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Abstract. To date, five species of *Ceratolejeunea* are known from the East African Islands: *C. belangeriana* and *C. calabariensis* from a number of localities, *C. variabilis* from three, and *C. papuliflora* and *C. umbonata* from single stations. This paper newly establishes the synonymy of *C. calabariensis* with the Neotropical *C. cornuta* and of *C. stictophylla* with *C. papuliflora*, and reports several additional localities of the latter species. *Ceratolejeunea diversicornua*, previously known from West Africa only, is reported from Madagascar, and *C. andringitrae* and *C. saroltae* are described as new to science. A key to the species of *Ceratolejeunea* from the Indian Ocean Islands is provided. The taxonomic position of *C. boschiana* remains uncertain.

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EAST AFRICAN BRYOPHYTES XXIX. THE *CERATOLEJEUNEA* (LEJEUNEACEAE) SPECIES OF THE INDIAN OCEAN ISLANDS

TAMÁS PÓCS

Abstract. To date, five species of *Ceratolejeunea* are known from the East African Islands: *C. belangeriana* and *C. calabariensis* from a number of localities, *C. variabilis* from three, and *C. papuliflora* and *C. umbonata* from single stations. This paper newly establishes the synonymy of *C. calabariensis* with the Neotropical *C. cornuta* and of *C. stictophylla* with *C. papuliflora*, and reports several additional localities of the latter species. *Ceratolejeunea diversicornua*, previously known from West Africa only, is reported from Madagascar, and *C. andringitrae* and *C. saroltae* are described as new to science. A key to the species of *Ceratolejeunea* from the Indian Ocean Islands is provided. The taxonomic position of *C. boschiana* remains uncertain.

Key words: *Ceratolejeunea*, Comoro, Indian Ocean Islands, Madagascar, Mascarenes, Seychelles

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INTRODUCTION

The genus *Ceratolejeunea*, with ca 40 species, is distributed exclusively in the tropics. Its species occur on various substrates, mostly bark and living leaves. The name of the genus refers to the horned perianths of its members. The coloring of the genus varies from dark brown to olive, with a dull shine that is quite rare among Lejeuneoideae and is more typical of the Ptychanthoideae subfamily. The genus was established by Jack and Stephani (1892) from the subgenus *Cerato-Lejeunea* defined by Spruce (1884–1885). The following characters distinguish the *Ceratolejeunea* species from other Lejeuneoideae: their special color and shine; their imbricate leaves which frequently present utriculi and generally have various types of ocelli in the lobe; their small, single-toothed, inflated lobule; their predominantly bilobed underleaves (subgen. *Caduciloba* R. M. Schust. – though the underleaves are entire in the small subgen. *Ceratolejeunea*); by their *Lejeunea*-type branching; and their usually four-horned perianths with Pycnolejeuneoid innovation. In terms of continental distribution, America is the richest, with 23 species (Dauphin 2003a) to which two more have recently been added, one by Ilkiu-Borges and Alvarenga (2008) and the other by Reiner-Drehwald (2011).

From continental Africa, Vanden Berghen (1951, 1973) identified eight species. Five species have been identified from the East African Indian Ocean Islands (Grolle 1995; Pócs 1995; Pócs & Geissler 2002; Wigginton 2009). Some 15 species are known from Asia and the Pacific, some of which have been revised by Mizutani (1981). The exact number of all *Ceratolejeunea* species is not known, as only the Neotropical species have been monographed recently; a revision of species on other continents is much needed.

In the course of several collecting excursions throughout East African Islands from the Seychelles and Comoros to different parts of Madagascar and the Mascarenes (Réunion and Mauritius), and with contributions from my colleagues (from EGR, MO, NAI, EA and TANA), I have assembled a rich collection of *Ceratolejeunea* species. So far only a smaller portion of these materials have been revised, the results of which are summarized below.

On the basis of this initial revision, seven species can be said with certainty to occur in the area: *Ceratolejeunea andringitrae* Pócs sp. nov., *C. belangeriana* (Gottsche) Steph., *C. cornuta* (Lindenb.) Steph., *C. diversicornua* Steph.,

C. papuliflora Steph., *C. saroltae* Pócs *sp. nov.* and *C. umbonata* Steph. It is also clear that *C. calabariensis* Steph. and *C. variabilis* (Lindenb.) Schiffn. are synonyms of *C. cornuta*, and *C. stictophylla* Herzog a synonym of *C. papuliflora*. Although Grolle (1995) synonymized *C. boschiana* Steph. with *C. belangeriana*, its taxonomic position remains uncertain.

SPECIES KNOWN FROM THE EAST AFRICAN ISLANDS

1. *Ceratolejeunea belangeriana* (Gottsche) Steph.

Spec. Hep. 5: 396. 1913.

BASIONYM: *Lejeunea belangeriana* Gottsche in Gottsche *et al.*, Syn. Hep.: 398. 1845. TYPE: Mauritius, *Belanger s.n.* (Fragment only in G. ex hb. Lehmann).

IMPORTANT SYNONYMS

Lejeunea mascarena Steph., Bot. Gazette 15: 284. 1890, *Ceratolejeunea mascarena* (Steph.) Steph., Spec. Hep. 5: 397. 1913 (fide Grolle 1995).

Lejeunea mauritiana Steph., Bot. Gazette 15: 285 & 349. 1890, *Ceratolejeunea mauritiana* (Steph.) Steph., Hedwigia 31: 205. 1892 (fide Grolle 1995).

Lejeunea oceanica Mitt. in Seemann, Fl. Vitiensis: 414. 1871, *Ceratolejeunea oceanica* (Mitt.) Steph., Bot. Jahrb. Syst. 23: 310. 1897 (fide Zhu *et al.* 2005). Further synonymy of *C. oceanica* see in Mizutani (1981).

ILLUSTRATIONS: Bonner (1953: 169, Fig. 8; 1953: 215, Fig. 58 under *C. mascarena*), Schiffner in Engler & Prantl (1893: 126 under *C. mascarena*), Stephani (1890: 284; Pl. xvii, fig. 5), Bonner (1953: 169, Fig. 8 and 1953: 215, Fig. 58), Mizutani (1981: 306, Fig. 1, under *C. oceanica*), Herzog in Herzog and Noguchi (1955: 47, Fig. 11h–m under *C. exocellata* Herz.) and Amakawa (1970: 180, Fig. 28 under *C. ryukyuensis* Amak.).

According to the protologue and the above-cited illustrations, what distinguishes *Ceratolejeunea belangeriana* from the more widespread *Ceratolejeunea cornuta* is the length of its perianth. The perianth of *C. belangeriana* reaches up to 1.4 mm in length, as it has an attenuate, quasi-stalked, narrow conical base exerting it well above (more than half its length) the perichaetial leaves. Without the perianth it is difficult to dis-

tinguish *C. belangeriana* from *C. cornuta*. More Asian and Pacific populations need to be examined to determine whether *C. belangeriana* really merits species rank. If its perianth length remains the only difference, it should be distinguished at subspecific rank under *C. cornuta*. Mizutani (1981) differentiates *C. maritima* (= *C. cornuta*) from *C. oceanica* (= *belangeriana*) by its highly inflated, spherical lobules and its few-branched, usually long stems. *C. belangeriana* was previously known as widespread in the East African Islands only, but reports of its occurrence in the whole of Indomalaya and Oceania have been published more recently (Miller *et al.* 1983; Zhu *et al.* 2005).

DISTRIBUTION. Comores, Madagascar, Seychelles, Réunion, Mauritius, Indomalaya from Thailand to the Philippines and New Guinea, Melanesia and Polynesia.

SELECTED SPECIMENS WITH PERIANTHS INVESTIGATED. MADAGASCAR: Prov. Antsiranana, Réserve integrale Marojezy, montane rainforest on the sharp ridge N of Andampibe Falls at 780–1050 m a.s.l., on decaying wood, Pócs 90113/CN (EGR). Prov. Antsiranana, Réserve spéciale de Manongarivo Ambahatra, cours superior, camp 2, 1200 m a.s.l., on bark, Geissler 19850 (CJB-G, dupl. EGR). RÉUNION: 12 km W of Ste Anne, remnants of tropical rainforest alternating with secondary *Psidium cattleianum* bushes around 'le Grand Étang' reservoir, 500–550 m a.s.l., epiphyllous, Pócs, A. Szabó & Vojtkó 9433/AO, 29 Aug. 1994 (EGR). ILES DE LA SOCIÉTÉ: Mooréa, au-dessus du point de vue de Belvédère, forêt du *Inocarpus edulis*, 300 m a.s.l., sur tronc, De Sloover 20.979 (det. Grolle, NAM, dupl. EGR).

Grolle (1995) placed *Ceratolejeunea boschiana* Steph. (1913) (lectotype: Bonner 1953: 168, Fig. 9) in the synonymy of *C. belangeriana*. However, the lectotype specimen of *C. boschiana* has juvenile perianths only, which are much shorter than the perichaetial leaves. At the time of Grolle's publication, *C. calabariensis* (= synonym of *C. cornuta*, with almost the same vegetative characters as *C. belangeriana*) was not known from the East African Islands. On the basis of its juvenile perianth, *C. boschiana* could belong to either of these two species, hence its taxonomic position remains uncertain.

2. *Ceratolejeunea cornuta* (Lindenb.) Steph.

Figs 1–6

in Engler, Pflanzenwelt of Afrikas Theil C: 65. 1895.

BASIONYM: *Jungermannia cornuta* Lindenb., Acta Nova Acad. Caes. Leop.-Carol. Suppl. 14: 23. 1829. TYPE: Jamaica, on *Grammitis serrulatus*, Swartz s.n. (HOLOTYPE W, fide Dauphin 2003, not seen).

AFRICAN SYNONYMS

Ceratolejeunea calabariensis Steph., Hedwigia 34: 234. 1895, **syn. nov.** TYPE: West Africa, New Calabar (in the Niger Delta of present-day southern Nigeria), on tree trunks, 8 Oct. 1884. 'Mönkemeyer 5 sub 'Lejeunea variabilis' in Hb.G', as indicated by Bonner 1963: 640.

Ceratolejeunea jungneri Steph., Hedwigia 34: 234. 1895. LECTOTYPE (selected by Bonner 1953: 205): Cameroons, Ekunda N'dene, 10 Sept. 1892, Dusen 936 (G), seen by Vanden Berghen (1973: 381), who synonymized it with *C. calabariensis* Steph.

Ceratolejeunea usambarensis Steph. in Brotherus, Denk. Kaiserl. Akad. Wissensch. 88: 731. 1913; Stephani, Sp. Hep. 5: 446. 1913. LECTOTYPE (selected by Bonner 1953: 247): East Africa, Usambara, Amani, 800 m a.s.l., July 1909, Brunthaler 8 (G). Synonymized by Vanden Berghen (1973: 381) with *C. calabariensis* Steph.

