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**Key words:** East African Islands, *Drepanolejeunea*, *Microlejeunea*, *Rectolejeunea*, *Vitalianthus*

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## The reappraisal of *Capillolejeunea* S.W.Arnell (Marchantiophyta, Lejeuneaceae)

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### Abstract

*Capillolejeunea* (Lejeuneaceae), known only from the East African Islands, is resurrected. It is characterized by and easily separated from *Drepanolejeunea* by the unbroken basal vitta of 3–5(–9) ocelli in leaf lobes, absence of scattered ocelli in leaf lobes, outer lateral margin of the upright underleaf lobes with a tooth, and single, unicellular tooth of the leaf lobule. The Madagascan *Drepanolejeunea geisslerae* is transferred to *Capillolejeunea*. *Capillolejeunea* is the only liverwort genus endemic to Africa. A key to known species of *Capillolejeunea* is provided.

**Key words:** East African Islands, *Drepanolejeunea*, *Microlejeunea*, *Rectolejeunea*, *Vitalianthus*

### Introduction

*Capillolejeunea* Arnell (1965: 69), a monospecific genus, was established based on *Capillolejeunea mascarena* Arnell (1965: 69) from Mauritius. The most striking features of the plant are the asymmetrically falcate leaves usually with ciliate teeth at apex, single, unicellular, somewhat curved, apical tooth of the leaf lobule with a hyaline papilla at its proximal base, unbroken basal vitta of 3–5 ocelli in leaf lobes, absence of scattered ocelli in leaf lobes, bilobed underleaves with upright lobes usually with a tooth on their outer margins, and gynoecial innovations with a pycnolejeuneoid leaf sequence (Arnell 1965; Zhu & Grolle 2003). Owing to the above-mentioned features of the species also occurring in *Drepanolejeunea* (Spruce 1884: 186) Stephani (1891: 209). Zhu & Grolle (2003) reduced *Capillolejeunea* to a synonym of *Drepanolejeunea*, and transferred *Capillolejeunea mascarena* to *Drepanolejeunea* as *D. mascarena* (Arnell 1965: 69) Zhu & Grolle (2003: 467).

In the course of our studies on the taxonomy and phylogeny of *Drepanolejeunea*, we found that the combination of several important features such as the 3–5 (–9) moniliate ocelli in a continuous row in the leaf lobes, lack of scattered ocelli in the leaf lobe, bilobed underleaves with upright lobes usually with a tooth on their outer margins, and a single lobular tooth is unique in two *Drepanolejeunea* species restricted to the East African islands (*Drepanolejeunea mascarena* and *D. geisslerae* Pócs (2001: 70)) and not found in any other species of this genus. Our unpublished molecular data (*rbcL*, ITS, *trnG* and *trnL-F*) also show that *Drepanolejeunea mascarena* and *D. geisslerae* are separated from the *Drepanolejeunea* clade, and that the two species form a monophyletic lineage near *Rectolejeunea* Evans (1906: 8). Morphologically *Rectolejeunea*, however, is immediately distinguished from *D. mascarena* and *D. geisslerae* by several reliable features such as the robust stem with 7–10 rows of medullary cells, the absence of oil bodies in ordinary cells of the leaf lobe, presence of scattered ocelli in the leaf lobe, and absence of an unbroken vitta of 3–5 moniliate ocelli. Therefore, morphological, molecular, and distributional evidence support that *Capillolejeunea* represents a good, natural group. The generic status of *Capillolejeunea*, thus, has to be resurrected and the following treatment is necessary.

## Taxonomic Treatment

***Capillolejeunea*** S.W.Arnell, Svensk Bot. Tidskr. 59: 69. 1965 (Arnell 1965).

Type:—*Capillolejeunea mascarena* S.W.Arnell, Svensk Bot. Tidskr. 59: 69. 1965 (Arnell 1965).

