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Crassiphyllum (Thamnobryaceae), a new moss genus from Madeira

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ABSTRACT: A morphological study of *Thamnobryum fernandesii* Sérgio, an endemic species of the island of Madeira in Macaronesia, and possible allies, shows that it constitutes a separate, new genus which is described as *Crassiphyllum* Ochyra, *gen. nov.* The only species of this genus *C. fernandesii* (Sérgio) Ochyra is fully described and illustrated. *Thamnobryum* Nieuwl. subg. *Parathamnium* (Fleisch.) Ochyra is briefly assessed and this subgenus is elevated to generic rank as *Parathamnium* (Fleisch.) Ochyra, *comb. nov.*, which includes *Parathamnium ellipticum* (Bosch. & Sande Lac.) Ochyra, *comb. nov.*, and *P. negrosense* (Bartr.) Ochyra, *comb. nov.* Additionally, *Porotrichum latinerve* Mitt. is transferred to *Thamnobryum* as *Th. latinerve* (Mitt.) Ochyra, *comb. nov.*

KEY WORDS: Musci, Thamnobryaceae, rheophytic mosses, taxonomy, Madeira, Macaronesia

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INTRODUCTION

In the early 1950s the Portuguese botanist Peré M. Nóbrega collected in a waterfall on the island of Madeira an aquatic moss which was subsequently determined and reported by Luisier (1953) as *Thamnium angustifolium* Holt [=*Thamnobryum angustifolium* (Holt) Crundw.]. Later this collection was entirely forgotten by bryologists and Furness and Gilbert (1980) seem to be the first, who intended to re-examine it while working on the taxonomic status of *Th. angustifolium*. Although they were unable to study personally the Madeira plant, Dr. C. Sérgio of Lisboa has compared it on their request with authentic British material of *Th. angustifolium* and found it is not the same species. She further stated that the Madeira plant is unlike any other species of the large genus *Thamnobryum* Nieuwl. and recognized it as the new species *Th. fernandesii* (Sérgio 1981). In addition to the plant reported by Luisier (1953) she discovered three other collections of this species from Madeira, but it is otherwise exceedingly rare on the island.

During the course of my revisionary study on the artificial genus *Sciaromium* (Mitt.) Mitt. (Ochyra 1986a) I had to study several rheophytic taxa of the Thamnobryaceae, including *Handeliobryum* Broth. (Ochyra 1986b) and *Limbella* (C. Muell.) Broth. (Ochyra 1987), since some taxa belonging to these genera were given names under this generic

name. In 1985 during the Bryological Meeting at Mont Rigi, Belgium, Dr. C. Sérgio called my attention to the peculiar aquatic species from Madeira and gave me some specimens of it. In addition, I found that the specimen reported as *Thamnium alopecurum* (Hedw.) Schimp. var. *protensum* (Turn.) Limpr. from Madeira by Winter (1914) also represents this species.

When examining *Th. fernandesii* for the first time I immediately associated it with *Touwia laticostata* Ochyra, another monospecific genus of the Thamnobryaceae I had just described from Queensland, Australia (Ochyra 1986c). Although the two species are aquatics and have leaves of comparable shape with broad costae occupying one-third the width of the lamina, I noted several distinct characters which definitely preclude their closer relationship. The absence of sporophytes makes it difficult to assess the interrelationships of *Th. fernandesii*, but the unusual structure of the stipe and branch leaves make it completely different from any other members of the Thamnobryaceae and on that basis alone the species deserves to be recognized as a separate genus as I already suggested elsewhere (Ochyra 1990). For its stiff and thick stipe and branch leaves I call this new genus *Crassiphyllum*.

DESCRIPTION

Crassiphyllum Ochyra *gen. nov. Thamnobryacearum* (Figs 1–24)

Sat robustum, rigidum, dendroideum, dense caespitosum, fuscum vel lutei-brunnescens, nitidum. Caulis primarius repens, secundarius simplex, erectus, usque ad 15 cm altus, stipitatus, in sectione transversa fasciculo centrali distincto, ramis elongatis irregulariter pinnatis, attenuatis vix complanatis, basi foliis squamaeformibus vel triangularibus, appressis, remotis, ecostatis, multistratosibus vestitus. Folia ramulina laxe imbricata, lanceolata vel oblongo-lanceolata, erecta vel erecto-patentia, margine inferne integris, superne et apice argute serrata vel eroso-dentata, nervo crassissimo, ubique aequilato vel inferne latiore, 1/2–3/4 basi folii occupante et in cellulas laminae inconspicue confluente, infra summam apicem folii evanido vel longe excendente, cellulis incrassatis, ovalibus vel hexagono-oblongis, bistratosibus, hic inde unistratosibus. Inflorescentia ut organa sexualia ignota.

