



Notes on Early Land Plants Today. 36. Generic treatment of Lophocoleaceae (Marchantiophyta)

LARS SÖDERSTRÖM¹, BARBARA CRANDALL-STOTLER², RAYMOND E. STOTLER², JIŘÍ VÁŇA³, ANDERS HAGBORG⁴ & MATT VON KONRAT⁴

¹Department of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway; lars.soderstrom@bio.ntnu.no

²Department of Plant Biology, Southern Illinois University, Carbondale, Illinois 62901-6509, USA; crandall@plant.siu.edu, stotler@plant.siu.edu

³Department of Botany, Charles University, Benátská 2, CZ-12801 Praha 2, Czech Republic; vana@natur.cuni.cz

⁴Department of Botany, The Field Museum, 1400 South Lake Shore Drive, Chicago, IL 60605–2496, USA; hagborg@pobox.com, mvonkonrat@fieldmuseum.org

Abstract

Recent molecular phylogenetic studies on Lophocoleaceae have recovered some well-supported monophyletic lineages within *Chiloscyphus s. lat.* that merit recognition at the generic level. As a consequence, *Chiloscyphus* is herein circumscribed to include only *Chiloscyphus* subgen. *Chiloscyphus*, *Chiloscyphus* subgen. *Connati* is elevated to generic rank to which the new name *Cryptolophocolea* is applied, and *Lophocolea*, *Pachyglossa* and *Clasmatocolea* are recognized as distinct genera. *Tetracymbaliella* is transferred to the Brevianthaceae, and a synopsis of the genera currently recognized in Lophocoleaceae is provided.

Current knowledge of the family Lophocoleaceae

During the last 50 years Lophocoleaceae Vanden Berghen (1956: 208) have (mostly as Geocalycaceae Klinggräff 1858: 34) mainly been circumscribed in a very broad sense. However, Hentschel *et al.* (2006a) showed that Lophocoleaceae is well separated from Geocalycaceae and Harpanthaceae Arnell (1928: 147), but remains a large and diverse family.

Lophocoleaceae is a family with a turbulent history and many taxa have been moved back and forth among genera. Engel & Schuster (1985) introduced a very broad concept of the genus *Chiloscyphus* including in it all species generally referred to *Chiloscyphus* and *Lophocolea* at that time. This concept was not adopted by several authors, including Grolle (1995), Paton (1999), Gradstein & Costa (2003), and Crandall-Stotler *et al.* (2009), but has been more widely accepted since molecular studies showed that *Chiloscyphus s. str.* nests within the traditionally circumscribed *Lophocolea* (He-Nygrén & Piippo 2003, Hentschel *et al.* 2006a). However, several later studies (Hentschel *et al.* 2007, Glenny *et al.* 2009, Engel *et al.* 2010, Engel & He 2010) have shown that unless the genus *Chiloscyphus s. lat.* is split into additional genera, *Pachyglossa*, *Leptoscyphus* and *Clasmatocolea* would also have to be included within it. But the same studies also show that there are several well-supported monophyletic lineages within the *Chiloscyphus s. lat.* clade that merit recognition at the generic level.

All molecular analyses resolve the taxa assigned to *Chiloscyphus* subgen. *Connati* in a strongly supported clade that is sister to the rest of *Chiloscyphus*, or even to a combined *Chiloscyphus-Leptoscyphus* clade (Hentschel *et al.* 2007). Recognizing *Chiloscyphus* subgen. *Connati*, as circumscribed by Engel (2010), at a genus level would allow the robustly supported clade of *Leptoscyphus* to be kept following Vanderpoorten & Long (2006) and Vanderpoorten *et al.* (2010), as discussed by Hentschel *et al.* (2007) and Crandall-Stotler *et al.* (2009).

Likewise, *Lophocolea*, which is resolved as the lineage labelled *Chiloscyphus* subg. *Lophocolea* (Dumortier 1831: 59) J.J.Engel et R.M.Schust. in Engel (1998: 42) by Hentschel *et al.* (2006b), can also be recognized as a distinct genus with moderate to strong support, especially since this fairly large clade includes the generitype of *Lophocolea*, but excludes that of *Chiloscyphus* (Crandall-Stotler *et al.* 2009). According to current molecular evidence (Hentschel *et al.* 2006a, 2006b, Glenny *et al.* 2009), the genus should comprise taxa previously assigned to *Chiloscyphus* subg. *Lophocolea* (excluding *Chiloscyphus* subg. *Lophocolea* sect. *Bicornuti* (Spruce 1885:424) Engel & Schuster (1985: 409), which was transferred to *Chiloscyphus* subg. *Connati* by Engel in 2010), *Chiloscyphus* subg. *Microlophocolea* (Spruce 1885: 426) Engel (1999: 22), *Chiloscyphus* subg. *Fragilifoliae* (Schuster 1978: 245) Engel & Schuster (1985: 409) and *Chiloscyphus* subg. *Spinoscaphus* Engel (2010: 1999).

