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A taxonomic revision of the Lophocoleaceae Vanden Berghen (Marchantiophyta) of New Caledonia

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ABSTRACT
Prior to this study, 51 species of Lophocoleaceae Vanden Berghen were reported from New Caledonia. Evolving taxonomic concepts have resulted in major recent changes in the taxonomy of Lophocoleaceae at generic level. This paper presents the results of taxonomic revision of the Lophocoleaceae of New Caledonia based on study of the types and further historical as well as recent collections. All accepted species are described and illustrated, with citation of types and synonyms. A key to the New Caledonian species and an index of species names, including those excluded from Lophocoleaceae, are provided. As a result of this revision, 27 species of Lophocoleaceae are accepted for New Caledonia. *Heteroscyphus* Schiffn. is the largest genus with 18 species, followed by *Lophocolea* (Dumort.) Dumort. (5 spp.), *Chiloscyphus* Corda (1), *Cryptolophocolea* L.Söderstr. (2) and *Otoscyphus* J.J.Engel, Bardat & Thouvenot (1). Seven species are excluded from the territory and one species is a doubtful taxon.

KEY WORDS
New Caledonia, liverworts, Lophocoleaceae, Acrobolbaceae, Brevianthaceae, determination key, lectotypifications, new synonyms, new combinations.

RÉSUMÉ
Révision taxonomique des Lophocoleaceae Vanden Berghen (Marchantiophyta) de Nouvelle-Calédonie.
Avant cette étude, 51 espèces de Lophocoleaceae Vanden Berghen étaient connues en Nouvelle-Calédonie. L'évolution des idées en taxonomie a conduit à d'importants changements dans la conception des genres de Lophocoleaceae. Cet article présente les résultats de la révision taxonomique des Lophocoleaceae en Nouvelle-Calédonie à partir de l'examen des types et des exemplaires disponibles dans les collections historiques ou contemporaines. Toutes les espèces acceptées sont décrites et illustrées avec la citation des types et des synonymes. Une clé de détermination des espèces de Nouvelle-Calédonie et un index des noms d'espèces, incluant celles qui ont été récemment exclues des Lophocoleaceae, sont fournis. Il résulte de cette révision une liste de 27 Lophocoleaceae acceptées pour la Nouvelle-Calédonie. *Heteroscyphus* Schiffn. est le genre le plus riche avec 18 espèces, suivi par *Lophocolea* (Dumort.) Dumort. (5 spp.), *Chiloscyphus* Corda (1), *Cryptolophocolea* L.Söderstr. (2) et *Otoscyphus* J.J.Engel, Bardat & Thouvenot (1). Sept espèces sont exclues du territoire et une garde un statut douteux.

MOTS CLÉS
Nouvelle-Calédonie, hépatiques, Lophocoleaceae, Acrobolbaceae, Brevianthaceae, clé de détermination, lectotypifications, synonymes nouveaux, combinaisons nouvelles.

INTRODUCTION

The taxonomy of the liverwort family Lophocoleaceae Vanden Berghen has been reviewed by Engel & Schuster (1984), He-Nygrén & Piippo (2003), Hentschel *et al*. (2006a, b), Crandall-Stotler *et al*. (2009), Söderström *et al*. (2013a) and others. Patzak *et al*. (2016) discussed the status of two important genera of this family, *Lophocolea* (Dumort.) Dumort. and *Chiloscyphus* Corda, which were treated in the "Checklist of the liverworts and hornworts of New Caledonia" (Thouvenot *et al*. 2011) and in many other publications as one single broad genus *Chiloscyphus* (with *Lophocolea* included as a subgenus), following Engel & Schuster (1984), but have recently again been reinstated as two separate genera based on molecular evidence (Hentschel *et al*. 2006a, b, 2007; Glenny *et al*. 2009), with recognition of a third genus, *Cryptolophocolea* L.Söderstr. (e.g. Söderström *et al*. 2013a, 2016).

Since Nees (1836), the most widely accepted criteria segregating the genera of Lophocoleaceae are the position and shape of the gametangia (Table 1; see also Engel & Schuster 1984). In addition, vegetative features like connate vs free underleaves are also of interest both at regional and wider scale. The recent clarification of the generic classification using a molecular approach (Hentschel *et al*. 2006b, 2007; Glenny *et al*. 2009) has confirmed the opinion of Grolle (1995) and others that *Chiloscyphus* is a small Laurasian genus (Söderström *et al*. 2013a). But a few species initially reported for this genus in New Caledonia are still pending further studies since the specimens available including types lack gametoecia of either one or both sexes. This is of critical importance to assign them to *Chiloscyphus* genus, as well as molecular analysis, but if that is confirmed, the range of this genus will be broadened to southern hemisphere.