Plants dendroid, medium-sized to relatively robust, coarse, stiff, rigid, in dense or loosely tangled mats, yellowish-brown to brown, blackish-brown with age, lustrous, often incrusted with silt and diatoms and then appearing dull. Primary stems stout, stoloniferous, creeping, densely covered with fascicles of blackish-brown, smooth, weakly branched rhizoids on the surface facing the substrate, remotely foliate with small, appressed, scale-like, triangular and mostly denuded leaves; secondary stems erect to ascending, distinctly dendroid from a woody, glossy, stipitate base, usually with varnish luster, in transverse section consisting of about 10 layers of small, cortical cells with the small and round lumina and brown and strongly incrassate walls, grading into 15–20 layers of large, hexagonal, hyaline medullary cells with relatively thick and yellowish-brown to brown walls; central strand small but conspicuous and sharply set off from the adjacent medullary cells; frond copiously, freely, fastigiately and profusely branched; branches erect, non-complanate, usually attenuate, sometimes flagelliform at tips, mostly defoliate in older parts and appearing bristly because of erosion of laminae except for

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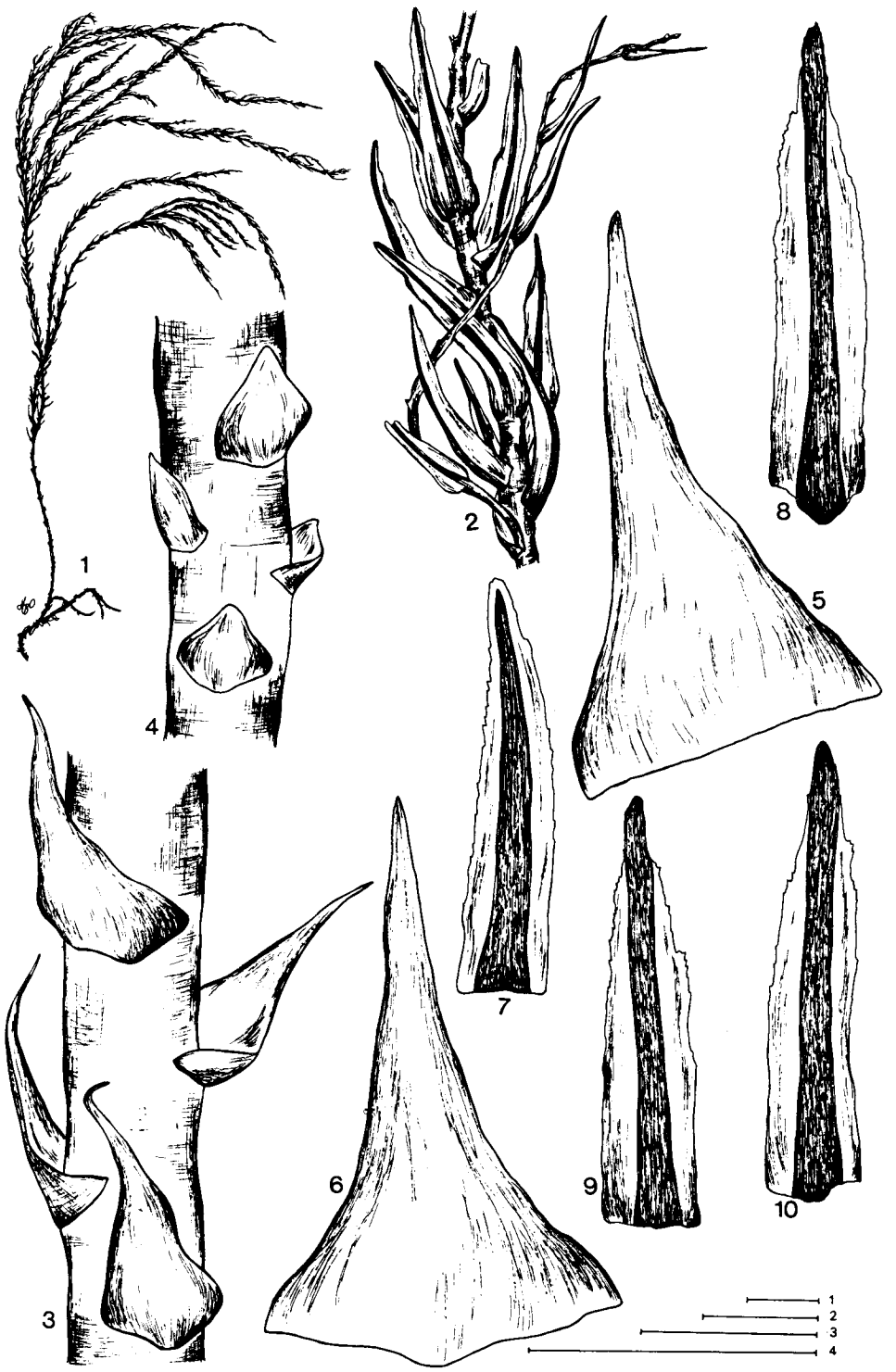
Figs 1–10. *Crassiphyllum fernandesii* (Sérgio) Ochyra. 1: habit; 2: portion of branch; 3: portion of the upper part of the stipe; 4: portion of the lower part of the stipe; 5–6: upper stipe leaves; 7–10: branch leaves. Scale bars: 1 – 1 cm (1); 2 – 1 mm (2); 3 – 1 mm (3, 4); 4 – 1 mm (5–10) (drawn from *Nóbrega*, IX–1950, paratype – KRAM).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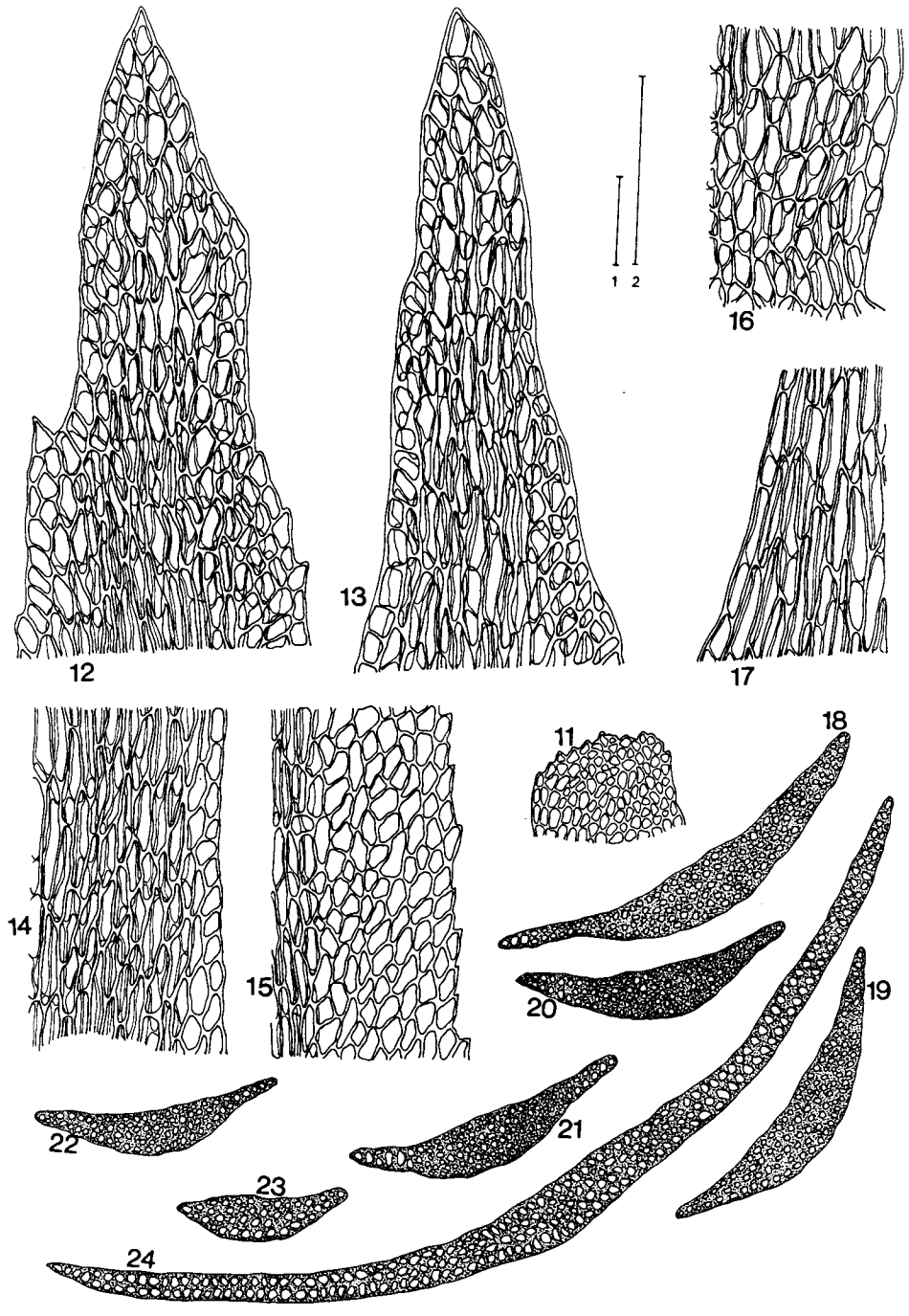