Of the remaining taxa included by Hentschel *et al.* (2007) in the "Chiloscyphus I" clade, *Chiloscyphus s.str.*, has been consistently resolved as a robustly supported, monophyletic lineage, comprising *Chiloscyphus polyanthos* (Linnaeus 1753: 1131) Corda (1829: 651) (the generitype of *Chiloscyphus*) and *Chiloscyphus pallescens* (Hoffmann 1796: 87) Dumortier (1831: 67). Recognizing *Chiloscyphus* to include only *Chiloscyphus* subg. *Chiloscyphus* is consistent with Grolle's (1995) contention that *Chiloscyphus* is a small, strictly Laurasian genus that is morphologically isolated from the more speciose, broadly distributed elements of the Lophocoleaceae, like *Lophocolea* and *Heteroscyphus*.

Disposition of the remaining taxa in the "Chiloscyphus I" clade is problematic. In Hentschel *et al.* (2006b, 2007), *Chiloscyphus* subg. *Notholophocolea* (Schuster 1980: 183) Engel & Schuster (1985: 410) is robustly supported as a monophyletic lineage, with *Pachyglossa tenacifolia* (Hook.f. et Taylor in Hooker 1845: 152) Herzog & Grolle (1959: 153) moderately supported sister to it. In the analysis of Glenny *et al.* (2009), on the other hand, *Chiloscyphus* subg. *Notholophocolea* is nested in *Lophocolea*. These contrasting results may be due to the use of different loci and/or different taxa by the two groups. The analyses of Hentschel *et al.* (2006b, 2007) include two accessions of *Chiloscyphus (Notholophocolea) gottscheoides* (Bescherelle & Massalongo 1886: 631) Engel & Schuster (1985: 415) and a single accession of *Chiloscyphus (Notholophocolea) austrigenus* (Hooker & Taylor 1844: 466) Engel & Schuster (1985: 411) subsp. *austrigenus* from southern South America in an nrITS dataset, while that of Glenny *et al.* (2009) is based on 3 plastid loci and a single accession of *Chiloscyphus (Notholophocolea) austrigenus* subsp. *okaritanus* (Stephani 1906: 785) Engel (1992: 113) from New Zealand. Obviously, more extensive molecular studies of this complex are needed to resolve unambiguously the relationships of these geographically separated taxa. However, on the basis of morphological similarities (Schuster 1980) and the more extensive sampling of Hentschel *et al.* (2007) *Chiloscyphus* subg. *Notholophocolea* should be transferred to *Pachyglossa*, and *Pachyglossa* should continue to be recognized as a genus.

A polyphyletic *Clasmatocolea* is also resolved within the "Chiloscyphus I" clade with most species currently included in molecular studies widely separated from *Clasmatocolea vermicularis* (Lehmann 1829: 361) Grolle (1960: 28), which is morphologically close to or conspecific with the generitype, *Clasmatocolea heterostipa* Spruce (1885: 441). These results are not surprising given the morphological heterogeneity of the six subgenera recognized to comprise the genus (Engel 1980). For example, *Clasmatocolea rigens* (Hooker & Taylor 1844: 461) Engel (1973: 156) (*Clasmatocolea* subg. *Protoclasmatocolea* Engel (1980:44)), not included in molecular studies, is morphologically very similar to species of the genus *Lophocolea* (s. str.), and it has been suggested that *Clasmatocolea cucullistipula* (Stephani 1900) Grolle (1960: 71) (*Clasmatocolea* subg. *Plicatocalyx* Engel (1980: 183)) should perhaps be separated at a generic level (Engel 1980). Since the molecular data of Hentschel *et al.* (2007), however, do not provide unambiguous resolution of the lineages within *Clasmatocolea*, it should be kept in its current form until the genus is more broadly sampled.

On the basis of molecular evidence, three monotypic genera have been recently reduced to older taxa. Specifically, *Amphilophocolea sciophila* Schuster (2001: 98) of the monotypic genus *Amphilophocolea* Schuster (2001: 98) has been shown by Engel *et al.* (2010: 47) to be conspecific with *Heteroscyphus knightii* (Stephani 1908: 129) Grolle (1987: 251), *Cyanolophocolea echinella* (Gottsche *et al.* 1847: 703) Schuster (2001: 102) has been transferred to *Heteroscyphus* (Engel & He 2010: 155), and *Physotheca autoica* Engel &

Gradstein (2003:764) has been transferred to *Leptoscyphus* (Vanderpoorten et al. 2012: 252). Until representatives of the genera *Bragginsella*, *Conoscyphus*, *Evansianthus*, *Hepatostolonophora*, *Leptoscyphopsis*, *Otoscyphus*, *Perdusenina*, *Pigafettoa*, *Stolonivector* and *Xenocephalozia* are included in molecular studies, and their relationships to other genera of the Lophocoleaceae are resolved, they should remain as currently defined. The generic status of *Xenocephalozia* is especially problematic. The genus was initially reduced by Grolle (1966) to *Clasmatocolea*, with affinities suggested to *Clasmatocolea trachyopa* (Hooker & Taylor 1844: 471) Grolle (1960: 73) and *Clasmatocolea obvoluta* (Hooker & Taylor 1845: 80) Grolle (1960: 72), taxa recognized by Engel (1980) to comprise *Clasmatocolea* subg. *Lacerifolia* Engel (1980: 50). Characters supporting the relationship of *Xenocephalozia navicularis* (Stephani 1915: 835) Schuster (1965: 25) to this subgenus of *Clasmatocolea* include the slightly armed and strongly adaxially concave leaves and relatively small underleaves, as also noted by Engel (1980). In Hentschel *et al.* (2007), *Clasmatocolea trachyopa* and *Clasmatocolea obvoluta* form a well-supported lineage within the "*Chiloscyphus* I" clade. The relationship of this lineage to *Xenocephalozia* and its status as a genus, however, cannot be determined without more extensive sampling.

