ones usually longer than sterile ones. Lamina pinnate to 3pinnatifid, herbaceous to coriaceous. Rachis terete or adaxially shallowly sulcate, set with indumentum similar to that on stipe. Pinnae proximally short-stalked and widely spaced, distally sessile and overlapping, adaxially with clavate and naviculate trichomes, often also with hairs and/or small scales, abaxially variously set with clavate and naviculate trichomes, hairs and scales. Pinnules opposite to alternate, widely spaced or overlapping, venation free, ending near margin in lobe or teeth apices. Stomata anomo-, copolo-, desmo-, euperi-, eupolo-, para- and/or tripolocytic, amphistomic, hypostomic in M. nudiuscula. Sporangia exindusiate, usually borne on distal pinnae, borne singly near vein endings on short, massive stalks, globose; annulus terminal, 8-22-celled; stomium well defined. Spores tetrahedral, trilete, radially symmetrical, with ridges and grooves parallel to the equatorial plane, variously sculptured, 70-120 µm in diameter. Chromosome *number*: 2n = 76, 152.

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KEY TO SPECIES

la Pinnae adaxially sparsely to densely hirsute:

2a Lamina pinnate, oblanceolate to linear-attenuate; abaxially hirsute or with a few narrow to broad-ovate scales along rachis; proximal pinnae not reduced in size to base, closely spaced; rhizome stoloniferous 2. M. marginalis

2b Lamina 2-pinnatifid to 2-pinnate, narrowly elliptic; abaxially sparsely to densely set with lanceolate to broad-ovate, pale to dark brown, entire scales; proximal pinnae widely spaced, decurrent, rhizome not stoloniferous 1. *M. lepigera*1b Pinnae adaxially glabrous or sparsely set with short or long hairs largely along secondary rachises and veins:

- 4a Fertile frond stipe significantly longer than sterile frond stipe; adaxial surface of pinnae with hairs only; hairs with sinuate transverse walls
 4b Fertile and sterile frond stipes of near equal length; adaxial surface of pinnae glabrous or with hairs and/or small scales,
 - especially along secondary rachises; hair cells sinuous-walled or ossiform: 5a Scales on abaxial surface of lamina narrowly linear to narrowly lanceolate, twisted; lamina usually >200 mm long, erect:

1. Mohria lepigera (Baker) Baker in Annals of Botany 5: 498 (1891).

Notochlaena lepigera Baker: 53 (1884). Type: Mount Dzomba, Zambesi-land (Malawi, Zomba Mountain), *Kirk s.n.* (K, lecto.!, here designated).

Mohria caffrorum (L.) Desv. var. multisquamosa Bonap.: 85 (1917). M. lepigera (Baker) Baker var. madagascarica Tardieu: 10 (1952). Type: Madagascar, Mont Intangabalala, près Ihosy, 1 000 m, Perrier de la Bâthie 7849 (P, holo.!).

Terrestrial or lithophytic. Rhizome prostrate, short, up to 4 mm in diameter, densely set with roots, stipe bases and scales; scales $0.8-5.0 \times 0.2-0.9$ mm, scarious, castaneous, adnate, linear to narrowly lanceolate, entire. Fronds few, erect, crowded; vernation non-circinate. Stipe terete, stramineous, up to 57.0×1.2 mm, set with hairs and scales; hairs up to 2.4 mm long, sinuous-walled; scales $0.9-3.8 \times 0.3-14$ mm, stramineous, adnate, cordate or cordate-imbricate, broadly ovate to lanceolate, entire. Lamina narrowly elliptic, up to 402 mm long, 2-pinnatifid to 2-pinnate, membranous to firmly herbaceous, with 12-39 pairs of pinnae. Rachis firm, proximally terete, distally adaxially shallowly sulcate, abaxially sparsely to densely set with stramineous scales similar in structure to those on abaxial lamina surface, reducing in size to frond apex, adaxially with naviculate trichomes and gland-tipped, straight-walled hairs similar to those on adaxial lamina surface. Pinnae 9.0–3.5 \times 6–14 mm, opposite to alternate, proximally widely spaced and decurrent, crowded near apex, ovate to linear, abaxially sparsely to densely set with hairs and scales; hairs 0.6-2.2 mm long, sinuous-walled; scales $0.2-1.3 \times 1.3-3.6$ mm, lanceolate to broadly ovate, adaxially with naviculate trichomes and sparsely to densely hirsute, with hairs 0.4-2.6 mm long. Pinnules or segments opposite, 4-8 pairs per pinna, widely spaced to overlapping, ovate to circular, margins shallowly crenulate or lobed, terminating in 1 or 2 acute, falcate or obtuse teeth. Spores stramineous, broadly ridged, ridges closely spaced, colliculate. Chromosome number unknown. Figure 1A-H.

Diagnostic features

Mohria lepigera is characterized by its generally long and narrow frond outline, the short stipe in relation to the lamina length ($\overline{x} = 1:10$; n = 30), the often greatly reduced and widely spaced proximal pinnae and the large, densely set stramineous to cream-coloured sinuous-walled scales which often cover the entire abaxial pinna surface. Clavate trichomes are $30.5-(42.52)-48.8 \ \mu m$ long and naviculate trichomes are $50.0-(113.44)-147.5 \ \mu m$ long.

Distribution and habitat

Mohria lepigera occurs in Tanzania, Burundi, Zaïre, Malawi, Mozambique, Zimbabwe and Madagascar (Figure 2). *M. lepigera* occurs from 1 200–2 400 m in habitats ranging from rock crevices or boulder bases and riverine fringes to moist open ground. Kornas (1979) dealt with the ecology of the taxon in Zambia.