Figs 11–24. *Crassiphyllum fernandesii* (Sérgio) Ochyra. 11: pseudoparaphyllium; 12–13: leaf apices; 14: angular cells of branch leaf; 15: median marginal cells of branch leaf; 16: angular cells of stipe leaf; 17: median marginal cells of stipe leaf; 18–23: transverse section of branch leaves; 24: transverse section of stipe leaf. Scale bars: 1 – 100 μm (11, 18–24); 2 – 100 μm (12–17) (drawn from *Nóbrega*, IX–1950, paratype – KRAM).

stout, bristle-like costae, in transverse section consisting of about 5–7 layers of small, thick-walled, yellowish-brown to brown cortical cells surrounding a smaller medullary area composed of 7–10 layers of large, hexagonal, hyaline cells with relatively thick and yellowish-brown walls and small and conspicuous central strand. Paraphyllia lacking; pseudoparaphyllia foliose, scattered. Lower stipe leaves small, 0.5–0.7 mm wide, 0.8–1.4 mm long, squamose, whitish and looking scarious when dry, non-decurrent, smooth, triangular, short acuminate, bluntly acute, distant, very often eroded or denuded, erect, tightly appressed; upper stipe leaves larger, 0.9–1.1 mm wide, 1.5–3.0 mm long, yellow-brown, gradually or suddenly tapering to a long, fine acumen from very broad basal part, erect to erecto-patent; margins plane, entire or sometimes abruptly notched or coarsely dentate at the apex; discrete costa lacking; lamina cells oblong- to linear-rhomboidal, 10–15 μm wide, 50–120 μm long, thin- to moderately thick-walled, 2–5-stratose throughout much of the lamina, with small, narrow unistratose areas along the margins in the lower half, imperceptibly merging into the multistratose area; cells at the insertion somewhat shorter, with incrassate walls and yellow-brown colouration. Branch leaves rigid and stiff, slightly shrivelled and incurved, loosely imbricate and erect when dry, erecto-patent when wet, 0.35–0.60 mm wide, 1.5–3.0 mm long, lanceolate to oblong-lanceolate, gradually acuminate, acute to bluntly acute, sometimes abruptly cuspidate and malformed or mis-shapen at the apex, not plicate, plane; margins entire below, serrate in the upper half, often abruptly notched or coarsely dentate on 1 or both sides of the cuspidate apex; costa single, yellow to yellow-brown or brown with age, strong, subpercurrent to excurrent as a stout, cuspidate point, very broad, usually occupying 1/2 to 3/4 the leaf base, in transverse section lacking internal differentiation and composed of many layers of small cells with strongly incrassate walls, well-defined above, imperceptibly merging into the lamina cells in the lower half; lamina cells rhombic, rounded-hexagonal to oblong-rhomboidal, 5–12 μm wide, 12–30 μm long, thick-walled, bistratose with occassional unistratose streaks, usually gradually merging into the costa composed of oblong-rhomboidal to linear-rhomboidal cells. Inflorescences and sexual organs unknown.

TYPE SPECIES: *Crassiphyllum fernandesii* (Sérgio) Ochyra, *comb. nov.* Basionym: *Thamnobryum fernandesii* Sérgio, Bol. Soc. Broter. sér. 2, **53**: 1125. *1 t. 1–8.* 1981. Type: Insula Madeira, in saxis innundatis rivuli «João Fernandes», pr. pagum vulgo dictum «Boaventura», ubi die 27–IX–1951 a *Nóbrega* sub n.^{0} 263, collectum (Holotype: MADS, not seen; isotype: S!).

