AN OVERVIEW OF THE GENUS *MARCHESINIA* (MARCHANTIOPHYTA: LEJEUNEACEAE), WITH SPECIAL ATTENTION TO THE SPECIES DESCRIBED FROM ASIA AND OCEANIA

S. ROBBERT GRADSTEIN

Abstract. Marchesinia Gray is a small genus of Lejeuneaceae subfam. Ptychanthoideae (Marchantiophyta) with eight species in two subgenera, one species in the atlantic-mediterranean subg. Marchesinia and seven in the tropical Afro-American subg. Marchesiniopsis. The checkered taxonomic history of the genus is briefly reiterated and the identities of three hitherto neglected taxa described from eastern Asia (M. gigantea Steph., M. sikkimensis Steph.) and Hawaii (M. mittenii A. Evans) are clarified based on examination of type material. Marchesinia gigantea is a synonym of Spruceanthus repandus (Nees) Verd. (new to Myanmar), M. sikkimensis is a synonym of Trocholejeunea infuscata (Mitt.) Verd. and M. mittenii is a synonym of the Afro-American Marchesinia brachiata (Sw.) Schiffn. The latter record extends the known distribution of M. brachiata to Hawaii and adds a further example of a bryophyte with a Neotropics–Hawaii range. Dicranolejeunea annobonensis S. Arn. from W Africa is reduced to a synonym of M. excavata (Mitt.) Schiffn. A conspectus of the genus Marchesinia and a key to the eight species in the genus are provided.

Key words: Dicranolejeunea annobonensis, Eastern Asia, Hawaii, Lejeuneaceae, liverworts, Marchesinia brachiata, Marchesinia gigantea, Marchesinia mackaii, Marchesinia mittenii, Marchesinia sikkimensis, Neotropics-Hawaii distribution, taxonomy

S. Robbert Gradstein, Muséum National d'Histoire Naturelle, Department Systématique et Evolution, Case Postale 39, 57 rue Cuvier, 75231 Paris cedex 05, France, gradstein@mnhn.fr

INTRODUCTION

Marchesinia Gray is a small liverwort genus of Lejeuneaceae subfamily Ptychanthoideae (Gradstein 1994; Wilson et al. 2007) with a checkered taxonomic history, which may be briefly reiterated. Originally spelled 'Marchesinius' (or 'Marchesinus') - after Joannes Gregorius Marchesinius, professor of medicine at the University of Florence in the early 18th century and one of the sponsors of P. A. Micheli's Nova Plantarum Genera (1729) – the genus was established in 1821 by the British naturalist Samuel Frederick Gray for the inception of a liverwort species described a few years earlier from the British Isles by William J. Hooker (1813) under the name Jungermannia mackaii Hook. (= Marchesinia mackaii (Hook.) Gray) (Fig. 1). Marchesinia mackaii is a locally frequent, atlantic-mediterranean taxon of western and southern Europe and Macaronesia, reaching

southwards to the Cape Verde Islands. In addition, the species occurs disjunctly on the Arabian island of Socotra (Kürschner 2000).

Almost at the same time, and unknowingly, the Belgian botanist and politician Barthélémy Charles (Comte) Dumortier (1822) created the genus *Phragmicoma* for *Jungermannia mackaii* Hook. The almost simultaneous publication of *Marchesinia* and *Phragmicoma* coincided with efforts by several workers in the early 19th century to split the large Linnean genus *Jungermannia*, which at the time comprised almost all species of leafy and simple thalloid liverworts, into more homogeneous genera (Schuster 1966). As the name '*Marchesinius*' due its male gender was considered inappropriate for a plant genus at that time, the name *Phragmicoma* Dumort. has been in use during much of the 19th century and no less than 114 (including 3 fossil) species were validly ascribed to it (Zijlstra 1989). The genus, defined by undivided underleaves and a more or less compressed perianth, was clearly a very artificial group and its species are nowadays placed in 26 different genera (Geissler & Gradstein 1994).