This study deals with Lophocoleaceae in New Caledonia with the aim of establishing a reliable and updated list of species present in the territory, and with removal of all unnecessary names (synonyms and erroneously reported taxa). None of the modern taxonomic studies have included New Caledonian species, so this work cannot benefit from recent data as to generic assignment. Because of the limited scope of the paper, the author follows the most recent generic classification of the family (Söderström *et al*. 2016). Difficulty in circumscribing the species due to their plasticity have been underlined by many authors (e.g. Jones 1953). In New Caledonia, a good example may be *Heteroscyphus grandiflorus* (Steph.) Hürl. whose variability is commented below (see comments in corresponding paragraph). Many species were described under several names based on small morphological differences which turned out to be variable in single specimens or within a range of samples. For example, *Heteroscyphus coalitus* (Hook.) Schiffn. currently includes five heterotypic synonyms in Japan (Yamada & Iwatsuki 2006) and four in Java (Söderström *et al*. 2010).

As mentioned, the Lophocoleaceae treatment in the checklist of the liverworts of New Caledonia (Thouvenot *et al*. 2011) essentially followed Engel & Schuster (1984), so that all species of *Lophocolea* were included in *Chiloscyphus*, and of *Tetracymbaliella* Grolle in *Heteroscyphus* Schiffn. Since then, *Lophocolea* has been reinstated as a genus in the classification of the Marchantiophyta (Crandall-Stotler *et al*. 2009) or the world checklist of hornworts and liverworts (Söderström *et al*. 2016), *Cryptolophocolea* and *Otosycphus* J.J.Engel, Bardat & Thouvenot (Engel *et al*. 2012) have been added, and *Tetracymbaliella* has been transferred to Brevianthaceae (Söderström *et al*. 2013a) and *Conoscyphus* Mitt. to Acrobolbaceae (Dimon *et al*. 2018).

This study deals with 45 species names listed by Thouvenot *et al*. (2011) together with four species that were subsequently described as new to science (Thouvenot & Price 2020; Thouvenot & Engel 2021; Engel *et al*. 2021), one species new to New Caledonia (Thouvenot & Müller 2021), two unpublished occurrences, and four new combinations published by Engel *et al*. (2012) and Thouvenot *et al*. (2018).

MATERIAL AND METHODS

For the purpose of updating the checklist of the liverworts of New Caledonia (Thouvenot *et al*. 2011), New Caledonian species of Lophocoleaceae were checked from type specimens and a few additional historic collections in G, PC, REN, BM, L, Z+Zt together with recent materials collected by Frank Müller (2001-2003) and the author (2008-2019) and kept in DR, PC and the author's private herbarium. In addition, the author had the chance to observe the single specimen of *Lophocolea muricata* (Lehm.) Nees hitherto reported from New Caledonia (Hürlimann 1998), and kept at Z, thanks to photos and comments from Heike Hofmann. The original diagnoses together with personal observations allowed us to check the discriminant characters and to provide concise descriptions and drawings from fresh material using a drawing tube. As to typification, original specimens were rarely fully cited by Stephani, Pearson and Mitten, but was usually done by Herzog. The loan of original specimens from BM allowed to select lectotypes for Pearson's new species. With regards to species described by Stephani, the citations in Bonner (1963, 1966) of original material present in the Stephani herbarium (G) have been taken into account. In view of the plasticity of the species, many specimens must be studied for their circumscription. Unfortunately, several species are only known from the type or few specimens. Nevertheless, the synonymy of many species names has been established. The possibility remains, however, that some of the species names accepted in this treatment will turn out to be synonyms of species described from other countries. When samples of related extraterritorial species could not be checked, the author has conservatively kept the New Caledonian species name, pending further study. In addition, a few species known only from limited type material unsuitable for detailed morphological analysis have been included under their original name.

Engel & Glenny (2019) highlighted the low reliability of taxonomic criteria used to define the genera of Lophocoleoideae. Here, the generic attribution of the New Caledonian species is largely based on characters of the gametangia, including

TABLE 1. — Discriminant features of Lophocoleaceae Vanden Berghen genera occurring in New Caledonia.