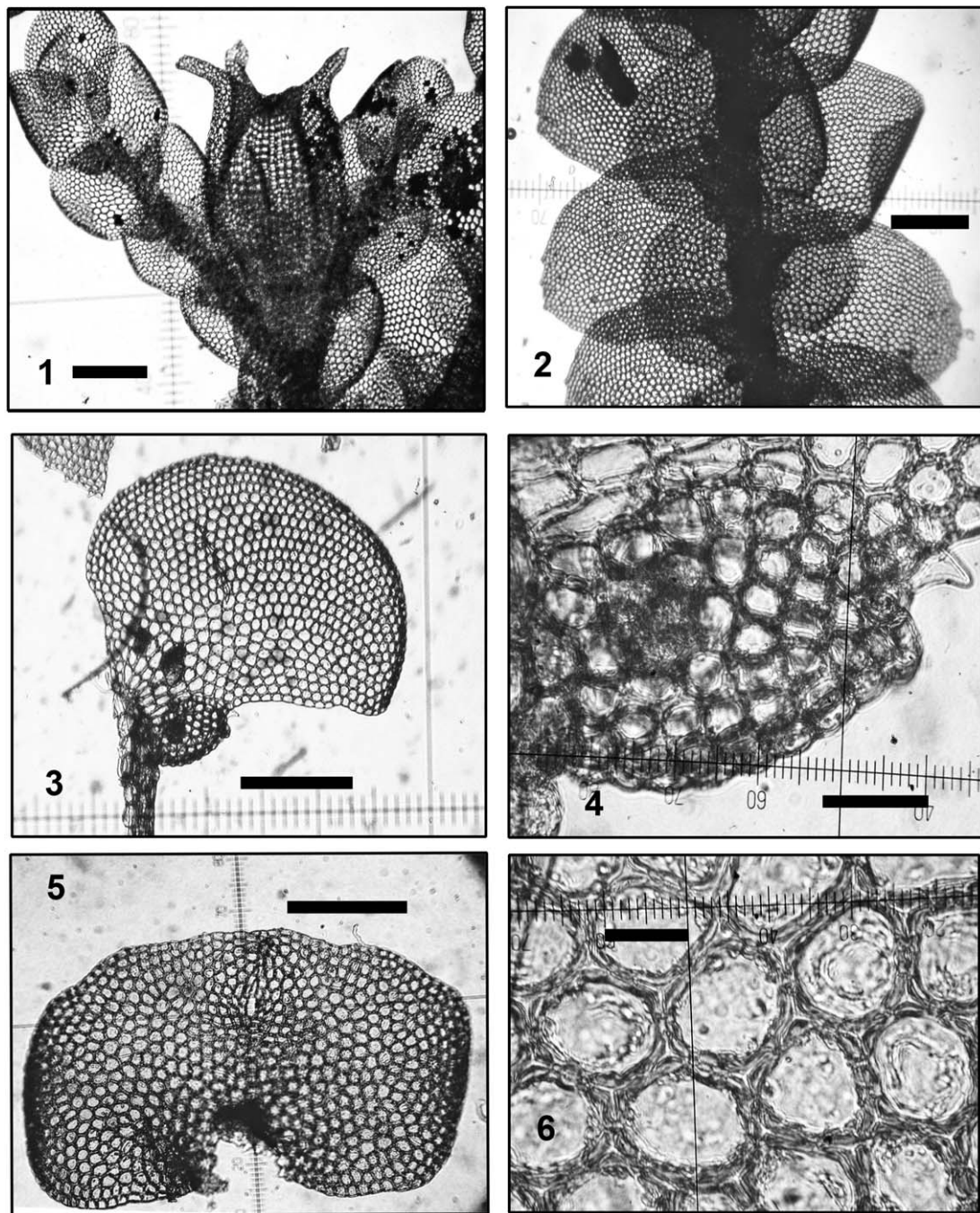
Lejeunea variabilis Lindenb. in Gottsche *et al.*, Synopsis Hepaticarum: 399. 1845, *Ceratolejeunea variabilis* (Lindenb.) Schiffn. in Engler & Prantl, Nat. Pflanzenfam. 1(3): 125. 1893. LECTOTYPE fide Grolle in sched.: Saint Kitts (W, ISOLECTOTYPES BM, M, G, S) according to Dauphin (2003a: 42). Although it was described from the Neotropics, Grolle (1995) cited several references from the East African Islands as well. For further American synonyms see Dauphin (2003a).

ILLUSTRATIONS: Fulford [1945: 389, Figs 53–59 under *C. maritima* (Spruce) Steph., Figs 60–64 under *C. valida* A. Evans, Figs 69–73 under *C. grandibracteata* Fulford], Bonner [1953: 205–206, Figs 47–48 under *C. involvens* (Nees & Mont.) Steph., 207, Fig. 49 under *C. jungneri* Steph. and under many other synonyms] and Vanden Berghen (1951: 73, Fig. 26 and 1973: 382, Fig. 6) as *C. calabariensis*.

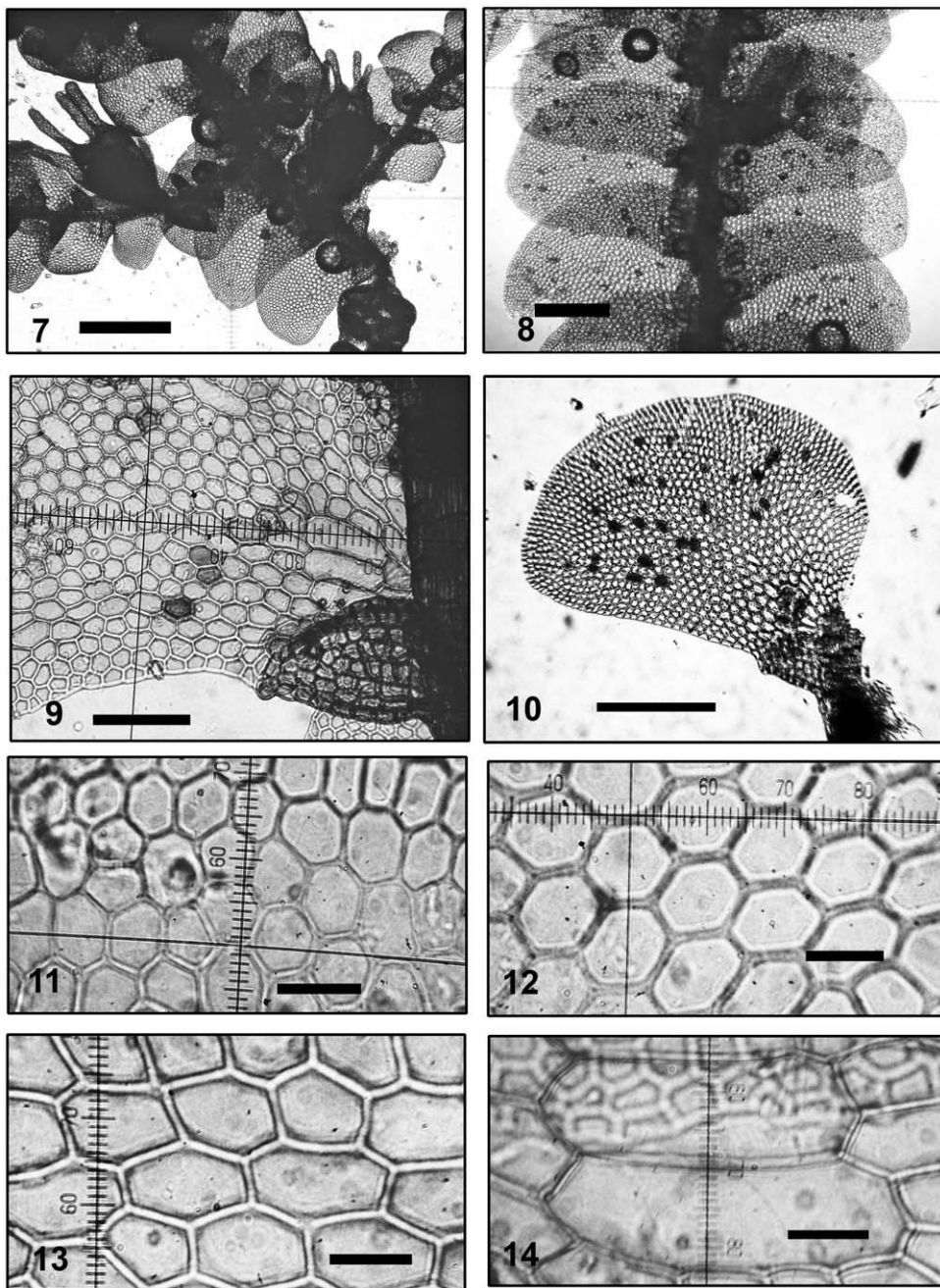
The plant known under the above synonyms is widespread all over the wetter parts of tropical Africa, including the Indian Ocean Islands (Pócs 1995; Pócs & Geissler 2002). I have examined a number of African plants and compared them both to various American *Cololejeunea cornuta*

specimens and to the detailed descriptions and illustrations given by Dauphin (2003a) as well as those of the authors of the two species. I could not find any difference between the African populations known under the name *Ceratolejeunea calabariensis* Steph. and the highly variable Neotropical *Ceratolejeunea cornuta* (Lindenb.) Steph. populations. The original description of *C. calabariensis* does not mention the utriculi (modified inflated lobules), while the detailed description of *C. cornuta* states that utriculi are rare, appear solitary or in pairs at the base of lateral branches, and are rounded to reniform in shape (Dauphin 2003a: 44). I have, in fact, also found African plants with the same type of utriculi. The perichaetial leaves of African plants are described as dentate, while those of the American plants as having 'margins dentate throughout or only distally'. The scattered, sometimes geminate basal leaf ocelli, the orbicular to wide reniform bilobed underleaves with a narrow incision and often auriculate basis, the perianth with 4 short or longer conical horns and other features of the African plants are all identical and fall well within the high variability of the widespread Neotropical *Ceratolejeunea cornuta* as established by Dauphin (2003a). The presence of enlarged, spherical lobules 'throughout or here and there' is emphasized by Dauphin (2003b), which is also true for certain African plants. Hence a typical case of Afro-American disjunction is at hand, as encountered by Gradstein, Pócs and Váňa (1984). If further investigation proves *C. belangeriana* to be only a subspecies of *C. cornuta*, the latter species should be considered a Pantropical flora element.

In fact, Gottsche *et al.* (1845: 399) had already reported *C. cornuta* from Madagascar, Stephani (1895: 65) had reported it from Réunion, and Miller *et al.* (1983) had reported it from Polynesia (under the name *C. maritima*). Bonner (1953) and Grolle (1995) both examined the Madagascar specimen from the Montagne Herbarium and identified it as *C. belangeriana*. On that basis, Grolle (1995: 142) concluded that the whole of the specimens reported from Réunion 'likewise has to be referred to *C. belangeriana*', but this has never been confirmed. *Ceratolejeunea variabilis* has on several occasions



Figs 1–6. *Ceratolejeunea cornuta* (Lindenb.) Schiffn. 1 – perichaetium with subgynoecial innovation (scale bar = 200 μ m), 2 – part of shoot, ventral view (scale bar = 200 μ m), 3 – leaf (scale bar = 250 μ m), 4 – lobule (scale bar = 50 μ m), 5 – under-leaf (scale bar = 200 μ m), 6 – median lobe cells (scale bar 20 μ m). Photographed from *Pócs 6100/AK*, Tanzania, Usambara Mts, Amani.



Figs 7–14. *Ceratolejeunea papuliflora* Steph. 7 – habit of fertile shoot (scale bar = 500 μm), 8 – shoot, dorsal view (scale bar = 250 μm), 9 – leaf base with lobule, seriate basal ocelli and scattered ocelli (scale bar = 100 μm), 10 – leaf (scale bar = 250 μm), 11–13 – lobe cells (11 – apical, 12 – median and 13 – basal; scale bars = 20 μm), 14 – serial basal ocelli (scale bar = 20 μm). 7 from Pócs *et al.* 90113/EW, Madagascar. Marojezy Reserve. 8 from Pócs & A. Szabó 9878/FE, Madagascar, Manananra Nord Biosphere Reserve, 9–14 from Pócs 9450/AB, Madagascar, Nosy Mangabe Island in Antongil Bay.

been reported from the East African Islands: from Madagascar (Gottsche 1882: 357), from Mauritius (Pearson 1892: 8) and from Réunion (Bescherelle 1895: 5) after Grolle (1995). All these records now belong to *C. cornuta* according to the synonymy given by Dauphin (2003a).

DISTRIBUTION (see map in Fig. 81). Ubiquitous all over Latin America from Cuba and Mexico to southern Brazil (Dauphin 2003a), also widespread in the wetter parts of tropical Africa from Sierra Leone and the Gulf of Guinea islands through Cameroon and Zaire to Tanzania and all East African Islands.