In 1865, Gray's generic name was resurrected by the British botanist William Carruthers, as Marchesinia Gray corr. Carruth., and the name Phragmicoma was reduced to synonymy. Twenty years later, the modern generic concept of Marchesinia was established by Richard Spruce in his masterly Hepaticae Amazonicae et Andinae (Spruce 1884–1885). Spruce treated Marchesinia as a subgenus of the large genus Lejeunea (subg. Homalejeunea) and characterized the group by the very flat, smooth perianth subtended by two repeatedly fertile, Radula-type innovations, the androecia on elongated branches, the frequently toothed leaf apex, and the undivided underleaves. Further diagnostic features added by later authors (e.g., Evans 1907; Gradstein & Geissler 1994) include the glossy dark-green to brown or black plant color, the robust stems with vegetative branches exclusively of the Lejeunea-type, the elongate leaves made up of isodiametric cells with radiate trigones, the rather flat lobules with 1-4 teeth, the non-articulate seta made up of 20 or more cell rows (15-25 outer rows, 4-20 inner rows) and its explosively dehiscent, 'ptychanthoid' capsule with a fenestrate layer of thickening on the inner surface of the valves, 72 elaters with well-developed spiral bands, and isodiametrical spores (van Slageren & Berendsen 1985). Chemically, the group stands out by the elaboration of eugenol-derivates and luteolin di-C-glycosides (Gradstein et al. 1981; Kruijt et al. 1986). Molecular-phylogenetic evidence has shown that Marchesinia is one of the basalmost genera in the family Lejeuneaceae (subfam. Ptychanthoideae), being a member of the basal lineage 'A1' together with the genus Frullanoides (Wilson et al. 2007). The genus is nowadays considered well-defined and most recent work has focused on species definition in Marchesinia, which has been considered difficult and has varied among authors.

Spruce (1884) included seven species in his

subg. Homalolejeunea, five from tropical America, one from Africa and Marchesinia mackaii from Europe. The fact that all of these species except one are still accepted today shows the exceptionally high quality of Spruce's work. It should be noted that Spruce was the first bryologist to study tropical species in the field. Before him, these species had generally been described based on dried herbarium material. Indeed, none of his predecessors including Hooker, Gottsche, Lindenberg, Nees von Esenbeck, Montage, Taylor, Mitten etc., had seen the tropics with the exception of the Swedish botanist Olov Swartz, nor had they been able to observe the species in the field, study their growth forms and branching patterns, their colors, habits etc. (Gradstein 1996). As Barbara Thiers wrote in her introduction to the reprint of Spruce's book: 'Hepaticae Amazonicae et Andinae displays a level of sophistication far beyond that of Spruce's predecessors or contemporaries in the field of 'exotic' hepaticology' (Thiers 1984).

The subgenus *Homalolejeunea* was soon elevated to generic rank with resurrection of the name *Marchesinia* (Schiffner 1893), and was considerably expanded by Franz Stephani in his *Species Hepaticarum* (Stephani 1912). The poor quality of this work and its negative consequences for hepaticology have been pointed out repeatedly (e.g., Verdoorn 1934; Gradstein 2006) and need not be related here. Stephani attributed 26 species to *Marchesinia*, half of them new to science: 4 from Africa (1 new), 18 from tropical America (10 new), 3 from Asia and Oceania (2 new), and 1 from Europe (*Marchesinia mackaii*).

The neotropical species were revised by Gradstein (1994) and Gradstein and Geissler (1994), who showed that they were a heterogeneous lot and included members of at least five different genera: Acanthocoleus, Archilejeunea Cheilolejeunea, Frullanoides and Marchesinia. The authors accepted only two species in tropical America, M. robusta (Mitt.) Schiffn. and the polymorhic M. brachiata (Sw.) Schiffn. Subsequent chemical, ecological and molecular evidence indicated the existence of a third neotropical species in lowland areas, M. bongardiana (Lehm. & Lindenb.) Trevis. (Geissler 1990; Schoeneborn 1996;



Fig. 1. Original illustration of *Jungermannia mackaii* Hook. (W. J. Hooker, *British Jungermanniae*, Part 14, Table 53. 1813) ≡ *Marchesinia* (subg. *Marchesinia*) mackaii (Hook.) Gray.

Geissler & Maier 1999; Gradstein 2008; Heinrichs *et al.* 2009). *Marchesinia bongardiana* had been considered a synonym of *M. brachiata* for more than a hundred years (e.g., Stephani 1890; Schiffner 1897; Evans 1907). In the Galapgos islands *M. bongardiana* it is a distinct taxon, occuring at lower elevations and in dryer environments than *M. brachiata* and being usually sterile or male, reproducing copiously by caducous leaves or leaf fragmentation (Gradstein 2008). Elsewhere, the morphological distinction between *M. bongardiana* and *M. brachiata* may be less clear and intermediate phenotypes occur.