Variation

Mohria lepigera shows a fair amount of plasticity in the degree to which the Jamina is divided, lamina size, texture and indumentum composition and density. Collections recorded from moist shaded conditions at higher elevations have relatively short, less dissected (2-pinnatifid) membranous fronds, whereas those from xeric environments have relatively long, 2-pinnate, firmly herbaceous fronds which are borne in an erect manner. The densely scaled abaxial surface which is typical of *M. lepigera* in some instances only bears filiform scales and hairs.

Vouchers: Brass 16484 (PRE, SRGH); Drummond & Hemsley 2557 (PRE); Pichi Sermolli 7042 (BOL, SRGH); Polhill & Paulo 1634 (K); Taylor 3279 (NBG).

2. Mohria marginalis (*Savigny*) *J.P. Roux* in South African Journal of Botany 56: 401 (1990b).

Osmunda marginalis Savigny: 655 (1798). Type: Bourbon (Réunion), Commerson s.n. (P. lecto.!, designated by Roux 1990b).

O. thurifraga Comm. ex Savigny: 655 (1798), nom. nud.

O. thurifraga Comm. ex Bory: 348 (1804), nom. nud.

O. crenata Desv.: 307 (1811). Type: habitat în însula Bourboniae (Réunion), sine coll. (P. lecto.!, here designated).

Mohria hirsuta J.P. Roux: 435 (1984). Type: Qwa Qwa, Tsheseng, near cave on road to The Sentinel, *Roux* 907 (NBG, holo.!; K, PRE, iso.!).

Terrestrial or lithophytic. *Rhizome* prostrate, short, up to 3 mm in diameter, irregularly branched, stoloniferous, sparsely set with scales; scales $0.8-3.3 \times 0.2-0.5$ mm, stramineous, scarious, cordate, linear to narrowly lanceo-late, entire. *Fronds* erect, crowded; vernation non-cir-

cinate. *Stipe* terete, firm, stramineous, up to 36×1 mm, sparsely set with naviculate trichomes, hairs and scales; hairs up to 2.7 mm long, sinuous-walled; scales $1.2-2.8 \times 0.3-0.9$ mm, cordate, narrowly lanceolate, narrowly ovate to linear-acuminate, entire or shallowly and uneven-

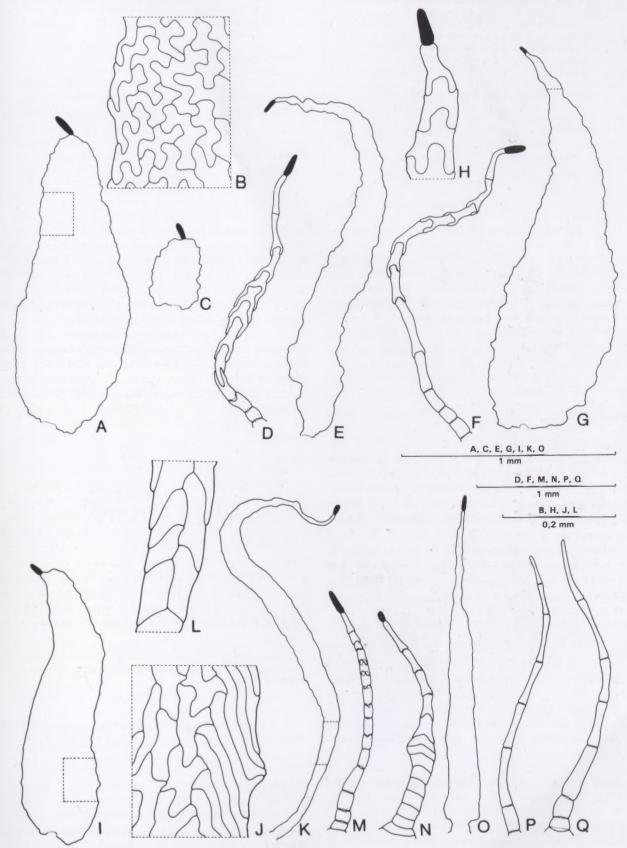


FIGURE 1.—Frond scales in Mohria. A–H, M. lepigera, Burrows 1686 (NBG). A–C, stipe; D, E, rachis; F, adaxial lamina surface; G, H, abaxial lamina surface. I–Q, M. marginalis, Roux 907 (NBG). I–M, stipe; N, O, rachis; P, adaxial lamina surface; Q, abaxial lamina surface. Scale bars: A, C, D–G, I, K, M–Q, 1 mm; B, H, J, L, 0.2 mm.

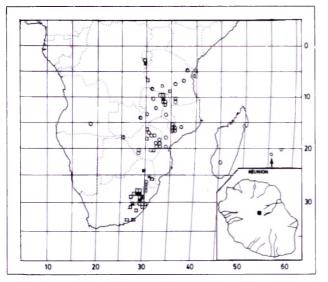


FIGURE 2.—Distribution of Mohria lepigera, ○; M. marginalis, ■; and M. nudiuscula, □.

ly crenulate. Lamina 33-131 mm long, oblanceolate to linear-attenuate, pinnate, firmly herbaceous, with 8-21 pairs of pinnae. Rachis terete, firm, distally somewhat flexuose, adaxially often shallowly sulcate, sparsely set with naviculate trichomes, hairs and filiform scales, which are absent at apex. *Pinnae* $4.4-14.7 \times 5.5-8$ mm, opposite to alternate, proximally widely spaced, crowded and overlapping distally, proximally short-stalked and circular to reniform, distally sessile and ovate to lanceolate, adaxially sparsely to densely hirsute, with straight-walled, often eglandular hairs, abaxially with sinuous-walled hairs up to 1 mm long and filiform scales; scales $1.6-2.6 \times 0.1-0.2$ mm, segments opposite, 2-5 pairs per pinna, usually overlapping slightly, rotund to ovate-obtuse, less deeply dissected towards lamina base and apex, shallowly crenulate to bluntly dentate. Spores stramineous, ridges widely spaced, ridges and grooves granulate, up to 82 µm in diameter. Chromosome number: 2n = 76. Figure 11-Q.