Many taxa that have been referred to *Chiloscyphus* in the past have not been included in molecular studies, so their phylogenetic affinities are unknown. None of them have been morphologically aligned with *Chiloscyphus* subg. *Chiloscyphus*, and should be excluded from *Chiloscyphus s. str.* as herein defined on the basis of morphology. Taxa included in *Chiloscyphus* subg. *Parachiloscyphus* Hässel (2000: 452) and *Chiloscyphus* subg. *Eurychiloscyphus* Hässel (2001: 38) show features in common with *Leptoscyphus*, where they were placed by Grolle (1962). *Chiloscyphus* subg. *Septati* Engel (2010: 125) is morphologically similar to *Stolonivector* and the two species in *Chiloscyphus* subg. *Phaeochiloscyphus* Engel & Schuster (1985: 409) have been previously aligned, respectively, with *Leptoscyphus* and *Heteroscyphus* (Hässel de Menéndez 1999).

Recent studies indicate that some elements included in Lophocoleaceae should be removed from the family. Engel and Schuster (1985) reduced *Tetracymbaliella* to a subgenus of *Heteroscyphus*, but in several molecular studies it is clearly resolved as a genus distinct from *Heteroscyphus* (e.g., Glenny *et al.* 2009; Engel & He, 2010). The genus is placed as sister to *Brevianthus* in He-Nygrén *et al.* (2006) and the two genera are sister to Plagiochilaceae Müll.Frib. et Herzog in Müller (1956: 877) instead of Lophocoleaceae in the same study, but sister to Lophocoleaceae in He & Glenny (2010). *Brevianthus* is monotypic but of the 3-5 species of *Tetracymbaliella*, only *Tetracymbaliella cymbalifera* (Hook.f. et Taylor in Hooker 1846: 151) Grolle (1961: 50) (the type of the genus) has been studied using molecular methods. Although morphologically quite different from each other, these two genera are tentatively placed in Brevianthaceae, pending additional studies. The genus *Deceptifrons* is provisionally placed in Lophocoleaceae pending further studies.

The genus *Pseudolophocolea* Schuster & Inoue in Schuster & Engel (1982: 71) was originally described as being closely related to *Pedinophyllopsis* Schuster & Inoue (1981: 311). The authors even speculated that the two genera might be regarded as subgenera of a single genus. Although both genera were placed in Geocalycaceae subfam. Leptoscyphoideae Schuster (1980: 267), an affinity with the plagiochiloid *Pedinophyllum* (Lindberg 1874: 366) Lindberg (1875: 504) was also noted. He-Nygrén & Piippo (2003) showed that *Pedinophyllopsis* is best placed in Plagiochilaceae, a hypothesis further supported by the molecular studies of Groth (2005). Based on the morphological similarities of *Pseudolophocolea* with *Pedinophyllopsis* and *Pedinophyllum* detailed in Schuster & Engel (1982), *Pseudolophocolea* is also placed in Plagiochilaceae.

Formal treatment

The format of this note follows Söderström *et al.* (2012) except that we use the Melbourne International Code of Nomenclature for algae, fungi, and plants (ICN; McNeill *et al.* 2012) instead of the Vienna International Botanical Code of Nomenclature (ICBN; McNeill *et al.* 2006).

Cryptolophocolea L.Söderstr., Crand.-Stotl., Stotler et Váňa, *gen. et stat. nov.*

Type:—*Cryptolophocolea ciliolata* (Nees) L.Söderstr., Crand.-Stotl., Stotler et Váňa.

Description:—Plants lophocoleoid in aspect; leaves opposite to subopposite, bifid, often with the ventral lobe larger than the dorsal; underleaves large, 2- or 4(6)-lobed, connate with the leaves on both sides, often broadly so; androecia on a leading stem or short lateral branch; antheridial stalks biseriate; gynoecia terminating the main shoot or a long leafy branch; perianths trigonous, with the mouth 3-lobed and the keels sometimes winged; inner capsule wall thickenings forming fenestrae.

= *Plagiochila* sect. V *Connatae* Lindenb., *Monogr. Hep. Gen. Plagiochilae*: XXIX, 1844 [1843] (Lindenberg 1843). Lectotype (Piippo 1985):—*Plagiochila ciliolata* (Nees) Lindenb. ≡ *Lophocolea* subgen. *Connatae* (Lindenb.) Piippo, *Acta Bot. Fenn.* 131: 165, 1985 (Piippo 1985) *nom. inval.* (ICN Art. 41.5, basionym cited erroneously); ≡ *Chiloscyphus* subgen. *Connati* (Lindenb.) J.J.Engel, *Novon* 9: 22, 1999 (Engel 1999), *nom. inval.* (ICN Art. 41.5; basionym cited erroneously); ≡ *Chiloscyphus* sect. *Connati* (Lindenb.) J.J.Engel, *Fieldiana, Bot., n.s.* 48: 133, 2010 (Engel 2010), *nom. inval.* (ICN Art. 41.5; basionym cited erroneously).