Based on molecular analysis, Heinrichs et al. (2009) found evidence for the existence of a further neotropical species, M. languida (Nees & Mont.) Steph., at high elevations. The latter differs from typical M. brachiata by having leaves with long ciliate teeth. Heinrichs et al. (2009) were also able to postulate a diversification of the neotropical Marchesinia species since the Late Oligocene, based on Miocenic fossil material described by Gradstein (1993) coupled with the molecular evidence. The authors were not able, however, to reconcile the large morphological variation in the M. brachiata-bongardiana-languida complex with the molecular results. Moreover, the taxonomic status of the numerous synonyms in this complex remained unresolved. This clearly needs more work.

The African *Marchesinias* were revised by Vanden Berghen (e.g., 1948, 1976) and Jones (1970; Wigginton 2004), who recognized three species: *M. excavata* (Mitt.) Schiffn., *M. madagassa* Steph. (with several synonyms) and the rare *M. deslooveri* Vanden Berghen from high mountains in Rwanda and Tanzania. In addition, *Marchesinia brachiata* has recently been reported from Africa where it is known from St. Helena (Geissler & Gradstein 1994) and Kenya (Heinrichs *et al.* 2009).

The species of *Marchesinia* from Asia and Oceania, including *Marchesinia gigantea* Steph. from Myanmar, *M. sikkimensis* Steph. from Sikkim and *M. mittenii* A. Evans from Hawaii, have not been studied since their original description. All three species are only known from type material. The main purpose of this paper is to clarify their taxonomic identity. The results, based on examination of the type specimens, are presented below.

RESULTS AND DISCUSSION

1. Spruceanthus semirepandus (Nees) Verd.

Ann. Bryol. Suppl. 4: 153. 1934. – Jungermannia semirepanda Nees, Enum. Pl. Crypt. Jav.: 39. 1830. TYPE: Java, Blume s.n. (HOLOTYPE, STR!; ISOTYPES, L!, S!). = Marchesinia gigantea Steph., Spec. Hepat. 5: 154. 1912. TYPE: Myanmar ('Birma'), Aracan Hills, 1888, Micholitz s.n., sterile (HOLOTYPE, G 19983!), syn. nov.

Although Stephani (1912) described the gynoecia of *Marchesinia gigantea*, the fragmentary type material of the species in the Stephani Herbarium in Geneva is sterile. Nevertheless, the material represents typical *Spruceanthus semirepandus*. The latter species seems to have not been reported previously from Myanmar and is apparently new to that country. As the species is known from neighboring countries (e.g., Verdoorn 1934; Lai *et al.* 2008), the occurrence of *Spruceanthus semirepandus* in Myanmar was to be expected.

2. Trocholejeunea infuscata (Mitt.) Verd.

Ann. Bryol. Suppl. **4**: 190. 1934; Mizutani (1989: 271). – *Lejeunea infuscata* Mitt., Proc. Linn. Soc. London **5**: 111. 1861. LECTOTYPE (designated here): Nepal, *Wallich s.n.* (NY, n.v., *fide* Mizutani 1989).

= Marchesinia sikkimensis Steph., Spec. Hepat. **5**: 155. 1912. TYPE: Sikkim (Himalaya), [*leg. Evans s.n.*, fide Stephani, Icon. Ined. 6698], ex herb. Kew, sterile (HO-LOTYPE, G 19984!), *syn. nov.*

The conspecificity of *Marchesinia sikkimensis* and *Trocholejeunea infuscata* was already noted *in sched.* (1988) by the late Patricia Geissler. *Trocholejeunea infuscata* is a widespread Himalayan species occurring at elevations ranging between 1500–2500 m. The species has been described over and over again by Stephani in at least eight (!) different genera (*Acrolejeunea*, Brachiolejeunea, Dicranolejeunea, Homalolejeunea, Lopholejeunea, Marchesinia, Omphalanthus, Ptychocoleus), and was finally assigned to the new genus Trocholejeunea by Schiffner (1932). The type material of Marchesinia sikkimensis is a phenotype of T. infuscata with long, somewhat attenuate branches.

3. Marchesinia brachiata (Sw.) Schiffn.

in Engler & Prantl, Nat. Pflanzenfam. **1**, 3: 128. 1893; *Jungermannia brachiata* Sw., Nova Gen. Spec. Pl. Prodr.: 144. 1788. TYPE (Gradstein & Geissler 1994): Jamaica, *Swartz s.n.* (HOLOTYPE, S!; ISOTYPE, BM!, E!, S!). (Fig. 2).