Bory has always been considered as the author of *Osmunda thurifraga* (Schelpe 1970, 1977; Schelpe & Anthony 1986) but the name was published without a description. Bory (1804: 348) merely noted 'Dans les environs je trouvai une belle fougère, dont les feuilles froissées répandaient l'odeur de l'encens: je l'ai vue depuis dans l'herbier de M. de Jussieu, elle lui venait de Commerson, qui l'avait appelée *Osmunda thurifraga*.' It is therefore evident that he did not describe, nor had any intention to describe, the species, as in other parts of this work he either provided a short description or gave a reference to a previous work where he thought a taxon to be new. The name is therefore a *nomen nudum*.

Savigny (1798) also published Commerson's manuscript name Osmunda thurifraga as a nomen nudum, citing it as one of the elements used in his description of O. marginalis, the other being a Sonnerat collection from Réunion. The Commerson specimen in the herbarium of the Muséum National d'Histoire Naturelle, Paris (P) was designated as the lectotype of O. marginalis Savigny (Roux 1990b). Desvaux (1811), in his description of *Mohria crenata*, gave the locality of the species as 'Habitat in insula Bourboniae' (Réunion), with no collector given. The specimen designated here as lectotype of *M. crenata* is a sheet which formerly formed part of Desvaux's herbarium and is currently housed in the herbarium of the Muséum National d'Histoire Naturelle, Paris (P).

Diagnostic features

Mohria marginalis is characterised by the relatively long and narrow, less dissected (2-pinnatifid) fronds, the usually eglandular, short-celled, straight-walled hairs on the frond, as well as the filiform scales and sinuous-walled hairs on the stipe, rachis and abaxial surface of the lamina. Clavate trichomes are $37.5-(48.75)-57.5 \ \mu m$ long and naviculate trichomes are $57.0-(104.3)-145.8 \ \mu m$ long.

Distribution and habitat

Mohria marginalis occurs from the southern Drakensberg in the northeastern Cape along the mountain ranges into central Africa, as far north as Burundi. It also occurs on Réunion (Figure 2). In the Drakensberg the taxon occurs in seasonally moist, often exposed situations at the rim of vegetation pockets commonly found in shallow depressions in the Clarens Sandstone formation, at boulder bases or among grass tussocks at higher elevations. Further north it has been recorded from rock crevices. The plants usually form large masses and may often grow alongside xerophytic ferns such as *Cheilanthes eckloniana* (Kunze) Mett., *Ophioglossum lancifolium* C. Presl and *M. rigida* J.P. Roux.

Variation

Slight variations occur in frond length, the number of segments per pinna and in the indumentum density on the stipe and rachis. Narrow hair-like scales often replace some of the hairs on the abaxial lamina surface.

Vouchers: De Marne s.n. (NBG); Leighton 3224 (BOL); Reekmans 8789 (PRE); Roux 907, 1524 (NBG).

3. Mohria caffrorum (L.) Desv. in Mémoirs de la Société Linnéenne de Paris 6, 2: 198 (1827). Type: habitat ad Cap. b. Spei., *König s.n.* [LINN 1251/67, lecto.!, designated by Schelpe & Anthony (1986)].

Polypodium caffrorum L.: 307 (1771); Adiantum caffrorum (L.) L.f.: 447 (1781); Lonchitis caffrorum (L.) Bernh.: 124 (1801); Colina caffrorum (L.) Greene: 247 (1893); Mohria thurifraga Sw.: 159, 385 (1806) nom. superfl.

Osmunda thurifera Sw.: 105 (1801). Type: C.B.S. Thunberg s.n. [UPS, lecto.!, designated by Schelpe & Anthony (1986)].

Cheilanthes fuscata Blume: 136 (1828), Type: Cape (L, holo.!).

Mohria thurifraga Sw. var. achilleifolia (as achilliaefolia) E.J. Lowe: 104, t. 62B (1862). Type; t. 62B (icono.!).

Lithophytic or terrestrial. *Rhizome* prostrate, short and stout or slender and creeping, 2–6 mm in diameter, irregularly branched, stoloniferous, clothed with roots and scales; scales $1.6-2.8 \times 0.3-0.8$ mm, castaneous, adnate, lanceolate to ovate, acute to obtuse, entire. *Fronds* erect, approximate to crowded, fertile ones usually longer than sterile ones; vernation non-circinate. *Stipe* terete, firm, castaneous throughout or proximally castaneous and dis-

tally stramineous, 17-162 mm long, up to 1.7 mm in diameter, fertile one significantly longer than sterile one, densely set with naviculate trichomes, uniseriate hairs and scales, becoming glabrous later; scales $0.5-3.8 \times 0.1-1.5$ mm, of two types, variable, stramineous-larger scales linear, narrowly elliptic or lanceolate or broadly ovate, entire-smaller scales sessile or cordate, irregularly shaped or with fimbriate base. Sterile lamina 37-235 mm long, elliptic to oblanceolate, fertile lamina 75-270 mm long, narrowly elliptic to narrowly oblanceolate, 2-pinnatifid to 3-pinnate, with 8-26 pairs of pinnae. Rachis proximally terete or shallowly sulcate, narrowly winged and distally often flexuose, densely set with indumentum similar to that on abaxial pinna surface. Pinnae 9-30 \times 6.5-12.6 mm, proximally widely spaced, distally crowded and overlapping, ovate to oblong, proximally shortstalked, becoming sessile distally, adaxially with clavate and naviculate trichomes and few short or long sinuouswalled hairs, 0.4-1.4 mm long, largely on secondary rachis; secondary rachis narrowly winged, abaxially with clavate and naviculate trichomes, hairs and scales; hairs and scales sparsely to densely set, pale brown to whitish; scales $0.2-3.5 \times 0.1-1.3$ mm, cordate to cordate-imbricate, narrowly linear to lanceolate, ovate or circular at base, terminating abruptly in a long and narrow entire apex, proximally with short and long, straight or curved marginal outgrowths. Pinnules opposite to alternate, 4-9 pairs per pinna, widely spaced or overlapping, segments lobed, each terminating in 1 or 2 cuneate or falcate teeth. Spores stramineous, ridges and grooves glebulate, pustulate, finely verrucous or reticulate-verrucous. Chromosome number: 2n = 76. Figure 3A–O.