	Heteroscyphus **Schiffn.**	***Chiloscyphus*** **Corda**	***Lophocolea*** **(Dumort.) Dumort.**	***Cryptolophocolea*** **L.Söderstr.**	***Otoscyphus*** **J.J.Engel, Bardat & Thouvenot**
Androecia position	On short lateral branches lacking normal leaves	On long normal leaved shoots	On long normal leaved shoots	On long normal leaved shoots	On long normal leaved shoots
Male bracts	Much smaller than leaves, fully saccate	Like the leaves but with small dorsal saccate base	Smaller than leaves, saccate at dorsal base, ventral lamina variously developed	Like the leaves but with dorsal saccate base, shorter than the lamina	Smaller than leaves, dorsal saccate base ½ bract length
Antheridia stalk	Biseriate to oligoseriate	Uniseriate	Uniseriate	Biseriate	Unknown
Gynoecial position	On short lateral branches lacking normal leaves	On short lateral branches lacking normal leaves	On normal leaved shoots, more or less elongate	On normal leaved elongate shoots	On normal leaved elongate shoots and short leafless ventral branches
Perianth	Cyathiform. Obscurely plicate	Cupulate. Obscurely plicate	Oblong. 3-keeled	Oblong. 3-keeled	Cyathiform. Obscurely plicate
Calyptra	Hidden deep within perianth	Reaching perianth apex to exserted	Hidden deep within perianth	Hidden deep within perianth	Hidden deep within perianth
Leaf insertion	Mainly subopposite	Mainly alternate	Alternate	Subopposite	Alternate
Underleaf connation	Typically bilateral and wide	Free or unilateral and narrow	Free or unilateral and narrow	Bilateral. Typically wide	Free
Cell walls	Thin, rarely thick	Thin	Thin	Thin	Thin
Trigones	Trigones typically large	Trigones small or lacking	Trigones small or lacking	Trigones small or large	Trigones large

their shape and their location on main shoots or on abbreviated branches, associated or not with normal vegetative leaves. This approach is marred, however, by the frequent absence of gametangia in historic specimens (Engel 2015). Additional relevant vegetative characters include leaf ornamentation and insertion, underleaf shape and connation to the leaves, as well as cell wall thickenings (Table 1).

When gametoecia are lacking, the original species names are kept in the *incertae sedis* group.

Collections by the author in New Caledonia were made on the basis of the following permits: Province Sud, nr 1238-2012, 794-2016, 2825-2019; Province Nord, nr 609012-1275-2016, 609011-45/2019. Unless otherwise specified, specimens cited are kept in the author's private herbarium.

RESULTS AND DISCUSSION

This treatment accepts 27 species of Lophocoleaceae in New Caledonia, plus one species whose generic assignation is doubtful, including seven that were described as new to science or reported as new to New Caledonia since the publication of the checklist (Thouvenot *et al*. 2011): *Chiloscyphus parapilistipulus* Thouvenot (here treated as *Heteroscyphus*), *Heteroscyphus assurgentissimus* J.J.Engel, Thouvenot & Frank Müll., *H. diestianus* (Sande Lac.) Piippo, *H. kanakensis* Thouvenot, *H. supinopsis* J.J.Engel, Thouvenot & Frank Müll., *H. succulentus* (Gott.) Schiffn. and *Lophocolea bidentata* (L.) Dumort. The genus *Heteroscyphus* is, by far, the richest Lophocoleaceae genus in New Caledonia with 18 species. In comparison, Papua New Guinea has 15 species (Piippo 1985, 1992). As explained by Engel & Schuster (1984), most of the former *Chiloscyphus* species in New Caledonia belong in *Heteroscyphus*. This includes specimens which have gametangial characters of *Heteroscyphus*, but with "lophocoleoid" vegetative features, e.g. underleaves deeply bifid and free from the leaves or connate on one side only, small trigones or none, and leaves dorsally free. However, a handful of former *Chiloscyphus* species included in the checklist (Thouvenot *et al*. 2011) seem to be nearer to *Chiloscyphus* than to *Lophocolea* or *Heteroscyphus* so that the strictly Laurasian range of *Chiloscyphus* can be questionable.

Besides members of *Heteroscyphus*, Lophocoleaceae of New Caledonia include five species of *Lophocolea*, one of *Chiloscyphus*, two of *Cryptolophocolea* and the monospecific genus *Otoscyphus*. A single further species is kept as *incertae sedis*, in the absence of fertile specimen available for examination. In addition, seven species names are excluded from the New Caledonian flora. In comparison, 41 Lophocoleaceae species were listed by Thouvenot *et al*. (2011) (apart from four that were recently classified in other families). Seventeen of these have been reduced to synonymy, among them five under *Heteroscyphus coalitus*, five under *Lophocolea convexula* Sande Lac. and one (*Chiloscyphus novae-caledoniae* J.J.Engel & R.M.Schust.) under *Goebelobryum unguiculatum* (Hook.f. & Taylor) Grolle, a member of the family Acrobolbaceae. In the index (Appendix 1), the synonyms are listed with the accepted names in bold face. The key to the species given below includes the genera recently transferred towards different families. To allow for identification of sterile specimens, the key uses primarily vegetative features.