SPECIMENS SEEN ADDITIONAL TO THE TYPE: MADEIRA. Serra da Boaventura, origem da Ribeira de João Fernandes, 8.1951, *Nóbrega s. n.* (S, topotype); vereda que desce do Pico Ruivo para o Caldeirão Verde, IX–1950, *Nóbrega* (KRAM, paratype); vereda entre Caldeirão Verde e Pico Ruivo, Santana, juncto a cascata ass. a *Tham. alopecurum*, 30.6.1982, *Nóbrega, Pita, Santos & Noia 4* (KRAM); im Wasserfall bei Rabaçal, V. 1912, *Winter s.n.* (as *Thamnium alopecurum* var. *protensum*) (KRAM).

DISCUSSION

Although *Crassiphyllum* is established on the basis of sterile material, it is a sound and well-defined genus and its placement in the Thamnobryaceae appears to be unquestionable and all gametophytic character states support this view. Among the features that suggest *Crassiphyllum* be assigned to this family are (1) frondose growth habit; (2) a marked dimorphism between stipe and branch leaves; (3) the lack of paraphyllia; (4) small, isodiametric to slightly elongate upper lamina cells; and (5) coarsely toothed leaf margins at the apex.

Crassiphyllum is a distinct and peculiar genus warranted by the combination of ga-

metophytic characters which make it immediately recognizable from all other thamnobryoid genera. Of these, the most unusual and unique feature is the structure of the stipe leaves, which are multistratose and can be interpreted as lacking a discrete costa. The lamina cells of these leaves are 3–5-stratose in the central part and are visible as a yellow-brown, obscure area with no internal differentiation gradually and imperceptibly diffusing on both sides of the lamina in areas of bistratose cells reaching the margins or occasionally merging in very narrow, obscure and irregular areas of unistratose cells in the lower half.

The multistratose stipe leaves are known only in the monotypic genus *Handeliobryum* Broth. from the Himalayan-Yunnan region. However, the costa in *H. sikkimense* (Par.) Ochyra – the only species of the genus – is well-defined and sharply demarcated from the bistratose lamina, which only occasionally has unistratose strands (Ochyra 1986b). In addition, this taxon is distinct at a glance from *C. fernandesii* by its strongly concave, rigid, oval to oblong-ovate and distinctly limbate branch leaves with broad, salient, 4–6-stratose marginal borders. In all other taxa of the Thamnobryaceae the stipe leaves are without exception unistratose and have distinct costae sharply set off from the laminae.

Crassiphyllum fernandesii is also definitely different from all other taxa of the Thamnobryaceae with regard to the branch leaves. Its lanceolate to oblong-lanceolate branch leaves admittedly resemble those of *Touwia laticostata* of Queensland, Australia (Ochyra 1986c) or *Thamnobryum angustifolium* of the British Isles (Furness & Gilbert 1980), but they are at once distinguishable by their entirely unistratose lamina cells. As well, *C. fernandesii* is very similar habitually and ecologically to some species of *Thamnobryum* from Juan Fernandez Islands on the Southeastern Pacific, including *Th. proboscideum* (Broth.) H. Robins. and *Th. assimile* (Broth.) Sérgio. These species have branch leaves of comparable size and shape and costae of similar texture and occupying at least one-third the width of the lamina. Nevertheless, the lamina cells are totally unistratose in the species from Juan Fernandez whilst those in *C. fernandesii* are bistratose throughout the lamina with only occasional unistratose streaks. This group of species from Juan Fernandez is otherwise an anomalous and discordant element in *Thamnobryum* and its taxonomic status will be dealth with in detail in a forthcoming account. It should be noted only that this complex includes one more species, *Thamnobryum latinerve* (Mitt. *in* Hemsley *in* Murray) Ochyra, *comb. nov.* (Basionym: *Porotrichum latinerve* Mitt. *in* Hemsley *in* Murray, Rep. Sci. Res. Voyage Challenger Bot. 1(3): 81. 1884), which was incorrectly synonymized with *Thamnobryum rigidum* (Mitt.) H. Robins. (Robinson 1975).