SELECTED SPECIMENS EXAMINED. PUERTO RICO: Sierra de Luquillo, Mt. Britton Loop Road, on bark. *Fulford, Crandall & Stotler* 334, 12–26 Feb. 1967 (EGR). REP: DOMINICANA: Prov. Monseñor Nouel. Cordillera Central, degraded cloud forest E of Jima, 1200–1300 m a.s.l., on decaying branch, *S. & T. Pócs* 03156/E, 22 Nov. 2003 (EGR). SURINAM: s.l., *Lanjouw* 831, 1933 (NY, dupl. EGR). FRENCH GUIANA: Kourou, Mt. des Signes, ‘sentier botanique’ in mixed rainforest, alt. ca 100 m a.s.l., epiphyllous on palm leaves, *Gradstein* 6271, 21 June 1986 (Bryophyta Neotropica Exsiccata No. 232, EGR). PANAMA: Prov. Panamá, nes summit of Cerro Jefe, alt. ca 1000 m a.s.l., on branches and twigs in scrubby secondary vegetation, *Salazar & Gradstein* 9405, 12 June 1991 (Bryophyta Neotropica Exsiccata No. 280 under *Ceratolejeunea maritima*, EGR). ECUADOR: Galápagos, Santa Cruz Island, *Miconia* scrub around Media Luna, on bark of a big avocado tree, 600–650 m. *Gradstein & Weber* H86, 1976 (U, dupl. EGR). SÃO TOMÉ: SE coast, W of São João dos Angolares, 20 m a.s.l., on palm trunk in grazed coconut and breadfruit tree plantation, *Pócs* 00145/G, 27 Aug. 2000 (EGR). Around Cascata Monte Café in the valley of Rio Manuel Jorge, in submontane rainforest, at 820 m a.s.l., on bark. *Pócs* 00148/A, 28 Aug. 2000 (EGR). PRINCIPE: E side of the island between Infante Henrique and Santo Antonio at the volcanic pinnacles called Twin Fingers, mixed hardwood forest, 115 m a.s.l., on volcanic boulder, *Shevock et al.* 34633, 9 March 2010 (CAS, EGR). IVORY COAST: Soubré, Parc National de Taï, *Aké-Assi* 12641, 1977 (EGR, UCJ). Chemin des Avodirés, sur tronc couché dans marais, 10 m a.s.l., *Assel RCI* 183, 16 Feb. 1968 (EGR). En direction de M’Ponto en forêt claire, sur tronc demi-sec, *Assel RCI* 1046, 23 Sept. 1969 (EGR). GHANA: Central Region, Pra-Suhien Forest Res., side of bough of fallen tree in gap, *Jones*

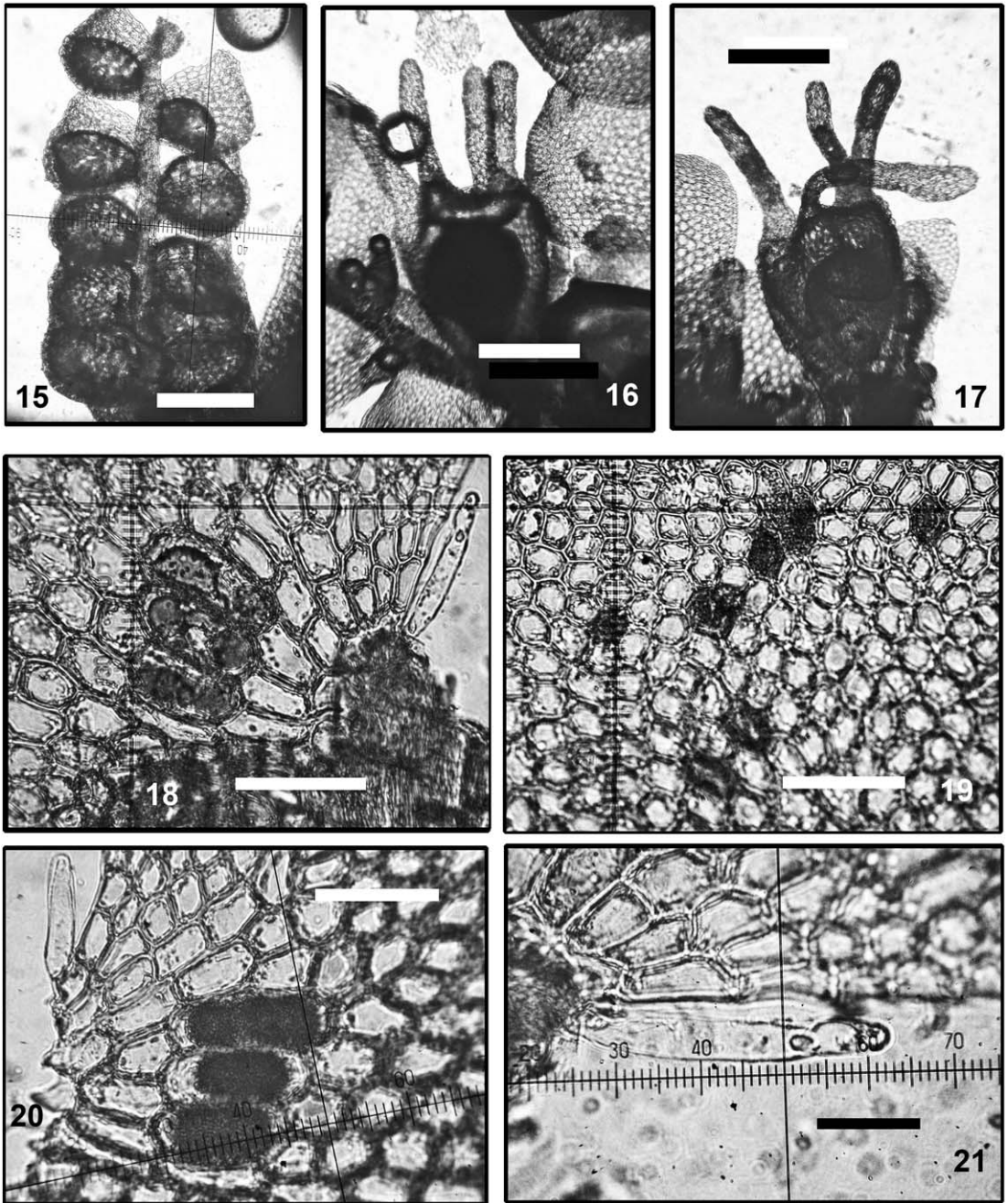
& *Hall* 1346, 11 Feb. 1971 (EGR). EQUATORIAL GUINEA: Muni, Cogo, on mangle trees in mangrove at Utoche, along River Mitong, 5 m a.s.l., *Heras VIT* 367/96, 28 Aug. 1996 (VIT, dupl. EGR). D. R. CONGO (former Zaire): Prov. Kivu, Irangi Forest Station 110 km W of Bukavu, in submontane rainforest near waterfalls at 900 m a.s.l., on branches above water, *Pócs* 6813 (EGR). UGANDA: Kalangala District, Ssesse Islands, Jungo Forest near Mweno village, Bugala Islands, 1170 m a.s.l., epiphyllous, *Pócs, Lye & Samuela* 97107/AH, 7 Sept. 1997 (EGR). TANZANIA: East Usambara Mts, Amani, on planted mango tree surrounded by submontane rainforest, 900 m a.s.l., epiphyllous, *Pócs* 6100/K, Dec. 1969 (EGR). Uluguru Mts above Morogoro town, Mwere Valley, submontane rainforest, 1450–1550 m a.s.l., epiphyllous, *Pócs* 6100/AK, 29 Dec. 1969 (EGR). COMORES: Ndzuani (Anjouan) Island, Col de Moya, intercropped submontane rainforest, 700–800 m a.s.l., on buttresses, *Pócs* 9166/X, 23 March 1991 (EGR). SEYCHELLES: Morne Seychellois Nat. Park, summit ridge of Morne Blanc, elfin forest, 590–669 m a.s.l., epiphyllous, *Pócs* 9323/BA, 12 Aug. 1993 (EGR). Mahé Island, Victoria – Port Glaud, Sentier Morne Blanc, 450–667 m a.s.l., epiphyllous, *Frahm SEY-032*, 9 Oct. 2008 (Hb. Frahm, EGR). Praslin Island, Vallée de Mai Nat. Park, palm forest along Cascade River, 150–180 m a.s.l., on bark, *Pócs* 9358/AL (EGR). MADAGASCAR: Prov. Antsiranana, Réserve intégrale Marojejy, montane rainforest on the sharp ridge N of Andampibe Falls at 780–1050 m a.s.l., on decaying wood, *Pócs* 90113/CN (EGR). Mananara Nord Biosphere Reserve. Mahavoho Hill, lowland rainforest at 220–300 m a.s.l., streamside, watered rocks, *Pócs & A. Szabó* 9878/AG (EGR, MO, TAN). MAURITIUS: Le Pouce, forest halfway to the top. On bark, *Een*, 7 Oct. 1962, Soc. D’Échange des Muscinées No. 2988, under *Ceratolejeunea renauldii* Steph. (EGR). Black River National Park, Piton Savanne, rainforest remnants, 700 m a.s.l., on bark. *Frahm MAU-010*, 28 Sept. 2007 (EGR).

3. *Ceratolejeunea diversicornua* (Steph.) Steph. Figs 54–63

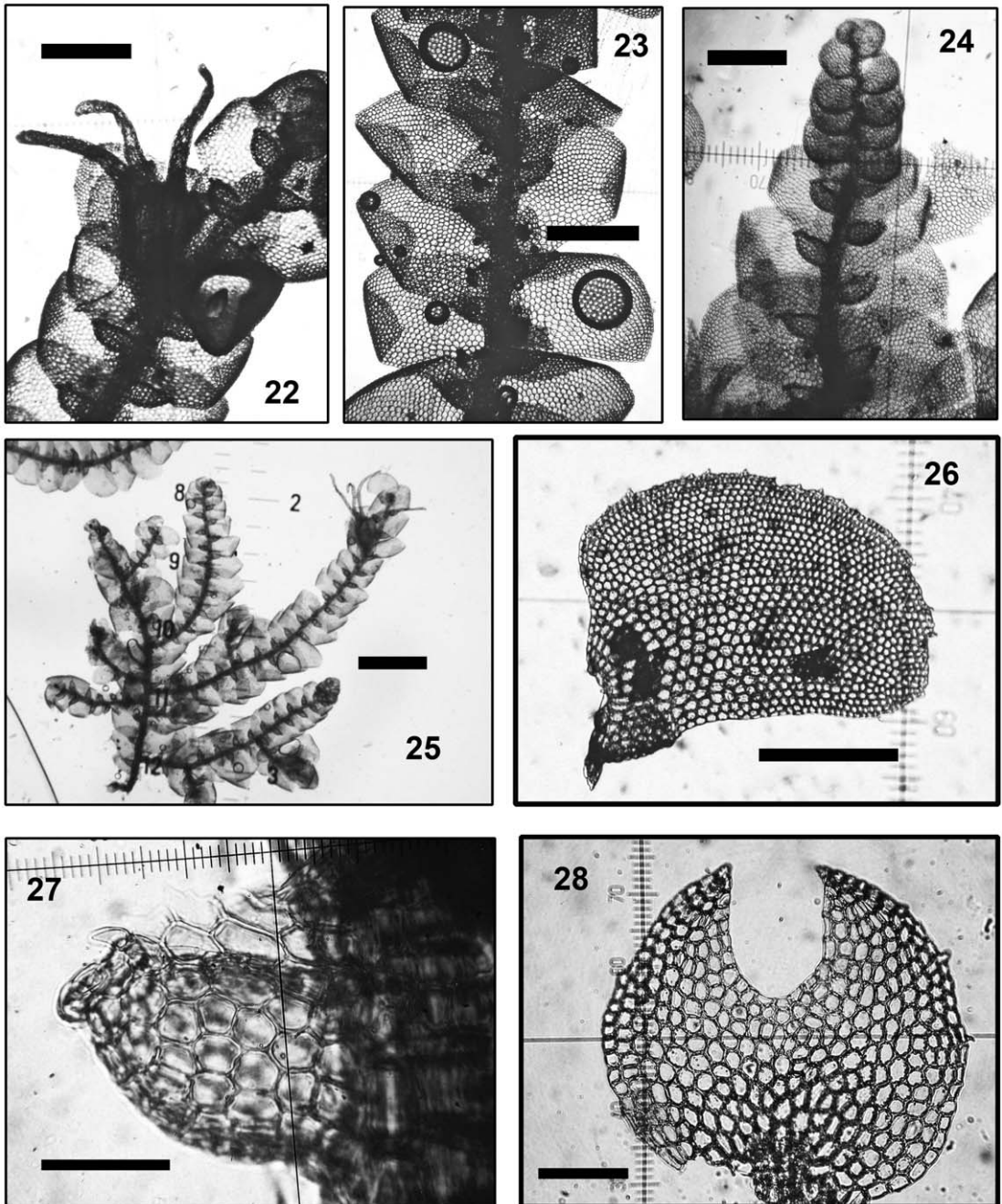
Species Hepaticarum 5: 410. 1913.