Distribution maps of the Lophocoleaceae species in New Caledonia are available on http://endemia.nc/flore/fiche7400.

Key to New Caledonian species of Lophocoleaceae Vanden Berghen and selected taxa recently transferred to other families

1. Basal parts of the leaves with pouches made of expanded or incurved parts of the lamina 2
— Leaves without pouches 3

2. Each pouch formed by the incurved basal margin of a single leaf or underleaf; underleaves without linear lobes; leaves widely ovate with shortly toothed margins ..... *Tetracymbaliella* Grolle (Brevianthaceae)
— Each pouch formed by two successive leaves, the dorsally enlarged base of a leaf set above the previous one; underleaves with spreading linear lobes; leaves rectangular in outline, entire margined, the apices deeply bifid ..... *Otoscyphus crassicaulis* (Steph.) J.J.Engel, Bardat & Thouvenot (Lophocoleaceae)

3. Plants brownish; leaf cells mammillose, with large contiguous spheroid trigones; underleaves reniform-rounded superficially toothed ..... *Conoscyphus trapezioides* (Sande Lac.) Mitt. ex Schiffn. (Acrobolbaceae)
— Plants green, rarely red tinged; leaf cells smooth, rarely bulging or papillose, with trigones null to large and rarely contiguous; underleaves of various shapes 4

4. Plants light green usually red tinged; underleaves vestigial or very small, narrower than the stem, and bifid with linear lobes, made of up to three short cells; fertile plants with a long cylindrical marsupium at the end of the fertile shoots ..... *Goebelobryum unguiculatum* (Hook.f. & Taylor) Grolle (Acrobolbaceae)
— Plants green when fresh, without red pigment; underleaves usually well developed, at least as wide as the stem; fertile plants without a marsupium ..... Lophocoleaceae Vanden Berghen

5. Leaves subopposite and underleaves connate to both nearest leaves, connation usually wide 6
— Leaves alternate, rarely subopposite, with underleaves at most narrowly connate to one of the nearest leaves or free on both sides 23

6. Gynoecia and androecia terminal on main shoots or long leaved branches; leaves asymmetrically oblong with the ventral base widened, leaf apices with 1-2 sharp lobes, lateral margins sharply toothed or not; underleaves ovate or reniform, shortly bifid and more or less toothed all around 7
— Gynoecia and androecia terminal on short leafless ventral-lateral branches; leaves and underleaves of various shapes 8

7. Normal leaves canaliculate, gradually narrowing from base to apex; lateral margins of leaves and underleaves usually toothed; leaf cells with strong trigones ..... *Cryptolophocolea subcostata* (Steph.) Thouvenot
— Normal leaves convex, ovate oblong to lingulate, the apex somewhat narrower; lateral margins of leaves usually naked or with a few teeth; lateral margins of underleaves with at most a single tooth on both sides; leaf cells without trigones ..... *Cryptolophocolea explanata* (Mitt.) Váňa & Crand.-Stotl.

8. Leaves entire or with the rounded apices superficially retuse but in a few shoots some of the leaves may be shortly bifid 9
— Leaves lobed, toothed or ciliate-laciniate, or at least with a small tooth at both angles of truncate apices 16

9. Underleaves widely reniform, the apices entire, margins with a few scattered small teeth; leaves entire except small teeth at the base of the dorsal margins ..... *Heteroscyphus diestianus* (Sande Lac.) Piippo
— Underleaves reniform or not, the apices at least superficially bifid, margins variously ornamented; leaves never with teeth restricted to the base of the dorsal margin 10

10. Leaves asymmetrically oval acuminate ..... *Heteroscyphus subacuminatus* (Herzog) Thouvenot, comb. nov.
— Leaves of various shapes, rounded, ovate or oblong, never acuminate 11

11. Underleaves shortly bifid with margins densely toothed all around ..... *Heteroscyphus splendens* (Lehm. & Lindenb.) Grolle
— Underleaves more conspicuously bifid with margins remotely toothed or laciniate 12

12. Leaves oblong; cells without trigones or with nodulose trigones 13
— Leaves widely ovate to rounded; cells with large nodulose or truncate trigones 15

13. Plants large, up to 5 mm wide; underleaves reniform in outline with lateral margins laciniate 14
— Plants smaller, up to 3.8 mm wide; underleaves ovate to sub-reniform with lateral margins remotely toothed ..... *Heteroscyphus supinopsis* J.J.Engel, Thouvenot & Frank Müll.

14. Plants fleshy; leaves dorsally free; cells without trigones ..... *Heteroscyphus succulentus* (Gott.) Schiffn.
— Plants rigid; leaves dorsally connate; cells with nodulose trigones .... *Heteroscyphus deplanchei* (Steph.) Schiffn.