Mohria thurifraga Sw. (1806) is a superfluous name for *Polypodium caffrorum* L. (1771). However, the concept of this species as construed by Swartz (1806) includes two different elements, namely a Cape taxon and a Réunion taxon. The latter was described as *Osmunda marginalis* Savigny based on collections by Commerson and Sonnerat from Réunion and is here upheld as a distinct species.

The description and illustration published by Lowe (1860) is that of *M. vestita* (No. 6). Here he mentions a dwarf form of this species which was known as *M. achilleifolia*. This he described as *M. thurifraga* var. *achilleifolia* in 1862. A Sim collection annotated by him as *M. thurifraga* var. *achilleifolia* from Zwaartberg near Pietermaritzburg, Natal, is housed in Pretoria (PRE) but this proved to be a variant of *M. vestita*. However, the illustration (t. 62B) provided by Lowe which is based on a Sim collection, judging by the size and laminar segmentation, appears to be a collection of *M. caffrorum*. The collection has obviously not been preserved and I therefore designate plate 62B as iconotype of *M. thurifraga* var. *achilleifolia*.

Diagnostic features

Mohria caffrorum is characterized by the branched, often widely creeping stoloniferous rhizome, the marked degree of dimorphism in the fertile frond stipe which is strikingly longer than the sterile frond stipe, indumentum structure and distribution, and spore ornamentation. Clavate trichomes are $55.0-(59.15)-67.5 \mu m$ long and naviculate trichomes are $147.5-(179.8)-222.5 \mu m$ long.

Distribution and habitat

Mohria caffrorum is found in the Northern, Western and Eastern Cape where it occurs in a wide range of ecological and climatic conditions (Figure 4). It grows at elevations ranging from almost sea level at Cape Point to $\pm 1\,000$ m in the Cedarberg. Plants are generally found in small clonal clusters at boulder bases, in rock crevices or in light shade of shrubs, or in large stands in seasonally moist exposed situations. Fires, which are prevalent in most of the vegetation types in which the species occurs, appear to have no ill effect on the plants but rather stimulate them.

Variation

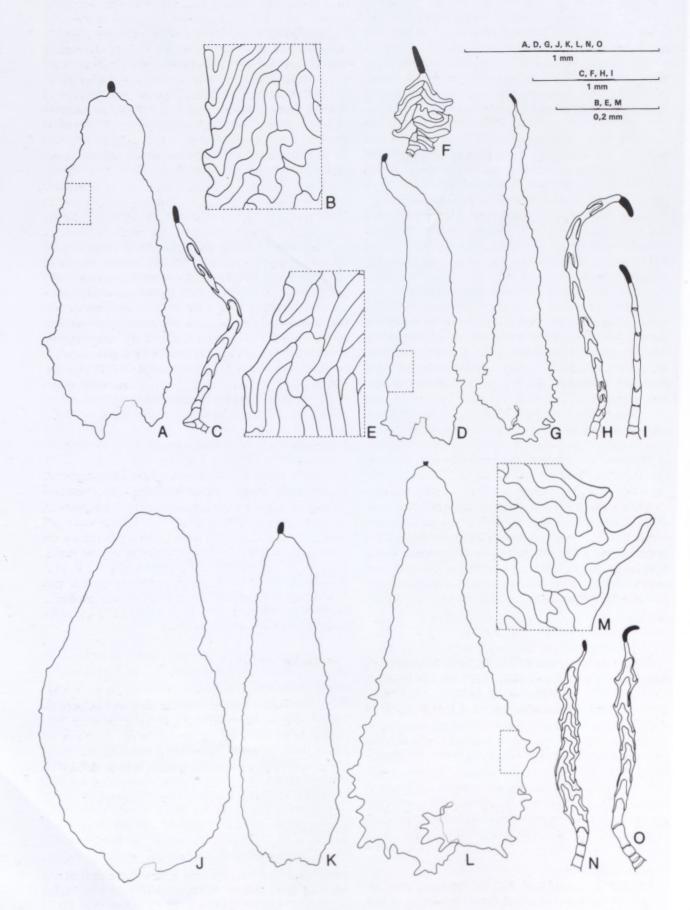
Scale density and scale outline or structure on the abaxial lamina surface show the most striking degree of variation. When scale variation throughout the distribution is viewed, a gradation in scale outline is detected from the west, becoming more complex to the east. Scale variation is especially apparent in the Gifberg/Vanrhynsdorp ecotype where the abaxial surface of the mature fronds of some plants is densely covered by large pale brown to whitish scales with sinuate-walled cells (Figure 3J–O).

M. caffrorum shows the highest degree of frond dimorphism. The difference between stipe length of the sterile and fertile fronds is the most significant. A relationship exists between frond and stipe length in the sterile frond (r = 0.724, P < 0.001) and the fertile frond (r = 0.530, P < 0.001). Fertile fronds proved to have a larger number of pinnae and pinnules than sterile fronds.

Vouchers: Barker 9790 (NBG); Dahlstrand 792 (GRA); Goldblatt 3667 (PRE); Perry 42 (NBG); Taylor 11833 (PRE, STE).