= *Chiloscyphus* sect. *Spiniferi* J.J.Engel, *Novon* 9: 22, 1999 (Engel 1999).

= *Chiloscyphus* sect. *Bicornutae* (Spruce) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 409. 1984 [1985] (Engel & Schuster 1985).

= *Chiloscyphus* sect. *Leucophylli* J.J.Engel, *Bryologist* 94: 312, 1991 (Engel 1991a).

Note:—This genus is based upon the expanded concept of *Chiloscyphus* subgen. *Connati* as treated by Engel (2010). Although we are changing the status of the Engel subgenus to the rank of genus, the name *Connatae* is a Latin technical term in use in morphology and cannot be used as a genus name following ICN Art. 20.2 (McNeill *et al.* 2012). In contrast to *Chiloscyphus s. str.*, which is characterized by undivided to retuse leaves, gynoecia borne on short, leafless lateral branches, and short inflated perianths with emergent fleshy calyptrae, *Cryptolophocolea* possesses bifid leaves, gynoecia that terminate leading shoots and elongate, trigonous perianths, often with winged keels. In these features it resembles *Lophocolea*. It is morphologically distinct from *Lophocolea*, however, in having large underleaves that are connate with the leaves on both sides, and in developing fenestrate, rather than unbranched, thickenings on the inner capsule wall. We have chosen a new name for the genus that reflects its morphological similarity to *Lophocolea*, while recognizing its "hidden" status as a distinct monophyletic lineage.

Cryptolophocolea ciliolata (Nees) L.Söderstr., Crand.-Stotl., Stotler et Váňa, *comb. nov.*

Basionym:—*Jungermannia ciliolata* Nees, *Enumer. Pl. Javae*: 68, 1830 (Nees 1830).

Type:—INDONESIA. Java: in ligno putrido, rara., *Blume, ex hb. Lehmann, misit Nees 1832.* (syntype S-B25177). ≡ *Plagiochila ciliolata* (Nees) Lindenb., *Spec. Hepat. (fasc.5)*: 143. 1843 (Lindenberg 1843). ≡ *Lophocolea ciliolata* (Nees) Gottsche, *Bot. Zeitung (Berlin)* 16, *Beil.*: 38. 1858 (Gottsche 1858). ≡ *Chiloscyphus ciliolatus* (Nees) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 413. 1984 [1985] (Engel & Schuster 1985).

Note:—Other combinations into this genus are being made elsewhere.

Synopsis of the Lophocoleaceae complex

Brevianthaceae J.J.Engel et R.M.Schust., *Phytologia* 47: 317, 1981 (Engel & Schuster 1981).

Brevianthus J.J.Engel et R.M.Schust., *Phytologia* 47: 317, 1981 (Engel & Schuster 1981).

Tetracymbaliella Grolle, *Nova Hedwigia* 3: 48, 1961 (Grolle 1961).

Lophocoleaceae Vanden Berghen, *Fl. Gén. Belgique, Bryoph.* 1 (2): 208, 1956 (Vanden Berghen 1956).

Bragginsella R.M.Schust., *Bryologist* 100: 363, 1997 (Schuster 1997). *Chiloscyphus* Corda, *Naturalientausch* 12: 651, 1829 "*Cheilocyphos*" (Corda 1829). *Clasmatocolea* Spruce, *Trans. & Proc. Bot. Soc. Edinburgh* 15: 440, 1885 (Spruce 1885). *Conoscyphus* Mitt., *Seemann, Fl. Vit.*: 404, 1871 [1873] (Mitten 1873). *Cryptolophocolea* L.Söderstr. *et al.*, *gen. nov.* *Deceptifrons* S.W.Arnell ex J.J.Engel et Váňa, *Mem. New York Bot. Gard.* 105: 54, 2012 (Váňa & Engel 2012). *Evansianthus* R.M.Schust. et J.J.Engel, *Bryologist* 76: 516, 1973 (Schuster & Engel 1973). *Hepatostolonophora* J.J.Engel et R.M.Schust., *J. Hattori Bot. Lab.* 46: 91, 1979 (Engel 1979). *Heteroscyphus* Schiffn., *Österr. Bot. Z.* 60: 171, 1910 (Schiffner 1910). *Lamellocolea* J.J.Engel, *J. Hattori Bot. Lab.* 70: 65, 1991 (Engel 1991b). *Leptoscyphopsis* R.M.Schust., *Phytologia* 39: 246, 1978 (Schuster 1978). *Leptoscyphus* Mitt., *Hooker's J. Bot. Kew Gard. Misc.* 3: 358, 1851 (Mitten 1851). *Leptophyllopsis* R.M.Schust., *J.*

Hattori Bot. Lab. 26: 269, 1963 (Schuster 1963). **Lophocolea (Dumort.) Dumort.**, *Recueil Observ. Jungerm.*: 17, 1835 (Dumortier 1835). Basionym: *Jungermannia* sect. *Lophocolea* Dumort., *Syll. Jungerm. Europ.*: 59, 1831 (Dumortier 1831). **Otoscyphus J.J.Engel, Bardat et Thouvenot**, *Cryptog. Bryol.* 33: 280, 2012 (Engel et al. 2012). **Pachyglossa Herzog et Grolle**, *Rev. Bryol. Lichénol.* 27: 150, 1958 [1959] (Herzog & Grolle 1959). **Perdusenina Hässel**, *Revista Mus. Argent. Ci. Nat., Bernardino Rivadavia Inst. Nac. Invest. Ci. Nat. Bot.* 7: 11, 1989 (Hässel de Menéndez 1989). **Pigafettoa C.Massal.**, *Nuovo Giorn. Bot. Ital.* 17: 237, 1885 (Massalongo 1885). **Platycaulis R.M.Schust.**, *Phytologia* 39: 245, 1978 (Schuster 1978). **Stolonivector J.J.Engel**, *J. Hattori Bot. Lab.* 69: 80, 1991 (Engel 1991c). **Xenocephalozia R.M.Schust.**, *Nova Hedwigia* 10: 25, 1965 (Schuster 1965).