Multistratosity of the lamina cells, at least partial, is not rare in the Thamnobryaceae. This family includes many taxa which show the strong predilections for aquatic habitats and multiplication of the layers of lamina cells can be interpreted as a structural adaptation for living in wet environment. Multistratosity of leaves finds most often expression in the form of limbidia, i.e. strongly thickened and distinct marginal borders. They are perfectly developed in *Handeliobryum* and *Limbella* but are also seen in *Thamnobryum* subg. *Parathamnium* (Fleisch.) Ochyra. I discussed at length the taxonomic status of the latter taxon elsewhere (Ochyra 1990) and found it occupies an isolated position within

Thamnobryum, but I hesitated to recognize it as a separate genus. Now I revised my original concept and consider this subgenus as the main discordant element in *Thamnobryum*. The distinctly limbate leaves and the lack of the leaf dimorphism set subgenus *Parathamnium* away from all other species traditionally allied with *Thamnobryum* and these characters seem to be sufficient for splitting *Th. ellipticum* and *Th. negrosense* into their own genus. Accordingly, the following nomenclatural changes are necessary:

Parathamnium (Fleisch.) Ochyra, *stat. et comb. nov.*

Basionym: *Thamnium* Schimp. *in* B., S. & G. sect. *Parathamnium* Fleisch., Musci Fl. Buitenzorg **3**: 930. 1908 ["*Para-Thamnium*"]; – *Thamnobryum* Nieuwl. subg. *Parathamnium* (Fleisch.) Ochyra, J. Hattori Bot. Lab. **68**: 301. 1990.

LECTOTYPE SPECIES: ***Parathamnium ellipticum*** (Bosch. & Sande Lac.) Ochyra, *comb. nov.* Basionym: *Porotrichum ellipticum* Bosch. & Sande Lac., Bryol. Jav. **2**: 70. *190.* 1863.

Parathamnium negrosense (Bartr.) Ochyra, *comb. nov.*

Basionym: *Thamnium negrosense* Bartr., Philip. J. Sci. **68**: 251. *19 f. 314.* 1939.

The modern concept of the Thamnobryaceae was outlined by Brotherus (1925), who considered it as a subfamily of the then all-encompassing Neckeraceae. He placed in it five genera, *Pinnatella* (C. Muell.) Fleisch., *Porotrichum* (Brid.) Hampe, *Porothamnium* Fleisch., *Handeliobryum* Broth. and *Thamnobryum* Nieuwl. (as *Thamnium* B., S. & G.). Since then, several other genera have been added to this family, including *Hydrocryphaea* Dix. (Manuel 1975), *Touwia* Ochyra (Ochyra 1986c), *Limbella* (C. Muell.) Broth. (Ochyra 1987), and *Bryolawtonia* Norr. & Enroth (Norris & Enroth 1990) as well as *Crassiphyllum* and *Parathamnium* in the present article. Nevertheless, additional work is necessary for a refinement of the concept of this family. It is primarily characterized by having the typically hypnaceous peristome whilst in *Pinnatella* and *Hydrocryphaea* frondose growth habit is coupled with the presence of the distinctly neckeraceous peristome. Such a situation obscures the limit between the Neckeraceae and the Thamnobryaceae and suggests the closer interrelationships of these families.

Crassiphyllum fernandesii is a rheophilous moss growing on rocks in streams and waterfalls. The species is exceedingly rare and so far it has been recorded only from four stations on Madeira, where it occurs at higher elevations of 1200–1500 m (Sérgio 1981). Madeira is one of the five Macaronesian archipelagos situated in the eastern part of the Atlantic Ocean. This area has a complex origin and geological history and as a result its present-day flora includes plants belonging to several distinct distribution patterns, of which the most interesting and important are endemic taxa (Sunding 1973, 1979). The bryophyte flora of Macaronesia consists of no less than seven different floristic elements, and endemics constitute about 9% of the total number of taxa (Sérgio 1984). Apart from numerous endemic species, there are four monotypic moss genera that are strictly limited to the Macaronesian region, including *Alophozia* Card., *Tetrastichium* (Mitt.) Card., *Andoa* Ochyra and *Crassiphyllum* Ochyra. The first two indicate the Gondwanan connec-

tions, while the third one clearly shows for the Laurasian affinity of the bryophyte flora of Macaronesia. The case of *Crassiphyllum* is more complex since the genus is related, from one hand, to the Laurasian *Thamnobryum angustifolium*, which is endemic to the British Isles, and from the other hand it shows the clear resemblance to the *Thamnobryum latinerve* complex of Juan Fernandez Islands.