4. **Mohria saxatilis** *J.P. Roux* in Journal of South African Botany 56: 399 (1990a). Type: Cape Province, 3219 (Wuppertal): Wuppertal, west-facing cliff near experimental forest plot on road to Heuningvlei, (–AA), *Roux 2012* (NBG, holo.!; K, PRE, iso.!).

Lithophytic. Rhizome prostrate, short, up to 5 mm in diameter, densely clothed with roots, closely spaced persistent stipe bases and scales; scales $1.0-3.7 \times 0.3-0.4$ mm, castaneous, adnate or cuneate, linear to narrowly lanceolate, entire. Fronds few, erect, caespitose, fertile ones slightly longer than sterile ones; vernation circinate. Stipe terete, firm, stramineous, 22.0-61.5 mm long, up to 1.2 mm in diameter, fertile one slightly longer than sterile one, densely set with scales; scales, $1.0-3.2 \times 0.5-1.1$ mm, stramineous, spreading, cuneate to cordate, narrowly lanceolate to ovate, shallowly and irregularly crenulate. Lamina elliptic to oblanceolate, 67-117 mm long, 2-pinnatifid, with 8-15 pairs of pinnae. Rachis proximally terete, distally narrowly winged and shallowly sulcate, adaxially with naviculate trichomes and sinuous-walled hairs, abaxially densely set with naviculate trichomes and scales similar in structure to those on stipe. Pinnae 11-24 \times 8–10 mm, opposite to alternate, oblong to ovate, obtuse, with 4-6 lobe pairs per pinna, each lobe terminating in a single tooth or paired acute teeth, abaxially densely set with naviculate trichomes and scales; scales 0.9–3.4 \times 0.3–0.9 mm, stramineous, spreading, cuneate to cordate, narrowly lanceolate to ovate, entire or shallowly and un-



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FIGURE 3.—Frond scales in Mohria. A–I, M. caffrorum, Roux 2014 (NBG). A–C, stipe; D–F, rachis; G, abaxial lamina surface; H, I, adaxial lamina surface. J–O, M. caffrorum, Roux 2015 (NBG). J, stipe; K, rachis; L, M, abaxial lamina surface; N, O, adaxial lamina surface. Scale bars: A, C, D, F, G–L, N, O, 1 mm; B, E, M, 0.2 mm.

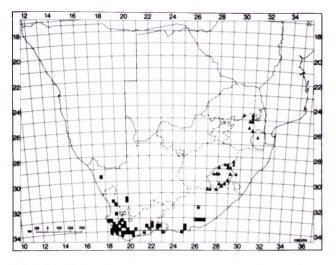


FIGURE 4.—Distribution of Mohria caffrorum, ■; M. saxatilis, O;and M. rigida, 🔺

evenly crenulate, adaxially with naviculate trichomes and sparsely set with straight or sinuous-walled hairs along broadly winged secondary rachis, 0.9-3.3 mm long. Spores stramineous, ridges broad, fossulate, sparsely and irregularly vertucous, 75.4-92.8 µm in diameter. Chromosome number: n = 76. Figure 5A-K.

Diagnostic features

Mohria saxatilis is distinguished by the short prostrate rhizome, short stipe, the crowded fronds, the large spreading scales on the stipe and on the abaxial lamina surfaces, and the broadly winged costa. Diagnostic micromorphological characters are the larger clavate trichomes which are 61.1-(68.11)-76.4 µm long (Roux 1992a), and epidermal cells and the occurrence of copolocytic and tripolocytic stomata not found in any of the other taxa (Roux et al. 1992). Naviculate trichomes are 97.7-(139.05)-177.19 µm long.

Distribution and habitat

Mohria saxatilis is confined to the Table Mountain Sandstone formation and occurs from the Cedarberg to the Langeberg in the Worcester District. The species grows at elevations ranging from $\pm 1~000$ to 1~500 m (Figure 4).

Vouchers: Bean 259 (in part, A & B only) (BOL); Compton 17993 (NBG); Roux 2000 (NBG); Roux 2003 (in part) (NBG); Roux 2012 (K, NBG, PRE).

5. Mohria rigida J.P. Roux in South African Journal of Botany 56: 268 (1990a). Type: Qwa Qwa, at Clarens Sandstone cave on road to The Sentinel, Roux 1910 (NBG, holo.!).

Lithophytic or terrestrial. Rhizome prostrate, short, up to 5 mm in diameter, densely clothed with roots, persistent stipe bases and scales; scales $3.6-5.6 \times 0.3-0.6$ mm, castaneous, adnate, narrowly lanceolate, entire. Fronds erect or spreading, caespitose, fertile ones slightly longer than sterile ones, vernation non-circinate. Stipe terete, firm, proximally castaneous, distally stramineous, 16-88 mm long, up to 1.3 mm in diameter, fertile one slightly longer

glabrous later; scales $0.5-3.4 \times 0.3-0.8$ mm, stramineous, variable, truncate, cordate or cordate-imbricate, narrowly lanceolate, ovate, broadly ovate or transversely broadly elliptic, terminating abruptly in long filiform, often uniseriate hair-like apex, entire or shallowly and irregularly crenulate or with a few long and/or short outgrowths at base. Lamina 43-197 mm long, elliptic to narrowly elliptic, 2-pinnate, with 7-21 pairs of pinnae. Rachis terete and rigid or distally shallowly sulcate, sparsely to densely set with naviculate trichomes and scales, adaxial scales similar in structure to those on abaxial surface. Pinnae $10-35 \times 4.5-9.5$ mm, opposite to approximate, proximally often alternate, distally alternate and closely spaced, often overlapping, mostly short-stalked throughout, narrowly ovate, adaxially glabrous, with naviculate trichomes or with few long ossiform-celled hairs, 0.9-2.7 mm long, or with small scales (similar to those on rachis); secondary rachis shallowly sulcate, distally winged, curves apically, abaxially sparsely to densely set with naviculate trichomes and scales; scales $0.5-3.1 \times 0.4-0.9$ mm, stramineous, cordate to cordate-imbricate, narrowly linear, triangular, lanceolate or ovate, crenulate or fimbriate. Pinnules opposite to alternate, 4-8 pairs per pinna, not or slightly overlapping, segments up to 3 pairs per pinnule, lobed, each terminating in 1 or 2 acute teeth. Spores stramineous, ridges widely spaced, ridges and grooves, granulate. Chromosome number: 2n = 152. Figure 5L–T.