BASIONYM: *Lejeunea diversicornua* Steph., Hedwigia 30: 207. 1891. **TYPE:** Cameroons, s.l., s.d., *Dusén* inter 37 (G, seen and drawn by Vanden Berghen 1951).

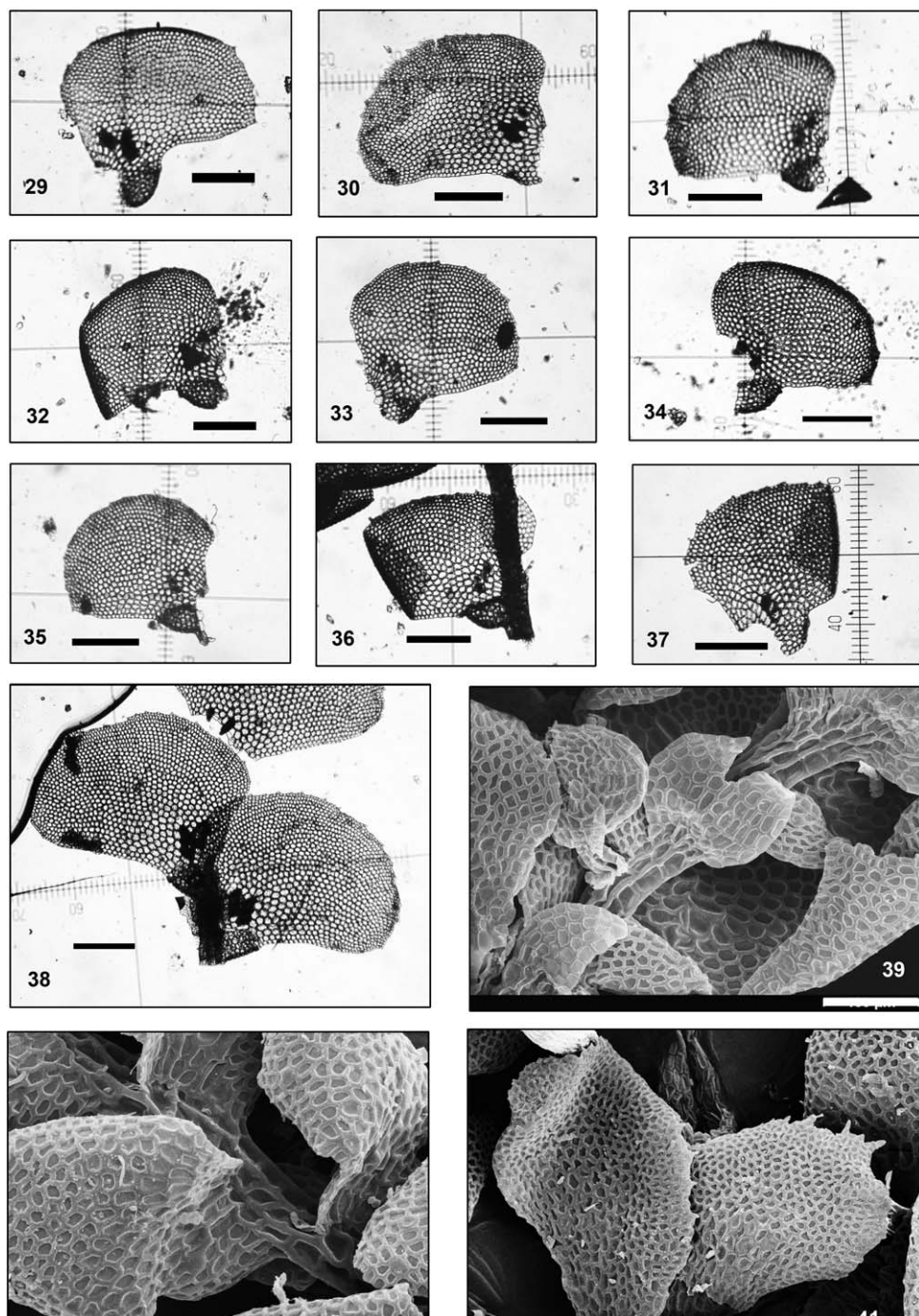
Ceratolejeunea cornutissima Steph., Hedwigia 31: 166. 1892; *Lejeunea cornutissima* (Steph.) Steph., Hedwigia 31: XVI. 1892, fide Jones in Wigginton et al. (1996: 41).



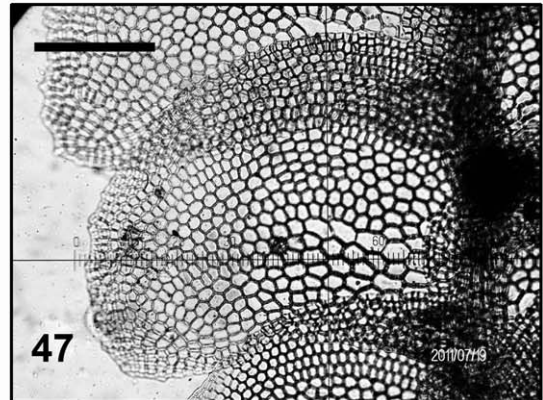
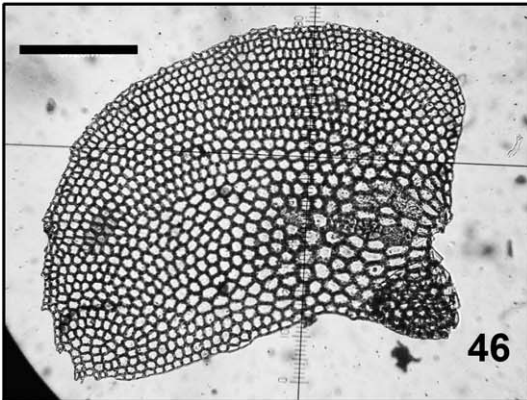
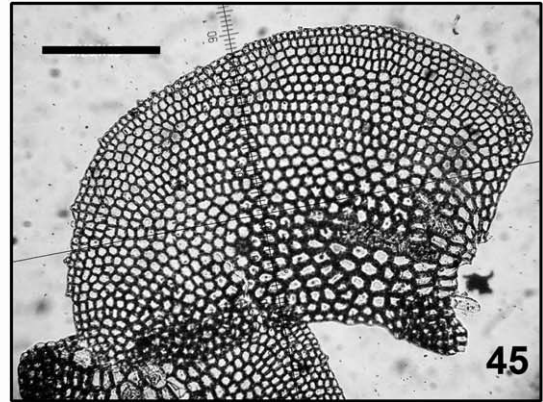
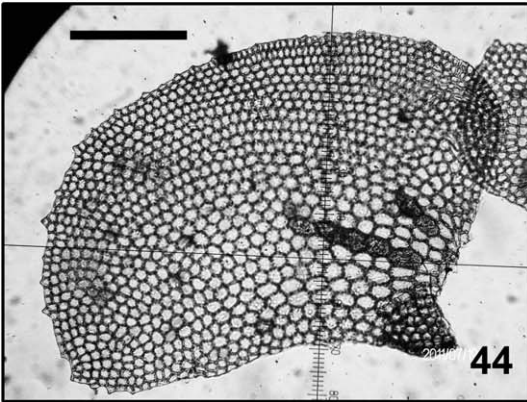
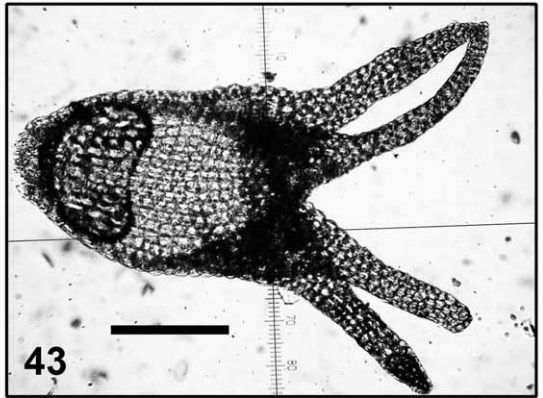
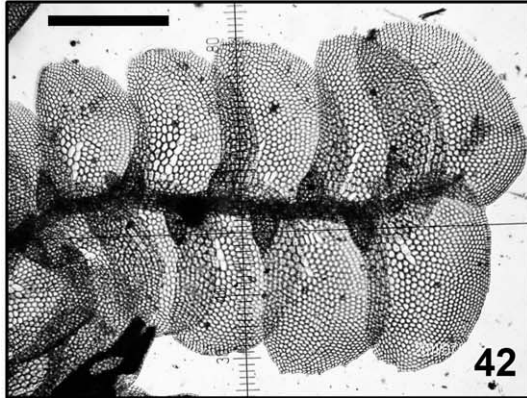
Figs 15–21. *Ceratolejeunea papuliflora* Steph. 15 – male branch (scale bar = 250 μ m), 16–17 – perianths (scale bars = 250 μ m), 18 & 20 – serial basal ocelli (scale bars = 60 μ m), 19 – scattered ocelli (scale bar = 50 μ m), 21 – two-celled style (scale bar = 50 μ m). 15–17 from Pócs *et al.* 90113/EW, Madagascar. Marojezy Reserve, 18–21 from Pócs 9450/AB, Madagascar, Nosy Mnagabe Island in Antongil Bay.



Figs 22–28. *Ceratolejeunea andringitiae* Pócs, sp. nov. 22 – habit with perichaetium (scale bar = 250 μ m), 23 – shoot, ventral view (scale bar = 250 μ m), 24 – androecium on branch apex (scale bar = 250 μ m), 25 – autoicous branching system (scale bar = 1 mm), 26 – leaf with ocelli groups (scale bar = 250 μ m), 27 – lobule (scale bar = 50 μ m), 28 – underleaf (scale bar = 100 μ m). All photographed from the type.



Figs 29–41. *Ceratolejeunea andringitrae* Pócs, *sp. nov.* 29–37 – leaves with different arrangements of grouped ocelli (scale bars = 250 µm), 38 – pair of leaves (scale bar = 250 µm), 39 – ventral view of shoot with antheridia on short side branch (scale bar = 100 µm), 40 – dorsal view of shoot (scale bar = 100 µm), 41 – female bracts, dorsal view (scale bar = 200 µm). All photographs and SEM micrograph made from the type.