Autoecious. Plants green to yellowish green, 2–12 mm long. Shoots 0.4–0.9 (–1.1) mm wide, irregularly branched, branching of the *Lejeunea*-type, leaf sequence of vegetative branches lejeuneoid. Stem 40–60 µm in diameter, in transverse section with 7 cortical cells and 3 medullary ones, ventral merophyte 2 cells wide. Rhizoids at base of underleaves, few, tufted, usually hyaline, rhizoid disc absent. Leaves contiguous to imbricate, diverging from stem at an angle of 50–60°; leaf lobes asymmetrically ovate or obovate, somewhat concave, falcate, 0.3–0.6 mm long, 0.2–0.3 mm wide, margin entire, dentate to ciliate, apex ± incurved; leaf lobules ovate, strongly inflated, ca. 1/3 as long as the lobes (up to 1/2 as long as lobes in some branch leaves), lateral free margin straight, usually slightly incurved (except for apex), bordered by 4 subquadrate to rectangular marginal cells, apex usually constricted, with a unicellular, usually curved apical tooth, directed towards leaf apex, keel arched, smooth, hyaline papilla subspherical to oblong, situated at the proximal base of apical tooth. Cells of leaf lobe with thin to moderately thickened walls and small trigones, usually without intermediate thickenings. Oil bodies small, compound (fide Arnell 1965). Ocelli oblong, 3–5 (–9) per leaf lobe, forming 1 (–2) longitudinal, unbroken row(s), the lowermost always basal (next to stem cell) or suprabasal (cf. Zhu & So 2001). Underleaves remote, longer than wide, 1.5–3 times as wide as stem, bilobed to 1/2 their length, sinus U- or V-shaped, lobes narrowly triangular, erect, acute at apex, 3–7 cells long, 3–4 cells wide at base, inner lateral margin nearly entire, outer lateral one usually with a small tooth, insertion line almost straight to subtransverse, base cuneate (never cordate). Androecia intercalary, rarely terminal, usually on long lateral branches or on main shoots, bracts in 2–8 pairs, hypostatic, antheridia 1–2 per bract, subspherical, bracteoles 1–3, borne only at the basal portion of androecium, similar to ordinary underleaves. Gynoecia usually on short or long branches, with 1(–2) pycnolejeuneoid innovations; bracts obovate, deeply and unequally bifid, the lobe broadly obovate, apical margin usually crenulate to slightly dentate, rarely with 1–several ciliate teeth, base with 3–8 ocelli as in leaf lobe, lobule oblong or lingulate, ca. 1/2 as long as the bract lobe, apex obtuse to acute, keel slightly sinuate to straight, ca. 2/3 as long as the lobule; bracteole connate with bracts on both sides at base, oblong, margin nearly entire to slightly dentate, apex bilobed to 1/5–1/4 its length, sinus usually obtuse. Perianths about 1/3–2/3 exserted, obovoid to obtriangular, 0.40–0.75 mm long, 0.23–0.40 mm wide at middle, inflated, with (4–) 5 keels, antical keel a little lower than the others and entire, but usually indistinct, keels entire to crenulate, sometimes with weak denticulations and ciliate or lacinate projections near apex, surface of perianth smooth, beak short, 1–3 cells long, ocelli in perianth several to numerous, scattered. Seta articulate, containing 12 outer cells rows surrounding 4 inner ones. Asexual reproduction not clear, possibly by slightly specialized branchlets.

***Capillolejeunea* is endemic to the East African Islands. It is also the only liverwort genus endemic to Africa. At present it contains two species which are keyed out in the following key.**

1. Lowermost ocelli suprabasal; dorsal margin of leaf lobe dentate to toothed, apical margin of leaf lobe dentate.....*C. geisslerae*
1. Lowermost ocelli basal; dorsal margin of leaf lobe almost entire; apical margin of leaf lobe usually ciliate .....*C. mascarena*

***Capillolejeunea geisslerae* (Pócs) R.L.Zhu, Qiong He, Y.M.Wei & Pócs, comb. nov.**

Basionym:—*Drepanolejeunea geisslerae* Pócs, Candollea 56(1): 70. 2001 (Pócs 2001). Type:—MADAGASCAR. Prov. Antsiranana: “Réserve Spéciale de Manongarivo (13°59'N, 48°26'E), Prov. Antsiranana, Nord-Quest de Madagascar”, abundant on palm stem, 950–1050 m, 5 March 1999, P. Geissler 19559 (holotype: G!, isotype: EGR!, HSNU! ex EGR, TAN).