Acknowledgements

The Early Land Plants Today project (ELPT) has been generously supported in part by the Global Biological Information Facility (GBIF) Seed Money Award No.2007-41, activities facilitated in part by funding from the Biodiversity Synthesis Center of the Encyclopedia of Life (BioSynC), partial funding from the National Science Foundation (Award No's 0749762, 1115002), the Warwick Foundation, and the Negaunee Foundation. NSF grant EF-0531750 (Assembling the Liverwort Tree of Life) to Crandall-Stotler & Stotler is gratefully acknowledged.

References

- Arnell, H.W. (1928) Levermossor. In: Holmberg, O.R. *Hartmans Handbok i Skandinavians Flora*. P. A. Norstedt & Söner Förlag, Stockholm, 224 pp.
- Bescherelle, E. & Massalongo, C. (1886) Hepaticae novae americanae-australes. *Bulletin mensuel de la société linnéenne de Paris* 1: 626–640.
- Corda, A.J.C. (1829) Genera Hepaticarum. Die Gattungen der Lebermoose. In: Opiz, P.M.. (Ed), *Beiträge zur Naturgeschichte als Fortsetzung des Naturalientausches No. 12*. Praha, pp. 643–655.
- Crandall-Stotler, B., Stotler, R.E. & Long, D.G. (2009) Phylogeny and classification of the Marchantiophyta. *Edinburgh Journal of Botany* 66: 155–198.
<http://dx.doi.org/10.1017/S0960428609005393>
- Dumortier, B.C. (1831) *Sylloge Jungermannidearum Europae indigenarum, earum genera et species systematice complectens*. J. Casterman, Tournay, 100 pp.
<http://dx.doi.org/10.5962/bhl.title.22343>
- Dumortier, B.C. (1835) *Recueil d'Observations sur les Jungermanniacées. I. Révision des genres*. J. A. Blanquart, Tournay, 27 pp.
<http://dx.doi.org/10.5962/bhl.title.731>
- Engel, J.J. (1973 "1972") *Chiloscyphus hookeri* n. sp. and nomenclatural changes in the genus *Clasmatocolea*. *Journal of the Hattori Botanical Laboratory* 36: 150–156.
- Engel, J.J. (1979) Austral Hepaticae X. A revision of *Hepatostolonophora* Engel et Schust., nom. nov. (Hepaticae). *Journal of the Hattori Botanical Laboratory* 46: 91–108.
- Engel, J.J. (1980) A monograph of *Clasmatocolea* (Hepaticae). *Fieldiana Botany, n.s.* 3: 1–229.
- Engel, J.J. (1991a) Studies on Geocalycaceae (Hepaticae). V. Comments on the *Leucophyllae* complex of *Chiloscyphus*. *Bryologist* 94: 311–314.
<http://dx.doi.org/10.2307/3243973>
- Engel, J.J. (1991b) Studies on Geocalycaceae (Hepaticae). IV. *Lamellocolea*, a new genus of Leptoscyphoideae from New Zealand. *Journal of the Hattori Botanical Laboratory* 70: 63–78.
- Engel, J.J. (1991c) Studies on Geocalycaceae (Hepaticae). II. *Stolonivector*, a new genus from New Zealand. *Journal of the Hattori Botanical Laboratory* 69: 79–86.
- Engel, J.J. (1992) Studies on Geocalycaceae (Hepaticae). VIII. A revision of *Chiloscyphus* subg. *Notholophocolea* (Schust.) Engel & Schust. *Journal of the Hattori Botanical Laboratory* 72: 105–115.
- Engel, J.J. (1998 "1997"). Studies on Geocalycaceae (Hepaticae). X. New taxa and new combinations in *Chiloscyphus* Corda for Australasia. *Phytologia* 83: 42–46.
- Engel, J.J. (1999) Studies on Geocalycaceae (Hepaticae). XI. Supraspecific new taxa and new combinations in *Chiloscyphus* Corda for Australia. *Novon* 9: 22–24.
<http://dx.doi.org/10.2307/3392110>