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STRESZCZENIE

Na początku lat 50. portugalski botanik Peré M. Nóbrega zebrał w wodospadzie na Maderze wodny mech, który został oznaczony i opublikowany przez Luisiera (1953) jako *Thamnium angustifolium* Holt [=*Thamnobryum angustifolium* (Holt) Crundw.]. Ponowne zbadanie tych okazów w ćwierć wieku później wykazało, że są one całkowicie różne od roślin z Wysp Brytyjskich i faktycznie należą do osobnego gatunku, który został opisany jako *Thamnobryum fernandesii* Sérgio (Sérgio 1981).

Chociaż kształtem liści i szerokością żebra *Th. fernandesii* przypomina bardzo australijski rodzaj *Touwia* Ochyra, to okazało się, że posiada on dwie wybitne cechy różniące go nie tylko od tego rodzaju, ale od wszystkich innych taksonów Thamnobryaceae. Po pierwsze liście łodygowe są pozbawione żebra; są one prawie całkowicie wielowarstwowe, w części środkowej 3–5-warstwowe, po bokach dwuwarstwowe, a tylko czasami w dolnej części na brzegach jednowarstwowe. Po wtóre liście gałązkowe są całkowicie dwuwarstwowe i tylko niekiedy blaszki są miejscami jednowarstwowe. Ponieważ tego typu kombinacja cech jest unikatowa w całej rodzinie Thamnobryaceae, został opisany nowy rodzaj *Crassiphyllum* Ochyra z jednym tylko gatunkiem *C. fernandesii* (Sérgio) Ochyra (Ryc. 1–24).

Crassiphyllum fernandesii jest pod wieloma względami podobny do grupy gatunków z rodzaju *Thamnobryum* Nieuwl. z archipelagu Juan Fernandez na Pacyfiku i wybrzeży Chile, a mianowicie *Th. proboscideum* (Bröth.) H. Robins., *Th. assimile* (Broth.) Sérgio i *Th. latinerve* (Mitt.) Ochyra, *comb. nov.* Różnią się one jednak od *C. fernandesii* całkowicie jednowarstwowymi blaszkami liściowymi. Wielowarstwowość liści, przynajmniej częściowa, jest zjawiskiem nierzadkim w rodzinie Thamnobryaceae, jako że jest to jedna z cech przystosowawczych do życia w środowisku wodnym, zwłaszcza w wodach płynących. Najczęściej przejawia się ona w formie wielowarstwowego obrzeżenia liści, które znane jest w rodzajach *Limbella* (C. Muell.) Broth. (Ochyra 1987) oraz *Handeliobryum* Broth. (Ochyra 1986b). Występuje ono również u dwóch wschodnioazjatyckich gatunków, *Thamnobryum ellipticum* (Bosch & Sande Lac.) Schu.-Mot. i *Th. negrosense* (Bartr.) Iwats. & Tan, zaliczanych do *Thamnobryum* subg. *Parathamnium* (Fleisch.) Ochyra (Ochyra 1990). Podrodzaj ten różni się ponadto szeregiem cech strukturalnych od podrodzaju typowego *Thamnobryum*, m.in. brakiem zróżnicowania morfologicznego liści łodygowych i gałązkowych, i został tu podniesiony do rangi rodzaju *Parathamnium* (Fleisch.) Ochyra, obejmującego dwa gatunki *P. ellipticum* (Bosch. & Sande Lac.) Ochyra i *P. negrosense* (Bartr.) Ochyra.

Crassiphyllum fernandesii jest gatunkiem reofilnym, endemicznym dla Madery, jednego z pięciu archipelagów wysp określanych mianem Makaronezji. Znany jest tu zaledwie z kilku stanowisk na wysokości 1200–1500 m n.p.m. (Sérgio 1981). Obszar ten ze względu na swe złożone pochodzenie i skomplikowaną historię geologiczną ma niezwykle zróżnicowaną florę roślin naczyniowych (Sunding 1973, 1979) oraz mszaków (Sérgio 1984), obejmujących szereg różnorodnych elementów florystycznych. Wśród mszaków około 9% taksonów to endemity, do których należą również 4 rodzaje mchów, *Alophozia* Card., *Tetrastichium* (Mitt.) Card., *Andoa* Ochyra i *Crassiphyllum* Ochyra.