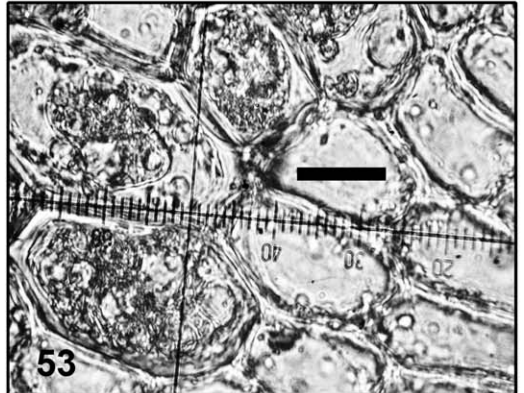
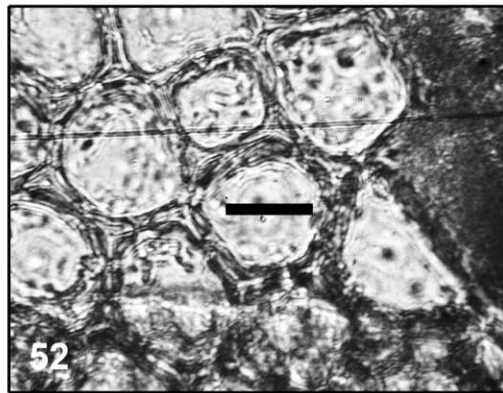
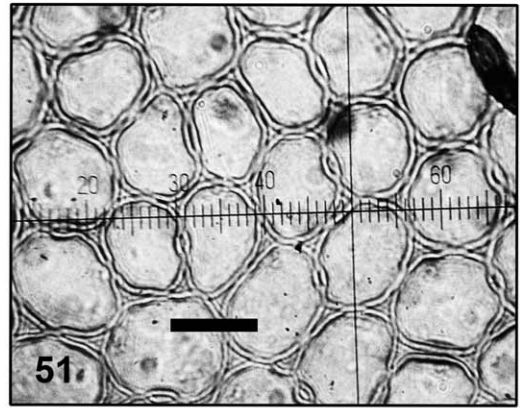
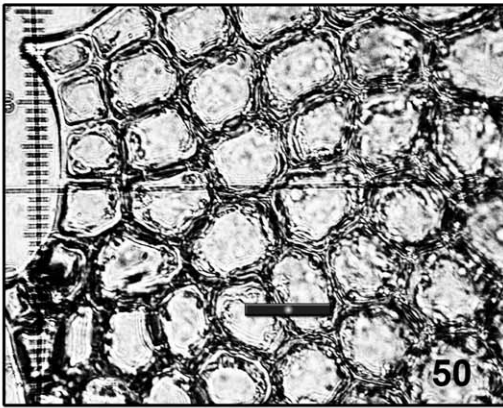
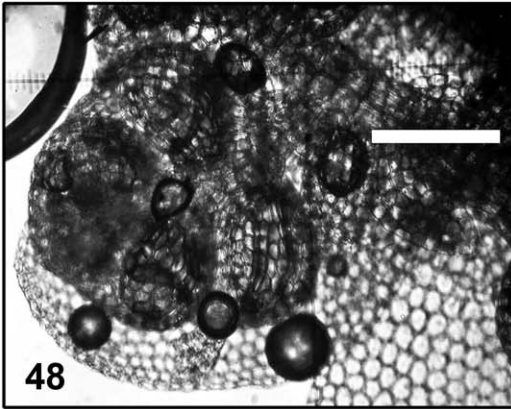


Figs 42–47. *Ceratolejeunea moniliata* Herz. for comparison. 42 – shoot, dorsal view (scale bar = 500 μ m), 43 – perianth (scale bar = 200 μ m), 44– 47 – leaves with moniliform ocelli (scale bars = 200 μ m). Photographed from Streimann & Naoni 16480, Papua New Guinea: Central Province, Ehu Creek 13 km SW of Sogeri, det. R. Grolle (H ex CBG).

ILLUSTRATIONS: Stephani (1892: 166, Tab. XII, figs 13, 14 under *C. cornutissima*), Vanden Berghen (1951: 67, Fig. D under *C. cornutissima*, Fig. E and 1951: 69, Fig. 25A under *C. diversicornua*) and Bonner (1953:

180, Fig. 20 under *C. cornutissima*, 1953: 186, Fig. 27 under *C. diversicornua*).

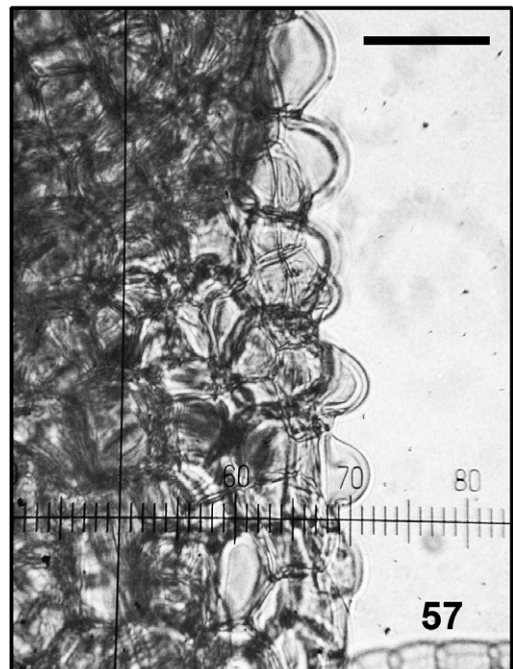
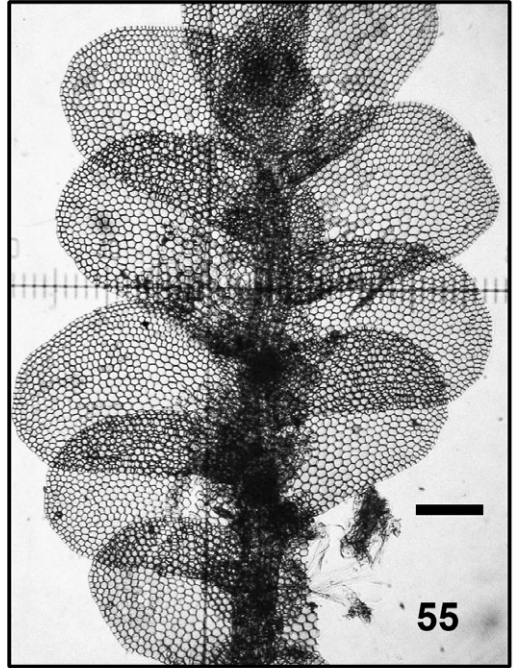
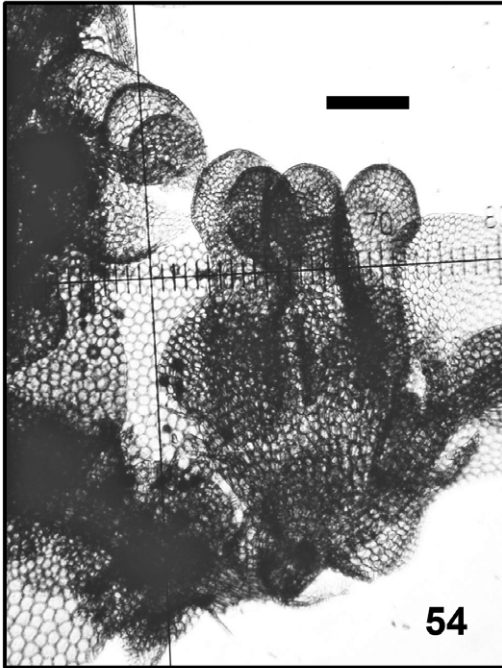
The distinctive characters of the species are



Figs 48–53. *Ceratolejeunea andringitiae* Pócs, *sp. nov.* 48 – male branch (scale bar = 100 μ m), 49 – perianth (scale bar = 250 μ m), 50–52 – lobe cells (50 – apical, 51 – median, 52 – basal; scale bars = 20 μ m), 53 – basal ocelli (scale bar = 20 μ m). All photographed from the type.

their four inflated perianth horns, often unequal in size, and their isolated or geminate basal ocelli. The lobe margin is often denticulate.

DISTRIBUTION. *Ceratolejeunea diversicornua* was considered a rare West African species known only from lowland rainforests of Cameroun,



Figs 54–57. *Ceratolejeunea diversicornua* Steph. 54 & 56 – female branches with perichaetium and subgynoecial innovation (scale bars = 50 μ m), 55 – shoot, ventral view (scale bar = 50 μ m), 57 – mamilllose surface of perianth (scale bar = 20 μ m). Photographed from Sarolta Pócs 9890/CA, Madagascar: Toamasina Province, Mt. Maromizaha, south of the Andasibe Nat. Park, on *Pandanus* leaf (EGR).

Ghana and Zaire. The species is new for Gabon and Madagascar. According to Vanden Berghen (1951), *C. cornutissima* may be synonymous with the Neotropical *C. plumula* (Spruce) Steph., which, according to Dauphin (2003), is a synonym of *C. coarina* (Gottsche) Schiffn. Vanden Berghen (1951) distinguishes *C. cornutissima* from *C. plumula* by its perianth horns which are longer than the urn and by the absence of utricles. However, I observed solitary utriculi at the base of lateral branches and shorter horns on the above-cited Gabon specimen; therefore it requires more material and a thorough comparison of the types to decide whether they are synonymous.

SPECIMENS EXAMINED. GABON: Forest Reserve 'ENEF Parcelle des Conservateurs, Sentier nature' between Libreville and Cap Esterias, epiphyllous in lowland rainforest at 10 m a.s.l. Pócs 00142/E, 25 Aug. 2000 (EGR). ZAIRE, Kivu, Irangi Forest Station, 850 m a.s.l., Fischer 8500-36, 22 Aug. 1991 (EGR). MADAGASCAR: Toamasina Province. Maromizaha forest. Mossy montane rainforest with bamboo (*Nastus* sp.) undergrowth on the summit ridge of Mt. Maromizaha, south of the Andasibe Nat. Park, 1080–1214 m a.s.l., on *Pandanus* leaf intermixed among *C. saroltae* Pócs. Sarolta Pócs 9890/CA, 26 August 1998 (EGR).

4. *Ceratolejeunea papuliflora* Steph.

Figs 7–21

Spec. Hep. 5: 430. 1913.

Ceratolejeunea papuliflora Steph. in Levier, Rev. Bryol. 28: 94. 1901, *nom. nud.*

TYPE: Madagascar: Tamatave, s.c., s.n., s.d. (BM, seen and drawn by Bonner 1953).

Ceratolejeunea stictophylla Herz. in Vanden Berghen, Bull. Jard. Bot. Bruxelles 21: 81. 1951, *syn. nov.* TYPE: Western Nigeria, Ijedu-Obe, Shasha Forest Reserve, on bark, Jones 17.251, March 1946 (BM, seen and drawn by Vanden Berghen 1951).

ILLUSTRATIONS: Bonner (1953: 221, Fig. 66) and Vanden Berghen (1951: 80, Fig. 28, under *Ceratolejeunea stictophylla* Herz.).

The particular arrangement of the ocelli of this plant, also seen on some Neotropical *Ceratolejeunea* and in the genus *Xylolejeunea* X.-L. He & Grolle, *Ann. Bot. Fenn.* 38: 25–44 (2001), is unique among African species. At the base of

the lobe are two transversely arranged rows of enlarged, elongate cells, the upper one of which constitutes the adjacently arranged serial ocelli (see Figs 10, 18, 20 in this paper, Pócs 1999: 286, Figs 6, 7 and 10 under *Trachylejeunea grolleana* and He & Grolle 2001: 33, Fig. 2). Each of these rows of ocelli consists of 3–5(–6) cells, filled with a large oil body. In spite of this interesting coincidence, other characters of *Ceratolejeunea papuliflora* are typical for the genus and differ significantly from *Xylolejeunea*. The similarity of the arrangement of ocelli between *Ceratolejeunea* and *Xylolejeunea* seems to be homoplasy, as molecular investigation has not revealed a close relationship between the two genera (Wilson *et al.* 2007). Apart from the serial ocelli, ocelli are also scattered in the lobes of *Ceratolejeunea papuliflora*. The perianth of *C. papuliflora* also bears important distinctive features: it is relatively small (320–400 × 280–320 µm), urn-shaped, with four 240–330 µm long, 30–40 µm wide fingerlike horns often slightly widening upwards, and a round apex similar to only a few species of the genus. The leaf lobe has a relatively long (50–70 µm), uni- or bicellular form.

DISTRIBUTION. Nigeria, Seychelles, Madagascar, Réunion.