15. Plants medium sized; leaves ovate, entire, up to 1.6 mm long; underleaves bifid with acute triangular lobes and shortly toothed margins ..... *Heteroscyphus kanakensis* Thouvenot & Engel
— Plants large; leaves rounded, apices retuse, 1.5-3 mm long; underleaves bifid with lanceolate lobes and laciniate margins ..... *Heteroscyphus giganteus* (Steph.) Hürl.

16. Leaves rounded, bifid, lobes short, narrow, acute, margins entire to superficially toothed; underleaves wide, rounded, bifid to 4-fid, margins toothed; cells with large nodulose trigones 17
— Leaves either oblong to rectangular with various apices, or rounded to oval with long toothed-ciliate margins; underleaves various; cells with minute to large trigones 18

17. Leaves asymmetrically bifid with dorsal margins straight or slightly convex, usually strongly recurved, ventral margins widely rounded, bifid apices shifted toward the upper dorsal margins; leaf and underleaf lobes usually acuminate with long linear apices ..... *Heteroscyphus aselliformis* (Reinw., Blume & Nees) Schiffn.
— Leaves symmetrically bifid with both margin curvatures similar and sinus set on the top of the rounded apex; leaf and underleaf lobes triangular acute, if acuminate, then with shorter apices ..... *Heteroscyphus confertus* (Steph.) Thouvenot

18. Leaves rounded to ovate, apices rounded or widely triangular with three long ciliate processes, triangular at base; margins usually with few to numerous cilia restricted to subapical and ventral parts; underleaves transversely elongate, 2-3 times as wide as the stem, bifid, lobes like the leaf appendages single or furcate, each lateral margins variously toothed to lobate ciliate ..... *Heteroscyphus grandiflorus* (Steph.) Hürl.
— Leaves elongate, oval-oblong to ovate trapezoid or rectangular, apices various, if rounded then with small teeth, if triangular then teeth spinose, not ciliate; margins entire except near apices or with a tooth more on ventral margins; underleaves various 19

19. Shoots canaliculate with the leaves dorsally assurgent, the abaxial surface of opposite leaves facing one another; leaves ovate trapezoid; leaf cell walls strongly thickened, with one thin pore on each side of the cells ..... *Heteroscyphus assurgentissimus* J.J.Engel, Thouvenot & Frank Müll.
— Shoots complanate with the leaves spreading out, the abaxial surfaces flat or convex, not facing to the opposite ones; leaves oblong to lingulate; leaf cell walls thin, with or without trigones 20

20. Underleaves transversally elongate in outline, bifid with triangular lobes acuminate and widely divergent, one or two small teeth on both lateral margins 21
— Underleaves either reniform with 4-6 subequal teeth or bifid with margins heavily lobate-laciniate 22

21. Leaf cells without trigones; leaf apices widely rounded to truncate, rarely acute, with 4-6 or more sharp teeth, roughly equal; underleaf lateral margins with one tooth on both sides ..... *Heteroscyphus argutus* (Reinw., Blume & Nees) Schiffn.
— Leaf cells with large nodulose trigones; leaf apices truncate, concave, with a single tooth at both angles; underleaf lateral margins with two teeth on both sides ..... *Chiloscyphus longifissus* Steph.

22. Underleaves strongly narrowed below and so narrowly decurrent and connate to the leaves by a band up to five cells wide; leaf cells with large nodulose trigones; leaves ovate-lingulate with apices variously shaped in a same shoot, entire rounded, or acute to bifid, or acute with 1-2 subapical teeth so that the leaf apices seem bifid or trifid ..... *Heteroscyphus deplanchei*
— Underleaves not narrowed below and so widely decurrent and connate to both adjacent leaves by a band of cells usually more than six cells wide; leaf cells with minute to inconspicuous trigones; leaves evenly shaped along the same shoot, leaf apices truncate with a single short to medium tooth at both angles ..... *Heteroscyphus coalitus* (Hook.) Schiffn.

23. Leaf surfaces appearing rough because of many spinose projections ..... *Lophocolea muricata* (Lehm.) Nees
— Leaf surfaces smooth, rarely with cells at most bulging 24

24. Plants small, shoots *c.* 1.5 mm wide; leaf and underleaf margins densely and sharply toothed; leaf cells less than 20 µm wide with relatively large trigones ..... *Lophocolea caledonica* Steph.
— Plants larger, shoots usually more than 1.5 mm wide, or, if smaller, with entire or emarginate leaves; underleaf lateral margins with at most two teeth on both sides; leaf cells more than 20 µm wide with trigones small or null 25

25. Leaves fully entire with rounded apices; plants medium to large 26
— At least some leaves toothed or lobed or emarginate at apices, plants small to medium 27

26. Leaves widely ovate, wider or as wide as long, 0.6-0.7 mm long, dorsally assurgent-convex, giving an inflate appearance to the shoots; shoots *c*. 2 mm wide when flattened; underleaves ½ bifid, 2-2.5 times the stem width, lobes erect ..... *Chiloscyphus trigonifolius* Steph.
— Leaves ovate-oblong, 1.6-2.2 mm long, horizontally spreading, shoots somewhat complanate, 3.5-4 mm wide; underleaves more than ½ bifid, 4-5 times the stem width, lobes widely spreading ..... *Heteroscyphus cornutistipulus* (Steph.) Thouvenot, comb. nov.