- Engel, J.J. (2010) Austral Hepaticae 45. A monograph of the genus *Chiloscyphus* Corda (Lophocoleaceae) for Australasia. *Fieldiana Botany*, n.s. 48: 1–209.
- Engel, J.J., Bardat, J. & Thouvenot, L. (2012) Studies on Lophocoleaceae XXI. *Otoscyphus* J.J.Engel, Bardat et Thouvenot, a new liverwort genus from New Caledonia with an unusual morphology. *Cryptogamie, Bryologie* 33: 279–289.
<http://dx.doi.org/10.2307/3647350>
- Engel, J. J. & Gradstein, S. R. (2003). Studies on Geocalycaceae XIV. *Physotheca* J.J. Engel & Gradst., a new genus of Hepaticae from Ecuador, belonging to a new subfamily, Geocalycaceae subfam. Physothecoideae J.J. Engel & Gradst. *Taxon* 52: 763–773.
<http://dx.doi.org/10.2307/3647350>
- Engel, J.J. & He, X.-L. (2010) Studies on Lophocoleaceae. XIX. The systematic identity of *Cyanolophocolea* R.M.Schust., an intriguing liverwort from New Zealand and Australia, based on morphological and molecular evidence. *Bryologist* 113: 149–163.
<http://dx.doi.org/10.1639/0007-2745-113.1.149>
- Engel, J.J., He, X.-L. & Glenny, D. (2010) Studies on Lophocoleaceae XXII. The systematic position of *Amphilophocolea* R.M.Schust. together with comments on the status of *Tetracymbaliella* Grolle and *Lamellocolea* R.M.Schust. *Phytotaxa* 9: 41–52.
- Engel, J.J. & Schuster, R.M. (1981) Austral Hepaticae XV. Brevianthaceae, fam. nov. and *Brevianthus*, gen. nov. from Tasmania. *Phytologia* 47: 317–318.
- Engel, J.J. & Schuster, R.M. (1985 “1984”) An overview and evaluation of the genera of Geocalycaceae subfamily Lophocoleoideae (Hepaticae). *Nova Hedwigia* 39: 385–463.
- Glenny, D., Engel, J.J. & He-Nygrén, X. (2009) The systematic identity of *Chiloscyphus trichocoleoides*, a new liverwort species from New Zealand, uncovered by morphological and molecular evidence. *Journal of Bryology* 31: 93–105.
<http://dx.doi.org/10.1179/174328209X427524>
- Gottsche, C.M. (1858) Uebersicht und kritische Würdigung der seit dem Erscheinen der Synopsis Hepaticarum bekannt gewordenen Leistungen in der Hepaticologie. *Botanische Zeitung*. (Berlin) 16, Beilage: 1–54.
- Gottsche, C.M., Lindenberg, J.B.G. & Nees von Esenbeck, C.G. (1847) *Synopsis Hepaticarum*, fasc. 5. Meissner, Hamburg, pp. 625–834.
- Gradstein, S.R. & Costa, D.P. (2003) Hepáticas e Antóceros do Brasil. *Memoirs of the New York Botanical Garden* 87: 1–318.
- Grolle, R. (1960) Nachtrag zur "Revision der *Clasmatocolea*-Arten". *Revue Bryologique et Lichénologique* 29: 68–91.
- Grolle, R. (1961) *Tetracymbaliella*, eine neue Lebermoosgattung. *Nova Hedwigia* 3: 47–53.
- Grolle, R. (1962) Monographie der Lebermoosgattung *Leptoscyphus* Mitt. *Nova Acta Leopoldina; Abhandlungen der Kaiserlich Leopoldinisch-Carolinisch Deutschen Akademie der Naturforscher*, n.s. 25: 1–143.
- Grolle, R. (1966) Miscellanea hepaticologica (61–70). *Journal of Japanese Botany* 41: 225–232.
- Grolle, R. (1987 “1986”) Miscellanea Hepaticologica 241–250. *Journal of the Hattori Botanical Laboratory* 61: 249–255.
- Grolle, R. (1995) The Hepaticae and Anthocerotae of the East African Islands. An annotated catalogue. *Bryophytorum Bibliotheca* 48: 1–178.
- Groth, H. (2005) Molecular phylogeny and morphological reconstructions of Plagiochilaceae (Jungermanniopsida) with hypotheses on biogeography and divergence times. *PhD Dissertation, George-August-Universität, Göttingen*.
- Hässel de Menéndez, G.G. (1989) *Perdusenina rheophila* Hässel, a new genus and species of Hepatophyta from southern South America. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigacion de las Ciencias Naturales: Ciencias Botánicas* 7: 11–17.
- Hässel de Menéndez, G.G. (1999) *Chiloscyphus* subgenus *Phaeochiloscyphus* (Hepatophyta, Geocalycaceae) from southern South America. *Revista del Museo Argentino de Ciencias Naturales*, n.s. 1: 121–127.
- Hässel de Menéndez, G.G. (2000) *Parachiloscyphus* Hässel, a new subgenus of *Chiloscyphus* Corda (Hepatophyta) from southern South America, including a new species. *Nova Hedwigia* 70: 451–460.
- Hässel de Menéndez, G.G. (2001) *Eurychiloscyphus* Hässel, a new subgenus of *Chiloscyphus* Corda (Hepatophyta) from southern South America. *Lindbergia* 26: 37–42.
- He, X.-L. & Glenny, D. (2010) *Perssoniella* and the genera of Schistochilaceae: a new classification based on molecular phylogenies. *Australian Systematic Botany* 23: 229–238.
<http://dx.doi.org/10.1071/SB10007>
- He-Nygrén, X. & Piippo, S. (2003) Phylogenetic relationships of the generic complex *Chiloscyphus*–*Lophocolea*–*Heteroscyphus* (Geocalycaceae, Hepaticae): Insights from three chloroplast genes and morphology. *Annales Botanici Fennici* 40: 317–329.