= *Marchesinia mittenii* A. Evans, Trans. Connect. Acad. **10**: 422. 1900. TYPE: Hawaii ['Sandwich Is'], unknown locality, *Hillebrand s.n.*, 'taken out from a mixture with *Lej. subnuda*' [= the type specimen of *Lopholejeunea subnuda* (Mitt.) A. Evans], c. per. (LECTOTYPE, NY 01059494!; ISOLECTOTYPE, NY 01059495!), *syn. nov.*

Marchesinia mittenii is only known from the type material, which was part of a mixed collection and included also the type specimen of Phragmicoma subnuda Mitt. (= Lopholejeunea nigricans (Lindenb.) Schiffn.; Zhu & Gradstein 2005). The type material of M. mittenii (NY) consists of two sheets, each containing well-developed female plants in considerable quantity. I have chosen the sheet containing the most copious material (in two packets) and a sketch and brief description of M. mittenii, as the lectotype. Evans (1900) described the species as lacking perianths but I found one mature perianth in the lectotype. The plants obviously belong to Marchesinia and are briefly described here. They are apparently dioicous (androecia were not seen) and robust, with leafy shoots to 4 mm wide, stems 0.30-0.35 mm in diameter and ventral merophytes ca 10 cells wide. The leaves are imbricate and oblong, ca 2 mm long and 1.8 times as long as wide, and with a broadly rounded, entire to short apiculate apex, which occasionally (in a few leaves) bears 1-2 small, additional teeth on each side of the apex. The lobules are small (to 0.4 mm long) and provided with 3-4 small, one-celled teeth along the free margin. The underleaves are large and imbricate, $5-6 \times$ stem width, the underleaf margins are narrowly recurved and entire, and the insertion line is deeply arched (*ca* 0.4 mm deep); the margins are gradually narrowed in the lower half and long-decurrent, with a small auricle at the very base. The female bracts and bracteole (in one series) are toothed, the bract lobule is very small and reduced to a fold along the bract margin, and the bracteole is short bifid. The perianth, finally, is long exserted, to 4 mm long, obovate-oblong, very flat and with a wide and entire, truncate mouth.

The material of M. mittenii is morphologically similar to Marchesinia brachiata s.str. as defined by Heinrichs et al. (2009) and should be considered a synonym of the latter. Marchesinia brachiata s.str. (Fig. 2) is widespread in tropical America and also occurs in Africa (see above). The conspecificty of M. mittenii and M. brachiata extends the known distribution of M. brachiata to Hawaii and adds a further example of a bryophyte with a Neotropics-Hawaii range, besides e.g., Plagiochila deflexa Mont. & Gottsche (Heinrichs et al. 2002) and Streptopogon erythrodontus (Taylor) Mitt. (also Africa, like M. brachiata). The Hawaiian material of M. brachiata, collected in the mid 19th century by the Hawaiian plant collector William Hillebrand (http://en.wikipedia.org/ wiki/William Hillebrand), is the only gathering of M. brachiata known from Hawaii. The material is copious and the species that occurred mixed in the packet (Evans 1900), Lopholejeunea nigricans, is widespread in the Hawaiian archipelago (Staples & Imada 2006). It is unlikely, therefore, that the material was mislabelled; an effort should be made to confirm the presence of M. brachiata in Hawaii.

Its occurrence in the Hawaiian archipelago concurs with the suitability of the spores of the species for long-range dispersal (van Zanten & Gradstein 1988).

CONCLUSIONS AND CLASSIFICATION

This study has shown that *Marchesinia* is distributed in Europe, Africa, tropical America and the Pacific region. The conspecificity of *M. mittenii* and *M. brachiata* has extended the distribution of the Afro-American *M. brachiata* to Hawaii. The



Fig. 2. *Marchesinia* (subg. *Marchesiniopsis*) *brachiata* (Sw.) Schiffn. A – habit, with three gynoecia and one androecial shoot, B – leaf, C – lobule free margin, D – underleaves, E – gynoecial bracts and bracteole, F – leaf cells. From Galapagos Is., Isabela, volcán Alcedo, 1100 m, van der Werff 1439 (U); after Gradstein and Geissler (1994).

records of *Marchesinia* from continental eastern Asia are erroneous and belong to other genera of Lejeuneaceae.