27. Leaf apices widely rounded to truncate, with 4-6 or more sharp teeth, almost equal; cell walls evenly thickened without trigones; plants medium, shoot width 1.5-2.0 mm ..... *Heteroscyphus argutus*
— Leaf apices various, teeth if any restricted to distal angles; cell walls thin, trigones minute to absent; shoot width ranging from 1 to 6 mm 28

28. All leaf apices bifid, lobes triangular acuminate, with piliform apices usually 3-5 cells long ..... *Lophocolea bidentata* (L.) Dumort.
— Leaf apices various, when bilobate unevenly so in the same shoot and lobe apices not piliform 29

29. Underleaves reniform, lateral margins heavily toothed-laciniate; leaf apices usually shallowly triangular with spinosely toothed angles ..... *Heteroscyphus caledonicus* (Steph.) Schiffn.
— Underleaves reniform or not, lateral margins with 0-2 small teeth; leaf apices truncate, rounded or emarginate 30

30. Leaves rectangular, contiguous to distant, apices transversally concave, with distal angles sharply toothed or less frequently rounded, a third subapical tooth eventually present on the ventral margins; leaf cells without trigone; gynoecia and androecia on short latero-ventral leafless branches ..... *Heteroscyphus etesseanus* (Steph.) Thouvenot, comb. nov.
— Leaves ovate to oblong, more or less strongly imbricate, apices straight or varying from rounded to shallowly emarginate-bilobate often on the same shoot, angles or lobes rounded to acute; leaf cells with or without trigones; gynoecia or androecia or both on main shoots or long branches with normal vegetative leaves 31

31. Leaf cells with large nodulose trigones; underleaves very wider than the stems with lobes triangular and widely divergent ..... *Chiloscyphus longifissus*
— Leaf cells with small trigones or trigones lacking; underleaves not or hardly wider than the stems with lobes narrow, roughly parallel 32

32. Plants small, shoots 1-2 mm wide; leaves ovate, leaf apices conspicuously narrower that the bases, rounded to narrowly emarginate, margins crenulate by the bulging marginal cells; underleaf lobes lanceolate, rigid ..... *Lophocolea convexula* Sande Lac.
— Plants medium sized, shoots more than 2.5 mm wide; leaves oblong, leaf apices quite as wide as the bases, from widely convex or emarginate to shortly bifid, margins smooth; underleaf lobes linear, curved 33

33. Gynoecia and androecia on short latero-ventral leafless branches; perianths cupulate, without keels, bracts strongly differentiated from normal leaves, bracteole deeply bifid; underleaf insertions concave, discs more than 2 cells long, lobes with triangular bases ..... *Heteroscyphus parapilistipulus* (Thouvenot) Thouvenot, comb. nov.
— Gynoecia and androecia at the end of main shoots or long leafy branches, perianths oblong and 3-angled, bracts slightly differentiated from normal leaves, bracteole oblong, toothed, not deeply bifid; underleaf insertions in an inverted U, discs very short, two cells long, lobes sublinear ..... *Lophocolea savesiana* Steph.

TAXONOMIC TREATMENT

All New Caledonian species of Lophocoleaceae are described below. Their shared characters include essentially: 1) plants small to large, leaves succubous, obliquely inserted, alternate or subopposite, sometimes dorsally decurrent or fused, never duplicate; 2) leaf apices entire to incised or toothed, margins smooth or toothed to laciniate; 3) underleaves conspicuous, usually wider than the stem, connate or not with one or both nearest leaves; 4) cells hexagonal, with usually thin walls, rarely strongly thickened, trigones inconspicuous to large, acute or bulging, sometimes confluent; 5) plants usually dioecious, less commonly autoecious, rarely paroecious; 6) gynoecia terminal either on leading shoots or long branches with normal leaves, or on short almost leafless ventral-lateral branches, bracts and bracteoles variously toothed to laciniate, the latter usually bifid; 7) perianths well developed, oblong-cylindrical to cupulate in outline, from tri-carinate in the distal part to shallowly plicate, narrowly winged or smooth, mouth more or less deeply trifid, lobes possibly bifid, toothed to laciniate; and 8) androecia position either intercalary on leading shoots or vegetative branches, bracts smaller than the vegetative leaves, or in a spike at the apices of short almost leafless ventral-lateral branches with smaller inflated bracts, or, in paroecious species, at the base of gynoecia set at the end of normal-leaved shoots.