- He-Nygrén, X.-L., Juslén, A., Ahonen, I., Glenny, D. & Piippo, S. (2006) Illuminating the evolutionary history of liverworts (Marchantiophyta) - towards a natural classification. *Cladistics* 22: 1–31.
<http://dx.doi.org/10.1111/j.1096-0031.2006.00089.x>
- Hentschel, J., Wilson, R., Burghardt, M., Zündorf, H.-J., Schneider, H. & Heinrichs, J. (2006a) Reinstatement of Lophocoleaceae (Jungermanniopsida) based on chloroplast gene *rbcL* data: exploring the importance of female involucre for the systematics of Jungermanniales. *Plant Systematics and Evolution* 258: 211–226.
<http://dx.doi.org/10.1007/s00606-006-0408-y>
- Hentschel, J., Zündorf, H.-J., Hellwig, F.H., Schäfer-Verwimp, A. & Heinrichs, J. (2006b) Taxonomic studies in *Chiloscyphus* Corda (Jungermanniales: Lophocoleaceae) based on nrITS sequences and morphology. *Plant Systematics and Evolution* 258: 211–226.
<http://dx.doi.org/10.1007/s00606-006-0408-y>
- Hentschel, J., Feldberg, K., Zündorf, H.-J., Hellwig, F.H., Schneider, H. & Heinrichs, J. (2007) The systematic position of *Pachyglossa* and *Clasmatocolea* (Jungermanniopsida: Lophocoleaceae) inferred from nrDNA ITS sequences and morphology. *Taxon* 56: 1136–1142.
<http://dx.doi.org/10.2307/25065908>
- Herzog, T. & Grolle, R. (1959 “1958”) Was ist *Pachyglossa*? *Revue Bryologique et Lichénologique* 27: 147–165.
- Hoffmann, G.F. (1796) *Deutschlands Flora oder Botanisches Taschenbuch für das Jahr 1795*. Cryptogamie. Johan Jakob Palm, Erlangen, 200 pp.
- Hooker, J.D. (1845) *The Botany of the Antarctic Voyage of H. M. discovery ships Erebus and Terror in the years 1839-43. I. Flora Antarctica I. Lord Auckland's Group and Campbell Island*. Reeve, London, pp. 1–208.
- Hooker, J.D. (1846) *The Botany of the Antarctic Voyage of H. M. discovery ships Erebus and Terror in the years 1839-43. I. Flora Antarctica II. Antarctic regions (exclusive of Lord Auckland's Group and Campbell's Island)*. Reeve, London, pp. 209–574.
- Hooker, J.D. & Taylor, T. (1844) Hepaticae Antarcticae; being characters and brief descriptions of the Hepaticae discovered in the southern circumpolar regions during the voyage of H.M. Discovery ships Erebus and Terror. II. Species of the Falkland Islands, Cape Horn, and of Kerguelen's Land. *London Journal of Botany* 3: 454–481.
- Hooker, J.D. & Taylor, T. (1845) Hepaticae Antarcticae, supplementum; or specific characters, with brief descriptions, of some additional species of the Hepaticae of the Antarctic regions, New Zealand, and Tasmania, together with a few from the Atlantic Islands and New Holland. *London Journal of Botany* 4: 79–97.
- Klinggräff, H.V. (1858) *Die höheren Cryptogamen Preussens*. Wilhelm Koch, Königsberg, 220 pp.
- Lehmann, J.G.C. (1829) Hepaticarum Capensium a C.F. Ecklon collectarum brevem recensionem cum Schlechtendalio suo. *Linnaea* 4: 357–371.
- Lindberg, S.O. (1874) Manipulus muscorum secundus. *Notiser ur Sällskapetets pro Fauna et Flora Fennica Förhandlingar* 13: 353–417.
- Lindberg, S.O. (1875 “1874”) Hepaticae in Hibernia mense Julii 1873 lectae. *Acta Societatis Scientiarum Fennicae* 10: 465–559.
- Lindenberg, J.B.C. (1843) *Species hepaticarum. Fasc. 5*. Henry & Cohen, Bonn, pp. 121–164.
- Lindenberg, J.B.G. (1844) *Monographia Hepaticarum Generis Plagiochilae*. Henry & Cohen, Bonn, 29 pp.
- Linnaeus, C. (1753) *Species Plantarum, ed. 1*. Laurentii Salvii, Holmiae [Stockholm], 1200 pp.
- Massalongo, C. (1885) Epatiche raccolte alla Tierra del Fuoco del Dott. C. Spegazzini nell' anno 1882. *Nuovo Giornale Botanico Italiano* 17: 201–277.
- McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N.J. (2012) International Code of Nomenclature for Algae, Fungi and Plants (Melbourne Code). Adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. *Regnum Vegetabile* 154: 1–208.
- McNeill, J., Barrie, F.R., Burdet, H.M., Demoulin, V., Hawksworth, D.L., Marhold, K., Nicolson, D.H., Prado, J., Silva, P.C., Skog, J.E., Wiersema, J.H. & Turland, N.J. (2006) International Code of Botanical Nomenclature (Vienna Code) adopted by the Seventeenth International Botanical Congress Vienna, Austria, July 2005. *Regnum Vegetabile* 146: 1–260.
- Mitten, W. (1851) Catalogue of cryptogamic plants collected by Professor W. Jameson in the vicinity of Quito. *Hooker's Journal of Botany and the Kew Garden Miscellany* 3: 351–361.
- Mitten, W. (1873) Jungermanniae and Marchantiae. In: Seemann, B. (Ed), *Flora Vitiensis*. Reeve, London, pp. 325–453.
- Müller, K. (1956) *Die Lebermoose Europas (Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, 3. Aufl.) 6. Band, 6. Lieferung*. Akademische Verlagsgesellschaft: Leipzig, pp. 757–916.
- Nees von Esenbeck, C.G. (1833) Hepaticae Hedw. In: Martius, C.F.P., *Flora brasiliensis seu enumeratio plantarum 1*. Sumptibus J. G. Cottae, Stuttgart, pp. 294–390.
- Paton, J. A. (1999) *The Liverwort Flora of the British Isles*. Harley Books, Colchester, 626 pp.
- Piippo, S. (1985) Bryophyte flora of the Huon Peninsula, Papua New Guinea. XII. Geocalycaceae (Hepaticae). *Acta Botanica Fennica* 131: 129–167.