Diagnostic features

Mohria rigida is characterised by abaxially appressed, often broadly ovate, cordate-imbricate, often sinuouswalled scales, the crowded, caespitose frond arrangement, the rigid unwinged rachis, the often proximally unwinged secondary rachis, and sporangia generally borne on the entire frond or only the proximal pinnae may be sterile. In *M. rigida* the stipe/lamina ratio averages 1:2.45 (n = 45) whereas in *M. vestita*, with which this species may be confused, it averages 1:3.6 (n = 61). Clavate trichomes are 35.0-(45.76)-61.1 um long and naviculate trichomes are 77.5-(112.86)-164.97 µm long.

Distribution and habitat

Mohria rigida is restricted to elevations of 1 800-2 438 m along the Drakensberg, the adjacent mountainous Lesotho and the Transvaal Highveld and escarpment (Figure 4). In the Drakensberg the plants usually occur individually or in small groups consisting of a few plants in the alpine and subalpine vegetation belts as defined by Killick (1963). Almost without exception they occur in seasonally moist, often exposed, rock crevices.

Variation

Variation occurs in frond and pinna length and in the density, size and outline of the scales on the abaxial and adaxial lamina surfaces. In Mohria rigida the stipe/lamina ratio ranges from 1: 0.84 to 1: 7.0 ($\bar{x} = 2.45$; n = 45).

Vouchers: Roberts 3611 (PRE); Roux 1013, 1075, 1904 (NBG); Schweickerdt s.n. (PRE).

6. Mohria vestita Baker in Transactions of the Linnean Society, Botany 2: 328 (1887). Type: Tanzania, Kilimanjaro, ad rupium fissuras, 6 000 ft. Johnston s.n. (K, holo.!).

M. caffrorum (L.) Desv. var. vestita (Baker) F. Ballard: 561 (1954).

M. thurifraga sensu E.J. Lowe: 197, t. 70 (1860).

Lithophytic or terrestrial. *Rhizome* prostrate, short, up to 8 mm in diameter, irregularly branched, clothed with roots and scales; scales $1.7-6.3 \times 0.5-1.7$ mm, castaneous to ferrugineous, adnate, lanceolate to ovate, entire. *Fronds* erect, crowded, fertile ones generally longer than sterile

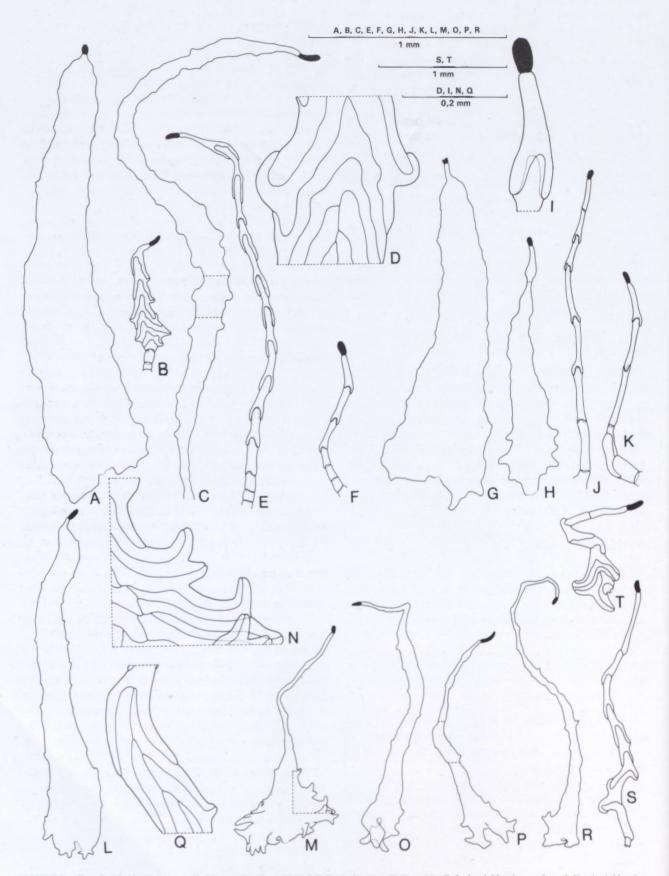


FIGURE 5.—Frond scales in Mohria. A–K, M. saxatilis, Roux 2002 (NBG). A–D, stipe; E, F, rachis; G–I, abaxial lamina surface; J, K, adaxial lamina surface. L–S, M. rigida, Roux 1910 (NBG). L, stipe; M, N, rachis; O–Q, abaxial lamina surface; R–T, adaxial lamina surface. Scale bars: A–C, E–H, J–M, O, P, R–T, 1 mm; D, I, N, Q, 0.2 mm.