The list of accepted species of Lophocoleaceae is followed by a commented dubious species, whose generic classification remains unresolved (*incertae sedis*), a list of species transferred to other families and a list of excluded taxa.

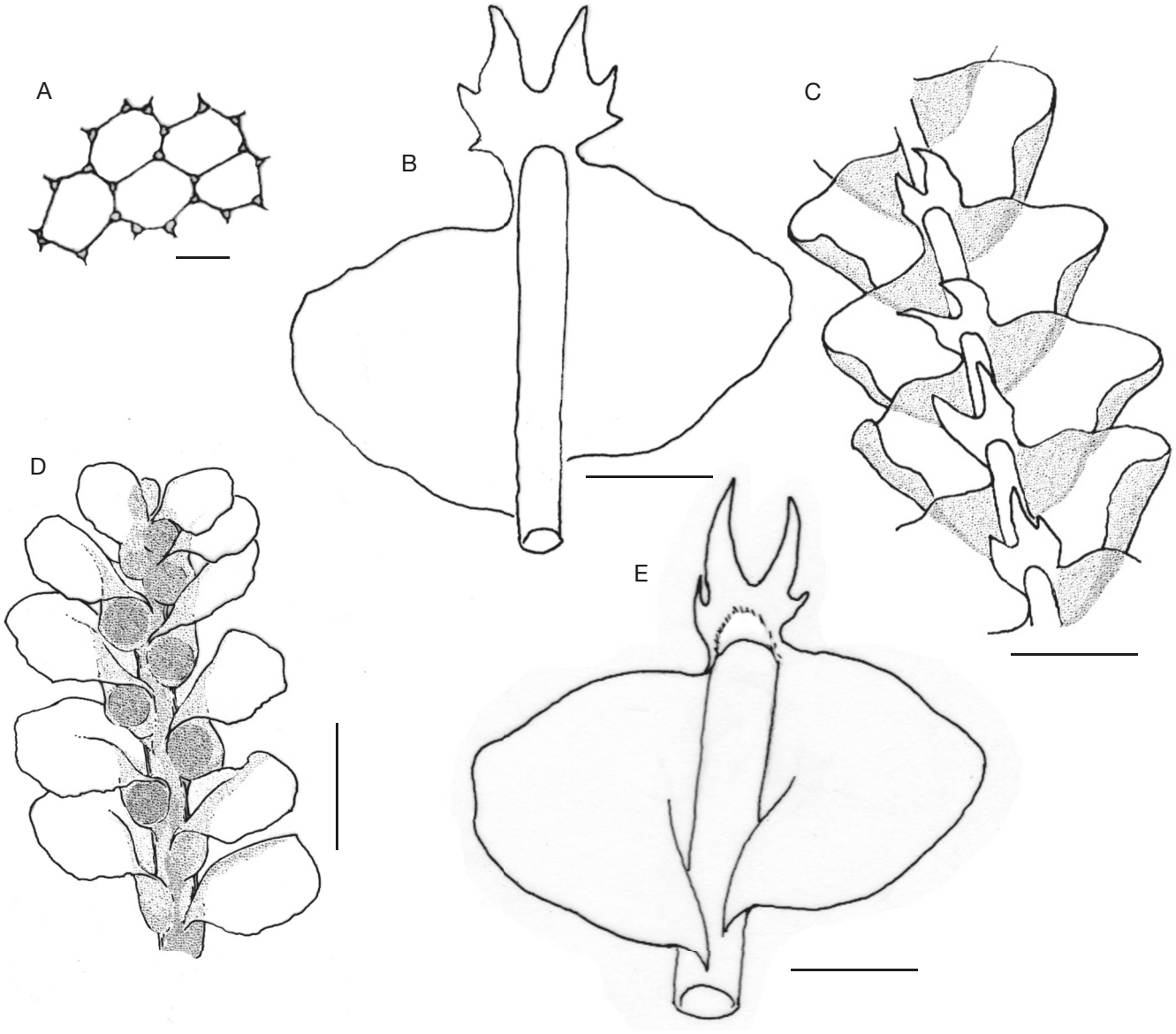

FIG. 1. — *Chiloscyphus trigonifolius* Steph.: **A**, leaf cells; **B**, leaves and underleaf in ventral view; **C**, shoot portion in ventral view; **D**, androecium; **E**, leaves and underleaf in dorsal view. **A**, **C**, drawn from the lectotype (G00069423); **B**, **D**, **E**, drawn from the isolectotype (PC0167659). Scale bars: A, 20 µm; B-E, 500 µm.