Currently, eight species are recognized in Marchesinia, in two subgenera (Schuster 1992, footnote!): subg. Marchesinia with M. mackaii and subg. Marchesiniopsis R. M. Schust. containing the remaining species. The two groups are distinguished by their different cell wall thickening patterns, oil bodies, underleaf insertions and distributional ranges (see below). Geissler and Maier (1999), in addition, showed that the two subgenera differ by characters of the spores and elaters. Species of subg. Marchesiniopsis have spores with distinct rosettes and elaters with 1-2spiral bands in the outer wall, being clearly visible with the light microscope and SEM. By the distinct rosettes and spiral bands, spores and elaters in subg. Marchesiniopsis are quite similar to those of other genera of Ptychanthoideae. Marchesinia mackaii (subg. Marchesinia), however, stands out by having spores with indistinct rosettes and elaters with a highly compressed spiral band, which is embedded within the strongly thickened wall of the elater. Spores with indistinct rosettes are found in many members of Lejeunoideae but not in Ptychanthoideae (Weis 2001). The embedded spiral band of the elaters, visible with the light microscope but not with SEM, has not been observed in any other species of Lejeuneaceae and seems to be unique to M. mackaii. Geissler and Maier (1999) furthermore found that species of the subg. Marchesiniopsis have different elaters. In M. excavata the elater is only twice as wide as the spiral while in the other species the elater is 4 to nearly 8 times as wide as the spiral. Moreover, the outer wall of the elater is quite thin in M. brachiata but thickened in M. madagassa, M. deslooveri and M. robusta. Geissler and Maier' work is of considerable importance for Lejeuneaceae systematics as it has for the first time demonstrated the taxonomic relevance of sporophyte characters at the infrageneric level. Previously, sporophytes were considered taxonomically informative only at suprageneric level (van Slageren & Berendsen 1985; see also Weis 2001 and Gradstein et al. 2003).

KEY TO THE SPECIES OF *MARCHESINIA* AND CONSPECTUS

Users of this key should note that the morphological differences between the neotropical species of the *Marchesinia brachiata* complex (*M. bongardiana*, *M. brachiata*, *M. languida*) are still unresolved and that intermediate forms do occur, which may not be identifiable with this key.

1. Trigones of leaf cells simple-triangular or lacking. Underleaf insertion shallowly curved. Oil bodies coarsely segmented, Calvpogeia-type. Spores without distinct rosettes. Europe, Macaronesia, Socotra (subg. Marchesinia) M. mackaii 1^{*} Trigones of leaf cells radiate. Underleaf insertion deeply arched. Oil bodies \pm homogeneous, *Bazzania*-type. Spores with distinct rosettes. Tropical America, tropical Africa, Hawaii (subg. Marchesiniopsis) 2 2. Underleaf apex toothed. Tropical America M. robusta 3. Leaf apex coarsely toothed by long and sharp teeth, the teeth (1–)2–10 cells long M. languida 3.^{*} Leaf apex entire or finely toothed, the teeth 1(-2)cells long 4 4. Well-developed lobules with only 1 tooth. Leaf apex apiculate. Caducous leaves lacking. Elaters narrow, only twice as wide as the spiral band. W Africa M. excavata 4.^{*} Well-developed lobules with (1-)2-4 teeth. Leaf apex rounded-entire or apiculate. Caducous leaves present or lacking. Elaters 4-8 times as wide as the spiral band. 5 5. Leaf apex rounded-entire. Underleaf margins plane. Female bracts and bracteole entire. E Africa (rare in W Africa) M. madagassa 5.* Leaf apex mostly apiculate to short acuminate (a few leaf apices may be rounded-entire). Underleaf margins recurved or plane. Female bracts and bracteole 6. Plants 1-2 mm wide, often sterile, dioicous. Leaves distant to subimbricate. Underleaves short decurrent, plane. Caducous leaves usually present. Tropical America M. bongardiana 6.* Plants 2-4 mm wide, often fertile, autoicous or dioicous. Leaves imbricate. Underleaves long decurrent, apex often recurved. Caducous leaves

- 7.* Margin of underleaf bases not undulate. Plants 2.0–3.5(-4.0) mm wide. Autoicous or dioicous. Tropical America, E Africa, St. Helena, Hawaii; 500–3300 m *M. brachiata*

Marchesinia Gray subgenus Marchesinia

TYPE: M. mackaii (Hook.) Gray (Fig. 1)

Cell walls thin or evenly thickened, trigones lacking or very small, simple triangular, not radiate. Oil bodies rather coarsely segmented with globules to 2 μ m in diameter, *Calypogeia*-type. Underleaf insertion rather shallowly curved. Spores without distinct rosettes. Spiral band of the elaters embedded within the thick elater wall (Geissler & Maier 1999). Autoicous.

DISTRIBUTION AND HABITAT. See under *M. mackaii*.