ones; vernation non-circinate. Stipe terete, firm, proximally castaneous, distally stramineous, 20-132 mm long, up to 4 mm in diameter, with naviculate trichomes and scales becoming glabrous later; scales $0.5-6.8 \times 0.1-1.5$ mm, stramineous to castaneous, variable, cordate or cordateimbricate, filiform or narrowly linear, shortly attenuate, hastate, or broad at base terminating abruptly in a long filiform apex, entire or with few short or long outgrowths at base curving apically. Lamina 53.5-380.0 mm long, herbaceous, sterile, narrowly elliptic, fertile, 79-464 mm long, narrowly oblanceolate, 2-pinnatifid to 2-pinnate, with 10-29 pairs of pinnae. Rachis proximally terete, distally shallowly sulcate and winged, sparsely to densely set with scales similar to those on abaxial lamina surface. *Pinnae* $8-44 \times 6.5-19.0$ mm, opposite to alternate, widely spaced proximally, distally crowded, often overlapping, ovate, proximally short-stalked, distally sessile; secondary rachis straight, winged throughout, shallowly sulcate adaxially, with clavate and naviculate trichomes and sinuous-walled and ossiform-celled hairs, 0.4-2.2 mm long, abaxially sparsely to densely set with scales; scales $0.7-3.2 \times 0.1-0.7$ mm, castaneous, variable, filiform or adnate, linear and shortly attenuate, or cordate to cordateimbricate, hastate to narrowly lanceolate, entire, irregularly crenulate or with short or long outgrowths at base, curving apically. *Pinnules* opposite to alternate, 4-9 pairs per pinna, generally not overlapping, segments up to 5 pairs, lobed, terminating in a single or paired, acute, often obtuse and falcate tooth. Spores stramineous, widely spaced ridges and grooves puncticulate. Chromosome number: 2n = 152. Figure 6A–L.

Diagnostic features

Mohria vestita is characterized by the short stipe/ lamina ratio, the reduction in size of the pinnae towards the lamina base, ossiform-celled hairs which adaxially are confined to the secondary rachis and veins, and the relatively small, generally hastate and sparsely set twisted scales which are also confined to the secondary rachis and veins on the abaxial surface. Clavate trichomes are $30.0-(51.31)-63.4 \mu m$ long and naviculate trichomes are $85.0-(138.32)-196.54 \mu m$ long.

Distribution and habitat

The distribution of *Mohria vestita* ranges from the southern Cape along the central mountain ranges as far north as Kenya. It also occurs on the higher lying areas of Angola and in Madagascar (Figure 7). *M. vestita* grows in habitats ranging from coastal subtropical conditions to elevations exceeding 3 000 m along the Natal Drakensberg. On Mount Kilimanjaro, *M. vestita* has been recorded at elevations ranging from 1 200–1 400 m and at Humpata in Angola it occurs at 2 220 m. Fires are common throughout the distribution area of *M. vestita*, but appear to have no effect on the subterranean rhizome.

Variation

Variation in frond length can be ascribed to the wide distribution and diverse environmental conditions throughout the range. In hostile environments the fronds may be merely 109 mm long but at lower, more favourable conditions the fronds may measure up to 690 mm. Irrespective of variation in frond length, a relationship exists between stipe and frond length in the sterile (r = 0.683, P <0.001) and fertile (r = 0.711, P < 0.001) fronds. Variation in the density and distribution of indumentum is most apparent. Hairs on the adaxial and abaxial lamina surfaces appear to increase as the distribution extends to the north. Slight variation in the cell structure may also be evident.

Vouchers: Daubenberger s.n. (PRE); Faden, Evans & Kabuye 70/344A (BOL); Janse 106 (GRA, PRE); Nicholas 497 (SRGH); Roux 2233 (NBG).

7. Mohria nudiuscula *J.P. Roux* in South African Journal of Botany 56: 266 (1990a). Type: Natal, Weenen Division, damp streambanks in the Mnweni area, Drakensberg, *Esterhuysen 14523* (NBG, holo.!; BOL, PRE, iso.!).

M. caffrorum (L.) Desv. var. *ferruginea* J.E. & S.M. Burrows in J.E. Burrows: 168 (1989). Type: Natal, (2929) Underberg: Drakensberg Mountains, Injasuti, below Women Grinding Corn, (-AB), *Burrows 360* (BOL, holo.!; K. PRE, iso.).

Terrestrial. Rhizome prostrate, short, up to 10 mm in diameter, densely clothed with roots and scales; scales $4.7-6.9 \times 0.3-0.5$ mm, castaneous to ferrugineous, adnate, narrowly lanceolate, entire. Fronds few, caespitose, spreading or erect, fertile ones slightly longer than sterile ones; vernation non-circinate. Stipe terete, firm, proximally castaneous, distally stramineous, 20-220 mm long, up to 3 mm in diameter, sparsely to densely set with naviculate trichomes and scales, becoming glabrous later; scales 0.5- 7.5×0.1 –1.2 mm, stramineous to castaneous, narrowly linear, narrowly lanceolate, triangular or hastate, terminating in a long filiform apex, entire, usually lignified at point of attachment. Lamina 53-635 mm long, often coriaceous, narrowly elliptic, pinnate to 2-pinnate, with 7-34 pairs of pinnae. Rachis shallowly sulcate for most of its length, densely set with naviculate trichomes and scales, similar but smaller than those along stipe. Pinnae $10-80 \times 6-15$ mm, proximally opposite to alternate, alternate and closely spaced distally, often overlapping, ovate to narrowly ovate, adaxially glabrous or with few naviculate trichomes and hairs, up to 1.8 mm long, often also with irregularly shaped filiform scales, up to $2.0 \times$ 0.2 mm, along secondary rachis, abaxially with clavate and naviculate trichomes, and few or numerous scales; scales stramineous to castaneous, $0.4-3.2 \times 0.1-0.8$ mm, attenuate or hastate, filiform or narrowly lanceolate; secondary rachis straight, winged throughout, shallowly sulcate adaxially, sparsely to densely set with scales similar to those along rachis. Pinnules opposite to alternate, 3-12 pairs per pinna, basal pair often smaller than the next, distant to crowded and overlapping, lobed, segments up to 3 pairs per pinnule, margins slightly revolute, shallowly crenulate or obtusely toothed. Spores stramineous, broad ridges and deep narrow grooves sparsely to densely set with verrucae or spherical deposits, 70-90 μ m in diameter. Chromosome number: 2n = 152 (Figure 6M-W).