Until published from Réunion Island (Ah-Peng *et al.* 2010) the species was only known from its type locality in Tamatave, Madagascar, deposited in the Kew Herbarium, and a specimen (No. 348) in Ténérive, Madagascar, both from unknown collectors. The specimens from Western Nigeria were collected by Jones in 1946 and published by Herzog in Vanden Berghen (1951) under the name *C. stictophylla* (see synonyms). At the time *C. stictophylla* was described the Stephani illustrations had not yet been published by Bonner (1953). Probably this is why Herzog did not realize the identity of the two species. After the protologue he mentions that the species is closely related to but distinct from *C. papuliflora* as it has numerous scattered and geminate basal ocelli – which, however, are characteristic of both. From Vanden Berghen's description (1951: 51) and illustrations (Fig. 28), it is clear that the plant described is

C. papuliflora. Interestingly, Jones (1957: 198–200, Fig. 3) published and illustrated another plant from the eastern part of Nigeria (Mamu River Forest Reserve, Awka, Onitsha Province, *E. W. Jones* 845, deposited in KEW, now transferred to BM), also under the name *C. stictophylla*, but his drawing and description show that the species examined was *C. zenkeri*, as Wigginton (2004: 296) has already pointed out. In Jones's illustration (1957: 199, Fig. 3) there are no real scattered ocelli shown, and he himself later adds on page 200 that in the type of *C. stictophylla* 'the scattered ocelli are rather more distinct, always being larger than the surrounding cells'.

SPECIMENS EXAMINED. SEYCHELLES: Val Riche, W of Copolia summit. Cinnamon coppice with many native trees (*Dillenia ferruginea*, *Phoenicophorum borsigianum*), 330–450 m a.s.l., on decaying logs, *G. Kis* 9333/BX, 17 Aug. 1993 (EGR). MADAGASCAR: Prov. Antsiranana, Reserve Integrale Nationale de Marojejy. Montane rainforest on the ridge N of Andampibe Falls, 780–1500 m a.s.l., epiphyllous, *Pócs et al.* 90113/EQ and EW, 24–29 March 1990 (EGR, MO). Masoala Peninsula, lowland rainforest on the W slopes E of Ambanizana village, at 100–300 m a.s.l., epiphyllous, *G. Kis*, 9447/T, 9–11 Sept. 1994 (EGR). Same place, in submontane rainforest above 450 m a.s.l., epiphyllous, *Pócs* 9448/N, 9448/P, 9 Sept. 1994 (EGR, MO, TAN). Antongil Bay, Nosy Mangabe Island, lowland rainforest, 200 m a.s.l., epiphyllous (with dentate underleaf lobes), *Pócs* 9450/AB, 13 Sept. 1994 (EGR, TAN). Prov. Toamasina, Mananara Nord Biosphere Reserve and National Park, lowland rainforest on the E slopes of Mahavoho Hill, 220–300 m a.s.l., epiphyllous. *Pócs & A. Szabó* 9878/FE, 16 Aug. 1978 (EGR). RÉUNION: Gîte Basse Vallée, *Cryptomeria* plantation, 625 m a.s.l., on *Cryptomeria* bark, *Vojtkó* 9604/BQ, 23 June 1996 (EGR).

5. *Ceratolejeunea umbonata* Steph.

Sp. Hepat. 5: 446. 1913.

TYPE: Cameroons, Bodjé, *Ledermann s.n.* (G, type seen and drawn by Vanden Berghen 1951).

ILLUSTRATIONS: Vanden Berghen (1951: 67, Fig. 24F) and Bonner (1953: 246, Fig. 94) and Wigginton (2004: 296, Fig. 196)

This species is unique among the African *Ceratolejeunea* as it has no real perianth horns; its 4

carinae end in rounded bosses only. In addition, it has only a single or no ocelli in the leaf. The underleaves are large, 5–6 times wider than the stem and orbicular to reniform, with a narrow incision and a slightly U-shaped insertion line. In tropical America some species of the genus also occur with reduced perianth horns, for example *Ceratolejeunea confusa* R. M. Schust., *C. fallax* (Lehm. & Lindenb.) Bonner and *C. minuta* G. Dauphin, but these all have basal ocelli.

As in some *C. umbonata* collections, both short-horned and hornless perianths occur (Wigginton 2004: 296); their relation to the highly variable *C. cornuta* is yet to be clarified (see perianth drawings in Bonner 1953: 246, Fig. 94 and Vanden Berghen 1973: 382, Fig. 6).

DISTRIBUTION. It was known as restricted to West Africa: São Tomé, Cameroons, Guinea and Liberia until discovered in Réunion Island (Ah-Peng *et al.* 2010).

SPECIMEN EXAMINED: RÉUNION: Grand Étang, forest margin by path to lake, 500 m a.s.l., epiphyllous *Porley* REU9719e (BM, REU).

6. *Ceratolejeunea andringitrae* Pócs, *sp. nov.*

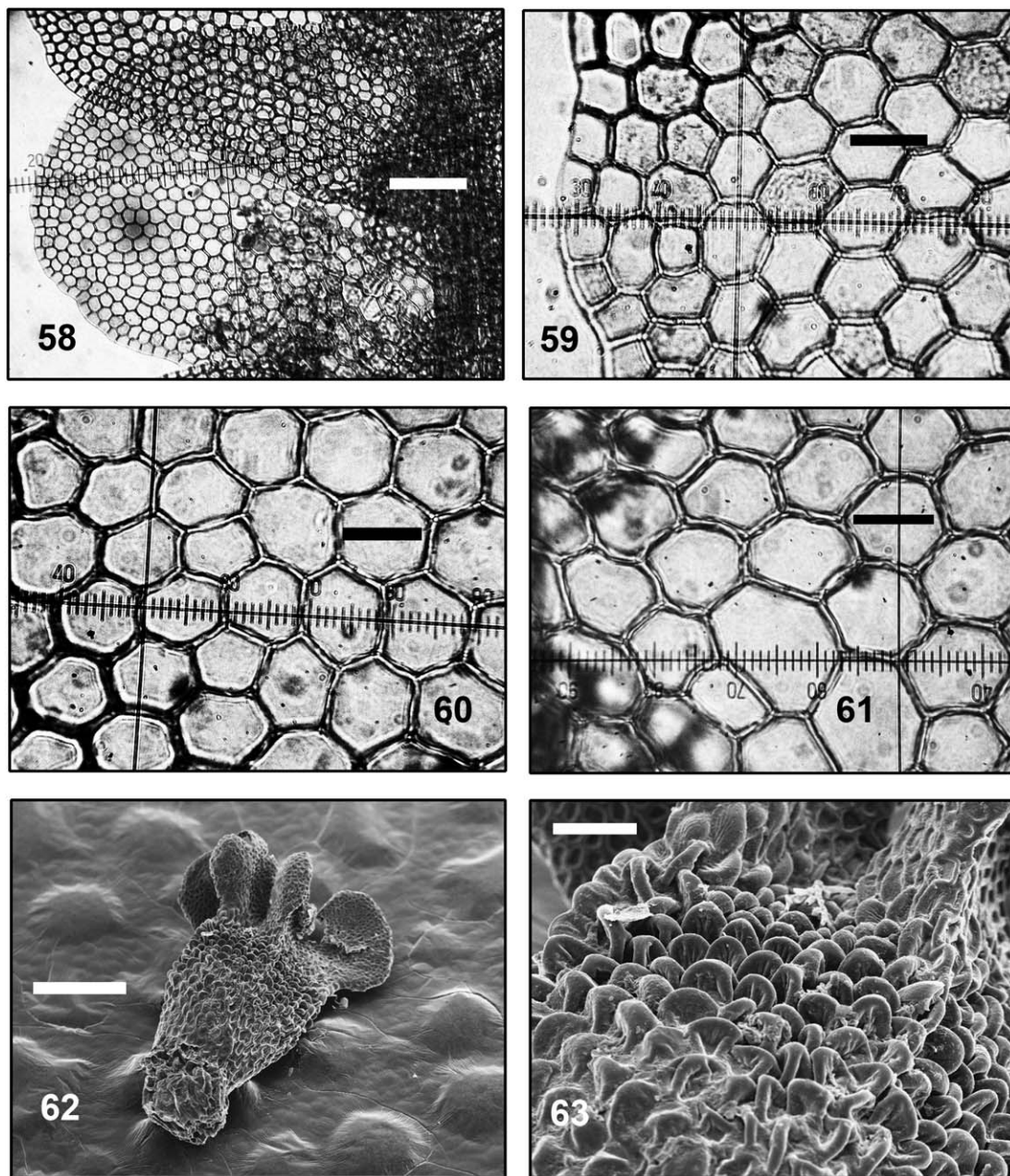
Figs 22–41, 48–53 & 76–77

Differt a Ceratolejeunea moniliata Herz., *cellis basilaribus aggregatis non moniliatis*.

TYPE: SE MADAGASCAR, Ihorombe Region in former Fianarantsoa Province, Andringitra National Park. Montane rainforests on W side of Korokoro River, around Camp II, at 750–1000 m a.s.l., 22°13'S, 47°1–2'E, epiphyllous. *Pócs & A. Szabó* 9472/AF, 20–23 Sept. 1994 (HOLOTYPE: EGR, ISOTYPES: MO, TAN).

ETYMOLOGY: Named after its locality, Andringitra National Park in southern Madagascar.

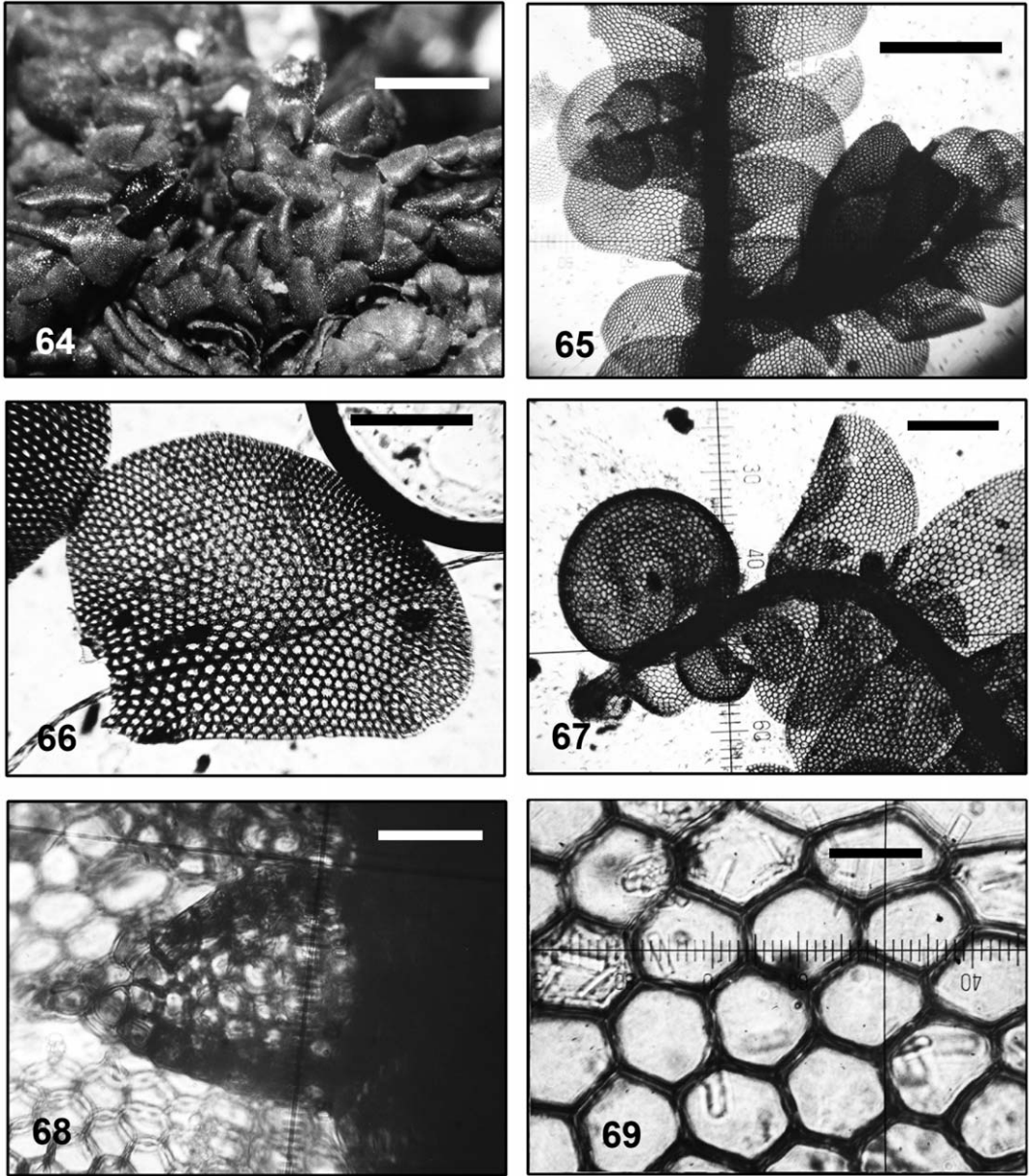
Small, rufous, epiphyllous plants, forming dense mats 2–5 mm diam. on leaves. Leafy shoots up to 1 cm long and 1.25 mm wide, densely and irregularly branched. Stems up to 100 µm wide, ventral merophyte cells rectangular, 35–40 × 18–22 µm. Leaves imbricate, 400–500 × 360–400 µm, slightly falcate, with entire or denticulate antical margin. Lobe with rounded apex and irregular groups of elongate hexagonal basal ocelli 30–60 × 25–40 µm