1. Marchesinia mackaii (Hook.) Gray

ILLUSTRATIONS: Hooker (1813: Tab. LIII; this paper: Fig. 1); Smith (1990: p. 279, Fig. 124); Paton (1999: p. 482, Fig. 237); Kürschner (2000: p. 506, Fig. 3, distribution map); Casas *et al.* (2009: p. 148, Fig. 54).

Atlantic-mediterranean species in W and S Europe, Macaronesia S to Cape Verde Islands, Socotra; on bark of trees and shrubs and on calcareous or somewhat acidic rock, in sheltered or exposed, oceanic habitats, 0–500(–1500) m (e.g., Geissler 1990; Birks 1991; Dierssen 2001). Monoicous.

Marchesinia Gray subgenus *Marchesiniopsis* R. M. Schust.

TYPE: M. brachiata (Sw.) Schiffn. (Fig. 2)

Cell walls thin, trigones radiate. Oil bodies \pm homogeneous, *Bazzania*-type. Underleaf insertion deeply arched. Spores with distinct rosettes. Spiral band(s) of the elaters not embedded within the elater wall (Geissler & Maier 1999). Autoicous or dioicous.¹

DISTRIBUTION AND HABITAT. Tropical America, tropical Africa, Hawaii, 0–3300 m; on bark in canopy and understory of primary and secondary evergreen and semi-deciduous moist tropical forests, also in humid scrubby vegetation and in plantations, usually growing in partial shade; occasionally on living leaves or on rock (Gradstein & Geissler 1994; Geissler 1997; Wigginton 2004).

1. *Marchesinia bongardiana* (Lehm. & Lindenb.) Trevis.

ILLUSTRATION: Herzog (1955: p. 174, Fig. 11, as *M. aquatica* Herzog); Geissler (1990: p. 357, Fig. 1, distribution map).

Widespread in tropical America, 0–1400 m. Dioicous.

2. Marchesinia brachiata (Sw.) Schiffn.

ILLUSTRATIONS: Evans (1900: Pl. XLVIII, figs. 12–14, as *M. mittenii*; 1907: Pl. 32); Gradstein & Geissler (1994: p. 105, Fig. 29); this paper: Fig. 2.

Widespread in tropical America; in addition on St. Helena, in E Africa (Kenya) and on Hawaii; 500–3300 m. Autoicous or dioicous.

3. Marchesinia deslooveri Vanden Berghen

ILLUSTRATION: Vanden Berghen (1976: p. 927, Fig. 2).

Rare species of E Africa (Rwanda, Tanzania), above 1900 m. Autoicous. Very similar to *M. brachiata* and may be a subspecies or synonym of the latter.

4. Marchesinia excavata (Mitt.) Schiffn.

Dicranolejeunea annobonensis S. Arn., Svensk Bot. Tidskr. 50: 531. 1956, syn. nov.

TYPE: Annobon, Santa Mina, *ca* 650 m, on stem of *Cyathea, Byström* 605 [UPS, n.v.]).

ILLUSTRATION: Arnell (1956: p. 531, Fig. 2); Wigginton (2004: p. 267, Fig. 174). Judging from the original

¹ According to Schuster (1992), subg. *Marchesiniopsis* also differs from subg. *Marchesinia* by having toothed female bracts (entire in subg. *Marchesinia*). However, entire female bracts are also found in *M. madagassa* and, occasionally, in *M. brachiata* s.l. (both members of subg. *Marchesiniopsis*).

description and illustration (Arnell 1956), *Dicranole-jeunea annobonensis* is a toothed-leaved form of *M. excavata*.

W and C Africa, at rather low elevations, 100–1500 m. Dioicous.

5. Marchesinia languida (Nees & Mont.) Steph.

ILLUSTRATION: Spruce (1884–1885: Tab. IV, as *Lejeunea* palaeflora Spruce); Stephani (1985: Fig. 6679).

Mountains of C and S America, above 1500 m. Dioicous.

6. Marchesinia madagassa Steph.

ILLUSTRATION: Vanden Berghen (1984: pp. 8–9, Figs. 1–2, as *M. obtusifolia* Vanden Berghen); Wigginton (2004: p. 268, Fig. 175).

Mountains of E Africa (very rare in W Africa), 1000–2000 m, at 500 m on La Réunion. Dioicous.

7. Marchesinia robusta (Mitt.) Schiffn.

ILLUSTRATION: Herzog (1955: p. 173, Fig. 10).

Mountains of C and S America, 650–2500 m. Dioicous.

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