- Schiffner, V. (1910) Über die Gattungen *Chiloscyphus* und *Heteroscyphus* n. gen. *Österreichische Botanische Zeitschrift* 60: 169–173.
<http://dx.doi.org/10.1007/BF01631854>
- Schuster, R.M. (1963) Studies on antipodal Hepaticae I. Annotated key to the genera of antipodal Hepaticae with special reference to New Zealand and Tasmania. *Journal of the Hattori Botanical Laboratory* 26: 185–309.
- Schuster, R.M. (1965) Studies on Hepaticae XXVI. The *Bonneria-Paracromastigum-Pseudocephalozia-Hyalolepidozia-Zoopsis-Pteropsiella* complex and its allies: a phylogenetic study (Part 1). *Nova Hedwigia* 10: 19–61.
- Schuster, R.M. (1978) Studies on Venezuelan Hepaticae. I. *Phytologia* 39: 239–251.
- Schuster, R.M. (1980) *The Hepaticae and Anthocerotae of North America. vol. IV.* Columbia University Press, New York, 1334 pp.
- Schuster, R.M. (1997) *Bragginsella*, a new genus of Jungermanniales from New Zealand. *Bryologist* 100: 362–367.
- Schuster, R.M. & Engel, J.J. (1973) Austral Hepaticae II. *Evansianthus*, a new genus of Geocalycaceae. *Bryologist* 76: 516–520.
<http://dx.doi.org/10.2307/3241410>
- Schuster, R.M. & Engel, J.J. (1982) Austral Hepaticae XVI. Gondwanalandic Leptoscyphoideae (Geocalycaceae). *Lindbergia* 8: 65–74.
- Schuster, R.M. & Engel, J.J. (1981) Austral Hepaticae XIII. Two new genera of Geocalycaceae (Lophocoleaceae). *Phytologia* 47: 309–312.
- Söderström, L., Hagborg, A. & von Konrat, M. (2012) Notes on Early Land Plants Today. *Phytotaxa* 65: 41–42.
- Spruce, R. (1885) Hepaticae Amazonicae et Andinae. Part II. *Transactions and Proceedings of the Botanical Society of Edinburgh* 15: 309–588.
- Stephani, F. (1900) Beiträge zur Lebermoosflora Westpatagoniens und des südlichen Chile. *Bihang til Kongliga Svenska Vetenskaps-Akademiens Handlingar* 26 (III,6): 1–69.
- Stephani, F. (1906) Species Hepaticarum 3. *Bulletin de l'Herbier Boissier, série 2* 6(9): 781–796.
- Stephani, F. (1908) Species Hepaticarum 3. *Bulletin de l'Herbier Boissier, série 2* 8(2): 125–148.
- Stephani, F. (1915) *Species Hepaticarum* 5. George & Cie, Genève & Bale, pp. 705–848.
- Váña, J. & Engel, J.J. (2012) The liverworts and hornworts of the Tristan da Cunha group. *Memoirs of the New York Botanical Garden* 105: 1–138.
- Vanden Berghen, C. (1956) *Flore générale de Belgique, Bryophytes, Vol. 1, Fasc. 2.* Jardin Botanique de l'État, Bruxelles, pp. 133–270.
- Vanderpoorten, A., Désamoré, A. Laenen, B & Gradstein, S.R. 2012. Striking autapomorphic evolution in *Physotheca* J.J.Engel & Gradst. (Marchantiophyta: Lophocoleaceae) blurred its actual relationships with *Leptoscyphus* Mitt. *Journal of Bryology* 34:251–256.
- Vanderpoorten, A. & Long, D.G. (2006) Budding speciation and neotropical origin of the Azorean endemic liverwort, *Leptoscyphus azoricus*. *Molecular Phylogenetics and Evolution* 40: 73–83.
<http://dx.doi.org/10.1016/j.ympev.2006.02.013>
- Vanderpoorten, A., Schäfer-Verwimp, A., Heinrichs, J., Devos, N. & Long, D.G. (2010) The taxonomy of the leafy liverwort genus *Leptoscyphus* (Lophocoleaceae) revisited. *Taxon* 59: 176–186.