Mohria nudiuscula was recently described by Burrows & Burrows in Burrows (1989) as M. caffrorum var. ferruginea. Unaware of this study, I described the same species as M. nudiuscula (Roux 1990a). However, when my manuscript was in press, *M. caffrorum* (L.) Desv. var. *ferruginea* J.E. Burrows & S.M. Burrows was published. Although the latter name antedates *M. nudiuscula* I found it to be a distinct taxon and believe it not to be related to *M. caffrorum*. In accordance with Article 11.2 of the International Code of Botanical Nomenclature (1994) the name *M. nudiuscula* is adopted.

Diagnostic features

Diagnostic features in *Mohria nudiuscula* are the thick, coriaceous texture of the lamina, the often less dissected lamina, the shallowly crenulate or obtuse teeth and the almost glabrous adaxial lamina surface (hence the specific epithet). In most cases, however, a few long hairs, or small

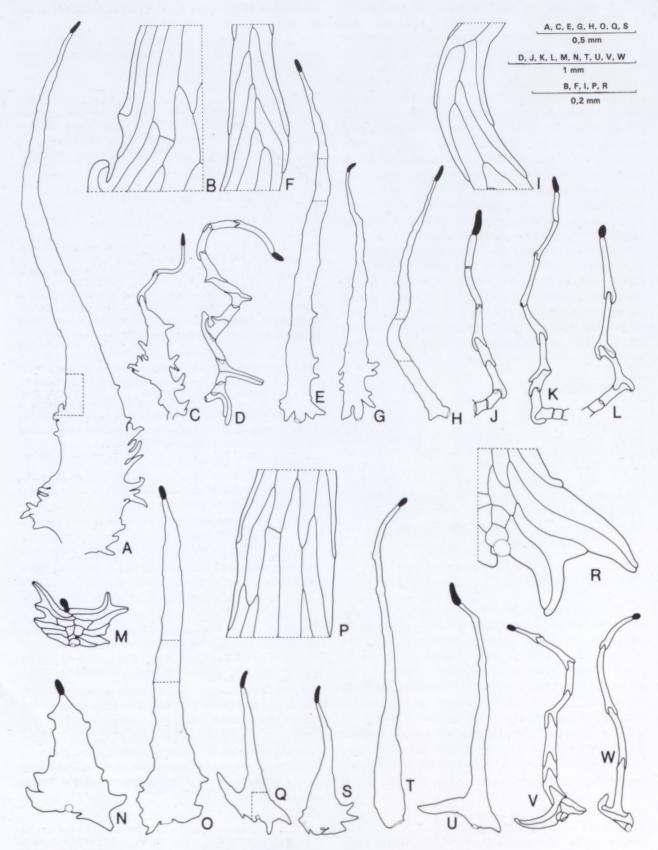


FIGURE 6.—Frond scales in Mohria. A–L, M. vestita, Roux 2219 (NBG). A–D, stipe; E, G, rachis; H–J, abaxial lamina surface; K, L, adaxial lamina surface. M–W, M. nudiuscula, Esterhuysen 14523 (NBG). M–P, stipe; Q–S, rachis; T, U, abaxial lamina surface; V, W, adaxial lamina surface. Scale bars: A, C, E, G, H, O, Q, S, 0.5 mm; D, J–N, T–W, 1 mm; B, F, I, P, R, 0.2 mm.

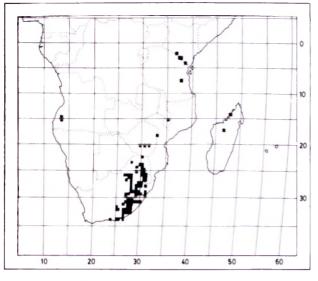


FIGURE 7.-Distribution of Mohria vestita.

scales, may occur adaxially along the secondary rachis; abaxially long filiform scales also occur along the veins on the stipe and rachis. Diagnostic micromorphological characters are the absence of stomata from the adaxial lamina surface, the presence of pericytic and paracytic stomata and the cuticular ridges occurring adaxially along the major veins (Roux *et al.* 1992). Clavate trichomes are $37.0-(50.5)-62.5 \ \mu m$ long and naviculate trichomes are $120.8-(156.4)-190.2 \ \mu m$ long.

Distribution and habitat

Mohria nudiuscula is largely confined to higher elevations with the distribution ranging from the Amatola Mountains in the Eastern Cape, along the KwaZulu-Natal Drakensberg, where this species has been recorded at elevations up to 2 400 m, and along the escarpment between the northeastern Orange Free State and KwaZulu-Natal. It is also widespread throughout the higher parts of Lesotho. Further north it occurs along the mountain ranges between Zimbabwe and Mozambique at elevations ranging up to 2 545 m, the Nyika Plateau in Malawi and the adjacent Rungwe Mountain range in Tanzania. In Zimbabwe, M. nudiuscula also occurs on serpentine-derived soils along the Great Dyke and as far west as the Victoria Falls (Figure 2). The habitat is subject to frequent burns which is evident from the fire scars borne by some collections.

Variation

When material throughout the distribution is viewed, an increase in frond length and pinna number becomes apparent towards the north. Fronds of plants occurring along the higher reaches of the Drakensberg are generally caespitose, firmly coriaceous and less dissected (2-pinnatifid) with the pinnae and pinnules crowded and overlapping. To the north, however, and especially along the mountains in eastern Zimbabwe, the fronds become erect and rigid. They are also more dissected (2-pinnate) with the pinnae and pinnules often distally spaced. The lamina texture along the northern limits of the distribution area also appears to be less coriaceous. Vouchers: Brass 17286 (PRE, SRGH); Brummitt & Synge 65 (SRGH); Last s.n. (K); Nicholson 97 (BOL); Roux 786 & 790 (NBG).

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