Figs 58–63. *Ceratolejeunea diversicornua* Steph. 58 – leaf (scale bar = 100 µm), 59–61 – lobe cells (59 – apical, 60 – median and 61 – basal; scale bars = 20 µm), 62 – perianth (scale bar = 250 µm), 63 – mammillose perianth surface (scale bar = 50 µm). Photographs and SEM micrographs made from the same specimen as in Figs 54–57.

in size, each filled with a large *Leucolejeunea*-type oil body as described by Kis and Pócs (1997). Scattered cells with different, darker content, but

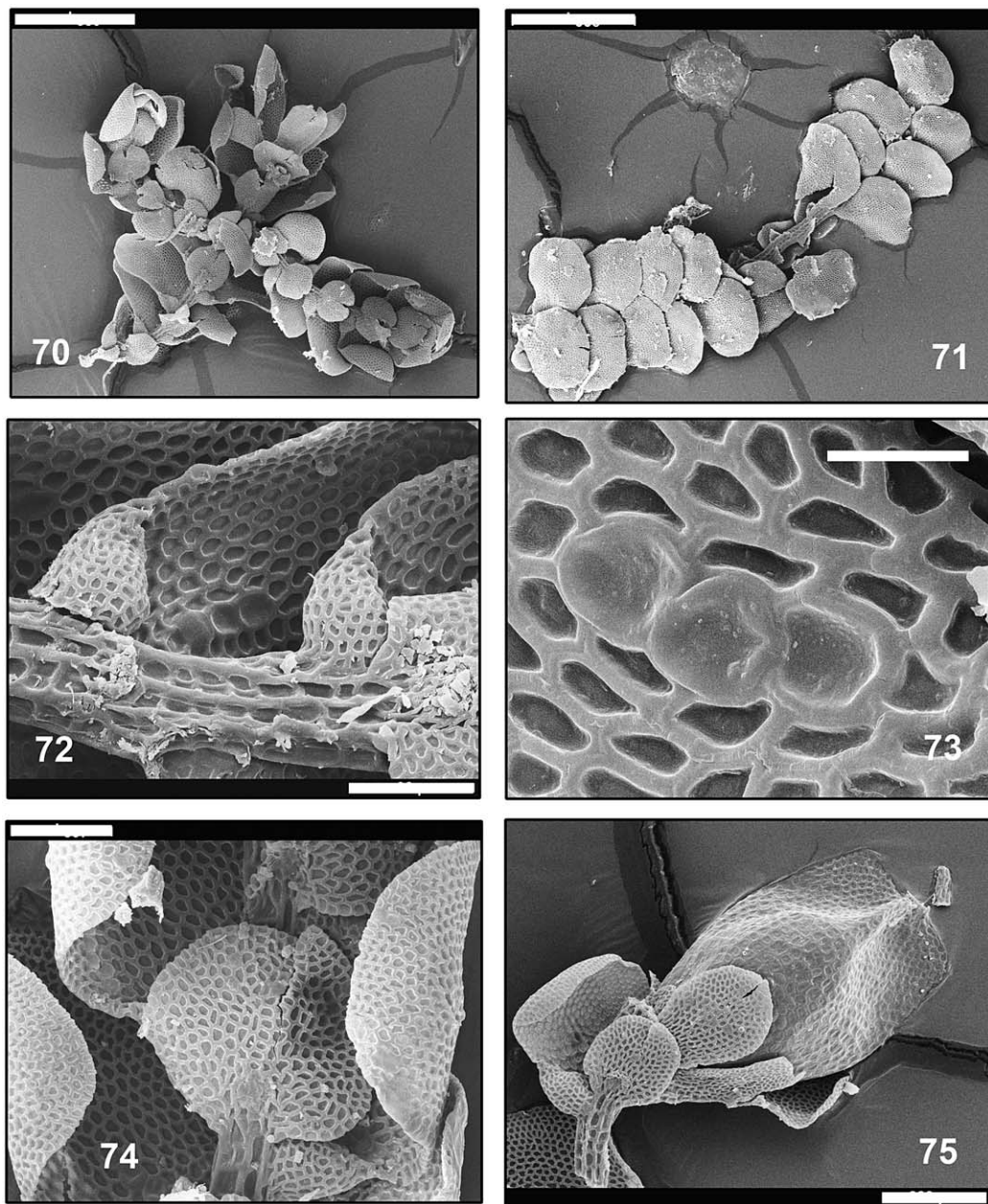
identical in shape and size to normal lobe cells, also occur. Apical cells rectangular, $10\text{--}20 \times 12\text{--}18$ µm, median cells $18\text{--}28$ µm diam., basal



Figs 64–69. *Ceratolejeunea saroltae* Pócs, *sp. nov.* 64 – habit, surface view (scale bar = 1 mm), 65 – habit with androecia and gynoecia, ventral view (scale bar = 500 μ m), 66 – lobe with moniliate and scattered papillae (scale bar = 200 μ m), 67 – branch with unequal utriculi at its base (scale bar = 250 μ m), 68 – lobule (scale bar = 50 μ m), 69 – median lobe cells (scale bar = 20 μ m). All photographs made from the type.

cells 25–36 μ m diam., all with relatively thin walls, moderate-size trigones, and intermediate thickenings. Lobule small, trapezoid-ovate, inflated, *ca* 1/4 leaf length, 9 cells long and 6 cells wide,

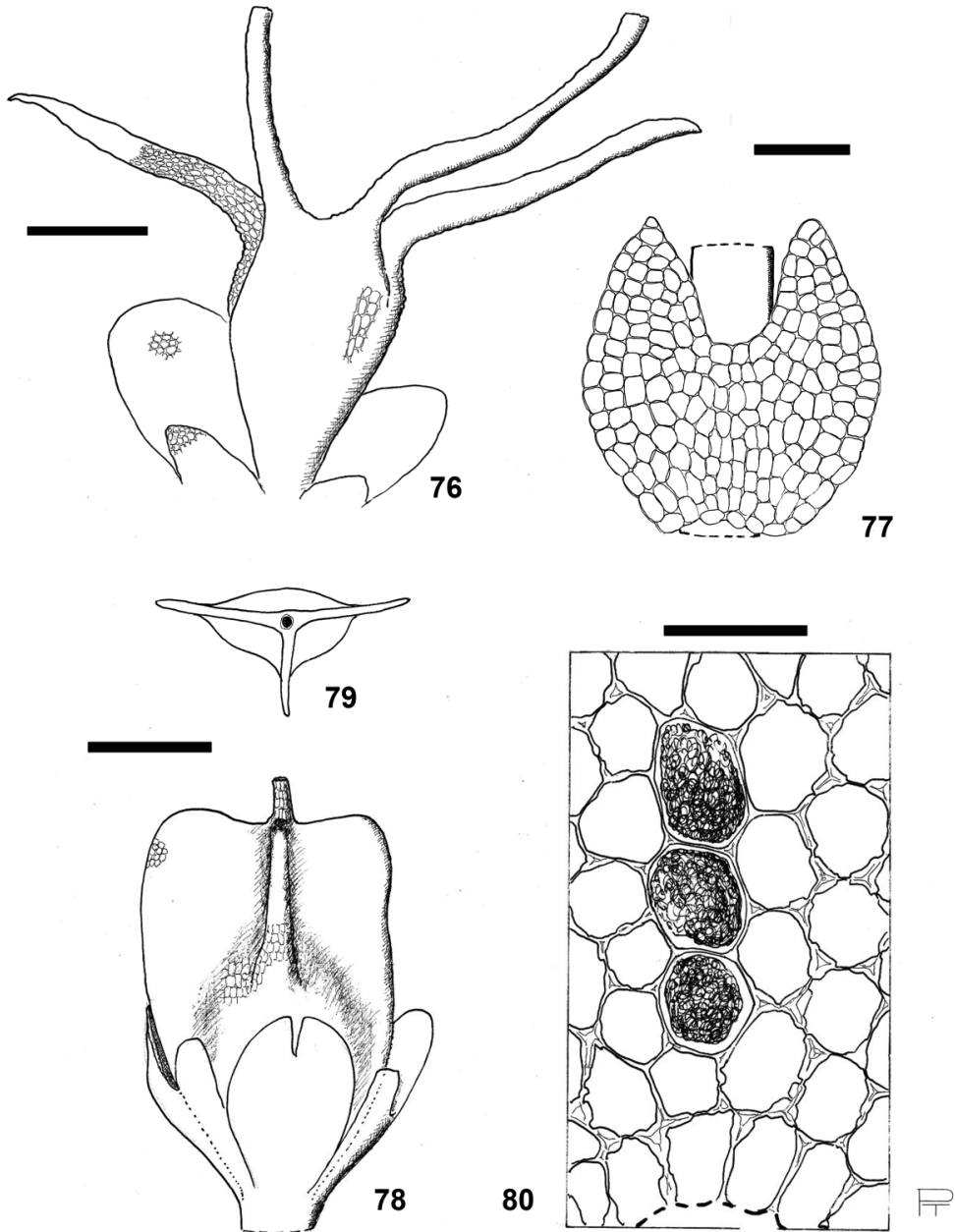
with involute margin and narrowing apex. Underleaves relatively small, orbicular, 2–3 times stem width, with U- or V-shaped incision to 1/3 depth and with entire or minutely denticulate margin.



Figs 70–75. *Ceratolejeunea saroltae* Pócs, *sp. nov.* 70 – habit, ventral view (scale bar = 600 µm), 71 – habit, dorsal view (scale bar = 800 µm), 72 – ventral merophyte and lobules (scale bar = 100 µm), 73 – moniliate ocelli (scale bar = 50 µm), 74 – underleaf (scale bar = 100 µm), 75 – perichaetium, perianth with broken beak (scale bar = 200 µm). All SEM micrographs made from the type.

Autoicous. Androecia on short side branches or on branch tips, consisting of 2–6 pairs of bracts. Gynoecia with one subgynoecial innovation. Fe-

male bracts dentate. Perianth with pyriform body 450–500 µm long and 290–330 µm wide, with mammillose walls and with four narrow horns



Figs 76–80. 76 & 77 – *Ceratolejeunea andringitiae* Pócs, *sp. nov.* 76 – perianth and bracts (bracteole removed), ventral view (scale bar = 250 µm), 77 – underleaf (scale bar = 100 µm). 78–80 – *Ceratolejeunea saroltae* Pócs, *sp. nov.* 78 – perianth with bracts and bracteole (scale bar = 250 µm), 79 – perianth seen from above (scale bar = 250 µm), 80 – leaf base cells with vittae (scale bar = 50 µm). All drawings made from the types.

which can far exceed body length (480–560 µm long and 40–60 µm, 3–5 cells wide), with acute or broken apex. The fragile apex possibly serves

vegetative reproduction. The perianth horns are erect or directed sideways, giving a spider-like aspect.