Illustrations:—Pócs (2001, p. 74, Tab. 1 as *Drepanolejeunea geisslerae*, p. 75, Tab. 2 as *D. geisslerae*, p. 76, Tab. 3 as *D. geisslerae*).

Habitat and distribution:—Corticulous and epiphyllous at altitudes of 800–1869 m, known only from Madagascar (Pócs 2001; Marline *et al.* 2012).

***Capillolejeunea mascarena* S.W.Arnell, Svensk Bot. Tidskr. 59: 69. 1965 (Arnell 1965).**

≡*Drepanolejeunea mascarena* (S.W.Arnell) R.L.Zhu & Grolle, Syst. Bot. 28: 467. 2003 (Zhu & Grolle 2003). Type:—MAURITIUS. Macabé: 1800 feet, Upland climax forest, 3 Oct. 1962, Een s.n. (holotype: S-14869!).

Illustrations:—Arnell (1965, p. 70, Fig. 2), Zhu & Grolle (2003, p. 468, Fig. 1 as *Drepanolejeunea mascarena*, p. 489, Fig. 2 as *D. mascarena*).

Representative specimens examined:—COMOROS. Ndzuwani (Anjouan) Island: submontane rain forest remnants intercropped with banana and taro, at the W side of Col De Moya, with Tambourissa and tree ferns, 700–800 m, corticolous, growing together with *Ceratolejeunea calabariensis* Steph., 23 March 1991, Pócs 9166/BB (JE). MADAGASCAR. Tamatave: route de Moramanga à Anosibe, au km 39, épiphylle, 15 Sept. 1953, Millot & Bosser 6320/4 (JE, PC); Masoala Peninsula: Montane rain forest on the summit ridge SE of Ambanizana village, 15°37'S, 50°0'E, 660–720 m, epiphyllous on Pandanus leaf, 11 Sept. 1994, Pócs 9449/AC, AF (JE). MAURITIUS. Macabé: sur les arbres d'une forêt climatique d'altitude, ca. 700 m, 19 Sept 1971, Onraedt 71.Ma.139 (JE); 1800 feet, Upland climax forest, 3 Oct. 1962, Een M23 (S-B7092); Black-River: Mont Cocotte, 700 m, sur un arbre d'une forêt climatique, 1971, Onraedt 71.Ma. 261 & 274 (JE); 700 m, on bark, 6 Aug. 1996, Pócs 9665/AA (PC).

Habitat and Distribution:—Corticulous and epiphyllous at 660–800 m, known from Comoro Islands, Madagascar, and Mauritius.