Most of the above characters quite agree with the properties of the Asian *Ceratolejeunea moniliata* Herz., *Mitt. Inst. Allg. Bot. Hamburg* 7: 205, Fig. 7a–f (1931). The most important difference is in the arrangement of ocelli. In *C. andringitrae* the ocelli are arranged in irregular groups, sometimes in rows perpendicular to the lobe axis, while *C. moniliformis*, as its name suggests, has moniliate basal ocelli consisting of 3–5(–6) cells arranged in a row parallel to the axis of the lobe, often accompanied by a second, short row of 2 cells. In addition, the apex of the perianth horns in *C. moniliata* is never as narrow and acute as in *C. andringitrae* (Herzog 1931; Mizutani 1981, and my own observations of a *C. moniliata* specimen from Papua New Guinea, Central Province, K. B. Sawmill, Ehu Creek, 13 km of Sogeri, 600 m a.s.l., on palm leaves, *Streimann & Naoni* 16480, 16 Feb. 1981, H, dupl. ex CBG). As the arrangement of the ocelli (compare Figs 26, 29–37 with figs 42, 44–47) is considered to be ‘the most important classification and identification character in the genus *Ceratolejeunea*’ (Dauphin 2003a: 7), I feel this difference is enough to justify the description of *Ceratolejeunea andringitrae* as an independent species. There is no doubt that the two species are closely related. *C. andringitrae* may be the African vicariant pair of the Asian *C. moniliata*, which is among the most common epiphyllous species in Papua New Guinea (Pippo 1994: 45).

DISTRIBUTION. At present only known from the type locality in the Andringitra Mts of SE Madagascar, where it seems to be abundant.

7. *Ceratolejeunea saroltae* Pócs, *sp. nov.*

Figs 64–75 & 78–80

Planta badius vel olivaceus, foliis cum ocellis tri- vel quadricellularis moniliatis. Utriculi inaequaliter binatis ad basim ramorum adsunt. Differt a toto speciebus alienis Ceratolejeuneae perianthis obconico cordatis acute tricarinatis sine cornibus.

TYPE: MADAGASCAR, Toamasina Province, Maromizaha forest, mossy montane rainforest with bamboo (*Nastus* sp.) undergrowth on the summit ridge of Mt.

Maromizaha, south of Andasibe Nat. Park, 1080–1214 m a.s.l., on twigs, *Sarolta Pócs* 9890/BJ, 26 Aug. 1998 (HOLOTYPE: EGR). At the same time and locality, on *Pandanus* leaf intermixed among *C. diversicornua* Steph., *Sarolta Pócs* 9890/CK (PARATYPE: EGR).

ETYMOLOGY: named in honor of its collector, my wife, Sarolta Pócs.

Shiny, olive to chestnut brown plants creeping on twigs or forming patches 1–3 cm diam. on leaves. Shoots densely pinnately branched, 10–40 mm long and with leaves 1.0–1.5 mm wide. Stem 80–105 µm diam., ventral merophyte cells rectangular, 15–20 × 8–12 µm. Unequal pairs of utriculi 250–500 µm in size at branch bases. Leaves concave, slightly asymmetric-ovate, 720–900 × 480–550 µm, apex rounded, often incurved, margin entire, the dorsal base straight, not auriculate, covering but not exceeding the stem. Ocelli 30–40 × 25–30 µm, moniliate with 3–4 cells in a row parallel with lobe axis. Apical lobe cells rectangular, 8–12 × 8–14 µm, median cells isodiametric penta- or hexagonal, 16–26 µm diam., the basal ones slightly elongate hexagonal, 28–40 × 21–39 µm. Cell walls thin with very small trigones, with no or very weak intermediate thickenings. Middle lamellae clearly visible but not darker in color. Oil bodies of *Calypogeia* type as described by Gradstein *et al.* (1977): 3–5 per cell, in ocelli *Leucolejeunea*-type: 1 per cell. Lobule triangular ovate, inflated with involute margin, about 1/5 lobe length when well developed, 100–200 × 180–240 µm, 8–11 cells long and 6–9 cells wide, with straight, smooth keel and with a 16–20 µm long, acute, somewhat falcate tooth directed away from the stem. Underleaves 3–4 times stem width, plane, orbicular or suborbicular, 280–320 × 250–320 µm, with entire margin and with a narrow slit between the 10–13-cell long and 10–13-cell wide obtuse segments. Autoicous, androecia on short lateral branches with 3–4 pairs of almost entire, acuminate bracts and with one basal bracteole. Gynoecia on lateral branches of different length, with or without one subgynoecial innovation. Female bracts nearly 1/2 the length of perianth, with entire lobe and a lobule 1/3 the length of perianth. Bracteole about the length of bract lobule, obovate

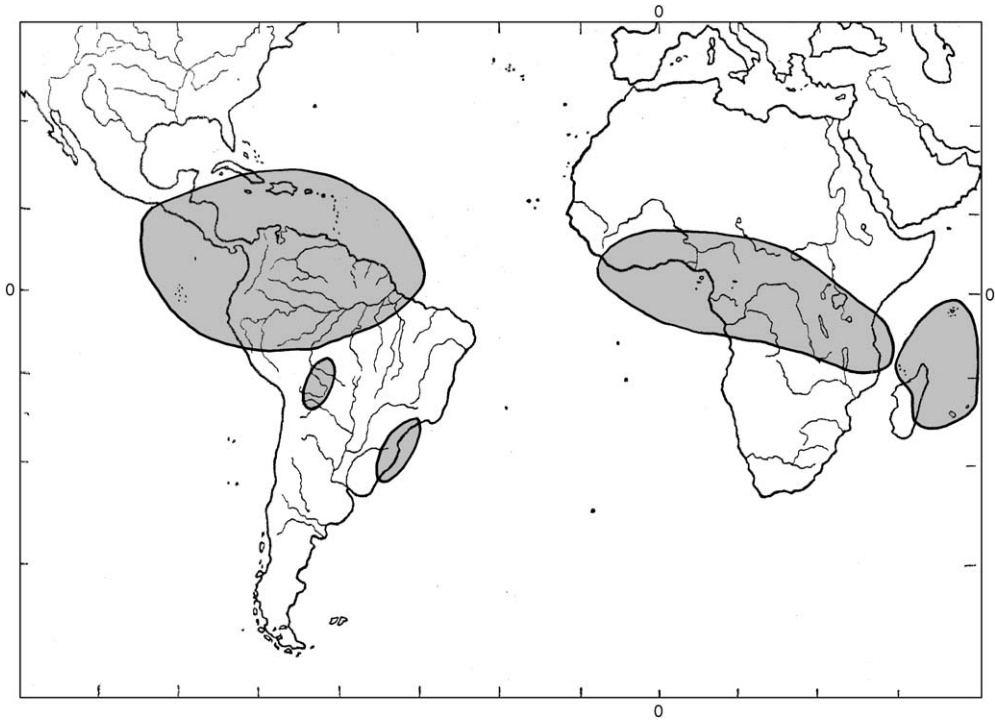


Fig. 81. World distribution of *Ceratolejeunea cornuta* (Lindenb.) Schiffn. The Neotropical part is based on the map of Dauphin (2003a: 45, Fig. 20).

with cuneate basis and with a short, narrow slit. Perianth shiny, dark brown, obconical-cordate with truncate apex, sharply tricarinate with two lateral and one ventral wing, $750\text{--}760 \times 480\text{--}490\text{ }\mu\text{m}$ not including beak. Beak tubular, relatively long, $60\text{--}80 \times 40\text{--}48\text{ }\mu\text{m}$, 3–5 cells long and wide, composed of elongate rectangular cells.

The plants are very fertile, with many tricarinate perianths, making the species easily recognizable. Due to its tricarinate perianths, hitherto unknown to occur within *Ceratolejeunea*, the new species appears to be quite isolated within its genus.

DISTRIBUTION. At present known only from its type locality in central eastern Madagascar. The species appears to be endemic to the area.

DISCUSSION

Ceratolejeunea is similar to several other cryptogamic and even phanerogamic genera (e.g.,

Colura, *Leucoloma*, *Adansonina*) in having as many or even more species in the East African archipelago than in the much larger African mainland. Among the seven species of *Ceratolejeunea* in the East African Islands, three species are known from the Seychelles, one from the Comores, six from Madagascar, three from Réunion and two from Mauritius. As is the case with other bryophytes (O'Shea 1997), the rate of endemism is relatively high on these islands: two of the seven species, *C. andringitrae* and *C. saroltae*, are known from here only. *Ceratolejeunea belangeriana* is an Afro-Asian-Pacific (Palaetropic) disjunct, while *C. cornuta* is of the Afro-American element. Interestingly, three species, *C. diversicornua*, *C. papuliflora* and *C. umbonata*, have a West-African – Indian Ocean disjunction, not occurring in the eastern half of continental Africa. Originally they may have occupied a continuous tropical African area and became extinct in the eastern part of the

mainland during drier climatic periods, probably in the Pleistocene.

Species of *Ceratolejeunea* do not occur in the dry tropics, although they prefer the well-illuminated and relatively dry upper canopy branches or openings in rainforest areas. Probably they cannot survive prolonged dry periods. As a consequence, they do not occur in savannah or other open woodland with an actual dry season, except for continually mist-affected areas.

KEY TO THE SPECIES KNOWN FROM THE EAST AFRICAN ISLANDS

A. SPECIMENS WITH PERIANTHS

1. Ocelli moniliate, forming a row of 3–4 cells parallel to the lobe axis. Perianth tricarinate with two lateral and one ventral wing. Bracts entire. 7. *C. saroltae*
- 1* Basal ocelli scattered or geminate or in groups of different shape. Bracts at least distally with dentate margin. 2
2. Basal ocelli in a row of 3–5 cells perpendicular to the lobe axis + scattered ocelli present. Perianth body small with four 240–330 µm long, finger-like horns with parallel or sometimes upwards-broadened sides and round apex. 4. *C. papuliflora*
- 2* Ocelli scattered, geminate or in irregular groups. 3
3. Ocellus basal, single or none. Perianth ovate without horns or wings. 5. *C. umbonata*
- 3* Ocelli different. Perianth with shorter or longer horns. 4
4. Perianth with short or longer, inflated, unequal horns with rounded apex. Basal ocelli isolated or geminate. 3. *C. diversicornua*
- 4* Perianth horns narrowing towards their apex, more or less equal in size. 5
5. Perianth horns equal or much longer than the perianth body (spider-like appearance), very narrow and acute. Ocelli in irregular groups. 6. *C. andringitrae*
- 5* Perianth horns shorter than the perianth body. Ocelli scattered or geminate, rarely in small groups. 6
6. Perianth half-immersed in the perichaetium. Underleaves of various width 2. *C. cornuta*
- 6* Perianth stalked, more than half of its body emergent from the perichaetial leaves. Underleaves never broader than 3× stem width. 1. *C. belangeriana*

B. SPECIMENS WITHOUT PERIANTHS¹

1. Ocelli moniliate, forming a single row of 3–4 cells parallel to the lobe axis. Female bracts entire. 7. *C. saroltae*
- 1* Basal ocelli scattered or geminate or in groups of different shape. Female bracts at least distally with dentate margin. 2
2. Basal ocelli in a row of 3–5 cells perpendicular to the lobe axis + scattered ocelli present. 4. *C. papuliflora*
- 2* Ocelli isolated or geminate or in irregular groups. 3
3. Ocellus basal, single or none. Underleaves mostly orbicular. 5. *C. umbonata*
- 3* Ocelli different. Underleaves of various shape . . . 4
4. Ocelli in irregular groups not farther than 2–3 cells distant from the lobe base. Underleaves orbicular without a cordate base, never wider than 3× stem width, with a U- or V-shaped incision. 6. *C. andringitrae*
- 4* Ocelli basal, isolated or geminate. Underleaf base often cordate. 1. *C. belangeriana*,
2. *C. cornuta*, 3. *C. diversicornua*²

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¹ Using this key, one should compare the plant with a detailed illustration or a correctly identified herbarium specimen

² These three species are hardly distinguishable without seeing their perianth

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