## Discussion

*Capillolejeunea* is well characterized by the 1) slender stem with seven cortical cells and three medullary ones in transverse section, 2) single, unicellular, curved tooth of the leaf lobule, 3) proximal hyaline papilla, 4) 3–5 (–9) moniliate ocelli in a continuous row in the leaf lobes, 5) lack of scattered ocelli in the leaf lobe, 6) free margin of the leaf lobule bordered by four rectangular cells, 7) outer lateral margin of the upright underleaf lobes with a tooth, 8) pycnolejeuneoid gynoecial innovation, and 9) absence of specialized cladia. The combination of several characters such as character 2, 4, 5 and 7 is unique in *Capillolejeunea* and not found in any species of *Drepanolejeunea*, the fourth largest genus of Lejeuneaceae (He *et al.* 2012a). Morphologically *Capillolejeunea* is most similar to *Drepanolejeunea* with about 110 species (He *et al.* 2012a). Several species also from the East African Islands in *Drepanolejeunea* subg. *Kolpolejeunea* Grolle (1976: 193), e.g., *Drepanolejeunea mauritiana* Tixier (1993: 47) and *D. madagascariensis* (Stephani 1913: 563) Grolle in Grolle & Onraedt (1974: 232) (Grolle 1976), also have 3–5 moniliate ocelli in a continuous row in the leaf lobes, but they differ from *Capillolejeunea* in the presence of scattered ocelli, two lobular teeth, and entire underleaf lobes widely spreading. Over three moniliate ocelli in a continuous row in the leaf lobes also occur in several genera of Lejeuneaceae, e.g., *Microlejeunea* (Spruce 1884: 286) Stephani (1888: 286). (Wei & Zhu 2013; Lee 2013), *Cheilolejeunea* (Spruce 1884: 251) Stephani (1890: 284). (Wei *et al.* 2013), *Vitalianthus* Schuster & Giancotti (1993: 447) (He *et al.* 2012b; Wei *et al.* 2013), *Otolejeunea* Grolle & Tixier in Tixier (1980: 609) (Grolle 1986), *Ceratolejeunea* (Spruce 1884: 198) Jack & Stephani (1892: 16) (Mizutani 1981; Dauphin 2003). *Vitalianthus*, a Brazilian and Chinese genus with two species (He *et al.* 2012b; Wei *et al.* 2013), also resembles *Capillolejeunea* in the moniliate ocelli in a continuous row in the leaf lobes, absence of scattered ocelli, and single, unicellular lobular tooth. The former, however, differs in the entire leaf margin, much smaller leaf cells, and non-falcate leaves. The taxa of *Microlejeunea* with the moniliate ocelli in a continuous row in the leaf lobes, e.g., *M. moniliata* (Mizutani 1979: 357) R.L.Zhu & Y.M.Wei in Wei & Zhu (2013: 308), are readily separated by the lejeuneoid gynoecial innovation, much smaller leaf cells, entire leaves, and keel of female bract usually winged (Dong *et al.* 2013; Wei & Zhu 2013). Three *Cheilolejeunea* species with an unbroken vitta of over 4 moniliate ocelli, *C. urubuensis* (Zartman & Ackerman 2002: 267) R.L.Zhu & Y.M.Wei in Wei *et al.* (2013: 50), *C. falsinervis* (Sande Lacoste 1855: 421) Schuster & Kachroo in Kachroo & Schuster (1961: 509) (Mizutani 1978; Zhu *et al.* 2002), and *C. insignis* Jovet-Ast & Tixier (1962: 25), are distinguished from *Capillolejeunea* by the distal hyaline papilla, multi-cellular lobular tooth, and the robust stem with over four rows of medullary cells. *Capillolejeunea* differs from *Otolejeunea* in the slender stem with seven cortical cells and three medullary ones in transverse section. Moreover, the perianths in *Otolejeunea* bear two auriculate or horn-shaped keels. *Ceratolejeunea* is readily separated from *Capillolejeunea* by the pale brownish plants and horn-like projections of the perianths.

*Capillolejeunea* may be close to the Neotropical genus *Rectolejeunea* with which it shares pycnolejeuneoid gynoecial innovations, single, unicellular, curved tooth of the leaf lobule with a proximal hyaline papilla, and absence of specialized cladia (Reiner-Drehwald & Grolle 2012). *Capillolejeunea* differs from *Rectolejeunea* in the slender stem with only 3 rows of medullary cells, the presence of oil bodies in ordinary cells of the leaf lobe, absence of scattered ocelli in the leaf lobe, and presence of an unbroken vitta of 3–5(–9) moniliate ocelli.

Gradstein (2003) established a new classification of Lejeuneaceae. He placed *Drepanolejeunea* in the subtribe Drepanolejeuneinae Gradstein (2003: 14), which contains two genera: *Drepanolejeunea* and *Vitalianthus*. Although *Capillolejeunea* is most similar to *Drepanolejeunea* in morphology, our preliminary molecular data reveal that *Capillolejeunea* is much closer to the subtribe Lepidolejeuneinae Gradstein (2013: 13), which includes two genera: *Lepidolejeunea* Schuster (1963: 139) and *Rectolejeunea*. The presence of oil bodies in green cells, the slender stem with seven cortical cells and only three medullary ones in the transverse section, and the absence of scattered ocelli in the leaf lobe, however, are rather different from Lepidolejeuneinae. The exact systematic position of *Capillolejeunea* still remains uncertain pending intensive sporophytic and molecular investigations of *Rectolejeunea* and *Lepidolejeunea*, and other related genera.

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