NEW CALEDONIAN SPECIES OF LOPHOCOLEACEAE

Genus *Chiloscyphus* Corda

Chiloscyphus trigonifolius Steph.
(Fig. 1)

Species Hepaticarum 6: 316 (Stephani 1922). — Type: **New Caledonia**. "In summo Mt. Dent de St Vincent, 1425 m", VII.1909, *L. Le Rat 101* (lecto-, here designated, G[G00069423]!; isolecto-, PC[PC0167659]!, REN[herb. E. G. Paris]!).

Chiloscyphus trigonifolius Steph. ex Paris, *Revue bryologique* 37: 129 (Paris 1910), nom. inval. (no description). — Material: REN[herb. E. G. Paris] **syn. nov.**

FURTHER SPECIMEN EXAMINED. — **New Caledonia**. South Province, in the vicinity of Nouméa, 1909, *Le Rat s.n.*, determinavit Stephani as "*Chiloscyphus cornutistipatus*" (PC[PC0167669]).

DISTRIBUTION IN NEW CALEDONIA. — Only known from the type locality, a remote place hard to reach, and one further historic specimen without precise location.

TOTAL RANGE. — Endemic.

DESCRIPTION
Dioecious.

Habit
Plant medium, moist shoots 1.00-2.00 mm wide, 2.50 mm wide when flattened; leaf bases dorsally assurgent, strongly

convex, masking the stem, the leaves distally curving downward, leaves second, imbricate, alternate, dorsally free, separated by a two ranked band of cortical cells.

Leaves
Ovate-triangular to rounded in outline, wider than long, 0.80-0.90 mm long, 1.10 mm wide at base, entire margined, apices rounded, margins convex, slightly crenulate by the prominent marginal cells.

Cells
Leaf cells 20-25 µm wide, thin walled with small acute trigones.

Underleaves
Small, 2 times the stem width, 0.60 mm long, 0.40-0.60 mm wide, connate to one adjacent leaf, bifid up to mid-length, sinus lunate, lobes lanceolate, acuminate to obtuse, upward directed, disc margins with 1-2 short teeth.

Gametangia
Androecia in series of numerous bracts and antheridia (10 pairs) inserted between normal-leaved sections of the main stems or at the end of long leafy branches; male bracts similar in size to vegetative leaves but with inflated dorsal base including antheridia; gynoecia not seen.

Comments
The alternate leaves, unilateral connation of underleaves with leaves, little differentiated male bracts and androecia on elongate shoots separate *Chiloscyphus trigonifolius* from *Heteroscyphus* while the entire leaves and, again, little differentiated male bracts with saccate dorsal base distinguish it from most *Lophocolea*. Unfortunately, gynoecia are unknown in *C. trigonifolius* and definitive evidence for its placement in *Chiloscyphus* vs *Lophocolea* is therefore lacking. But, since all known characters match *Chiloscyphus*, we conservatively keep the species in this latter genus pending further collections of female plants.

In the original publication of *Chiloscyphus trigonifolius*, Stephani mentions Franc as collector, but the label of the original material of *C. trigonifolius* in G mentions Louise Lerat as the collector. In the checklist of the New Caledonian liverworts, Thouvenot *et al*. (2011) stated that the identity of *Chiloscyphus trigonifolius* Steph ex Paris was unclear since Paris did not give any description of this taxon. The specimen kept in the herbarium of E. G. Paris at REN have been checked; its label is identical to the one in G; moreover, the plant exactly matches Stephani's diagnosis and drawing of *C. trigonifolius* and therefore constitutes a duplicate of the material used by Stephani to define his new species. A letter from Stephani (9 Febr. 1910) (Rennes 1 University Library) reports *Chiloscyphus trigonifolius* as a new species, cited as "nr 101", among the material collected by Mr. and Mrs. Le Rat and sent to Stephani by Paris. This confirms that the type is not from Franc and that the specimen at REN must be an isolectotype.

Heteroscyphus cornutistipulus is close to *Chiloscyphus trigonifolius*, with leaves and underleaves being superficially similar. It differs essentially by: 1) shoots complanate; 2) leaves slightly convex and horizontally spreading; 3) larger sizes in all dimensions: shoot width, leaf length and width, cell diameters, trigones width; and 4) androecia on very short ventral branches. Furthermore, the leaves are ovate oblong, longer than wide, instead of widely ovate, wider than long in the latter. Out of New Caledonia, *Heteroscyphus furcistipulus*, endemic to New Zealand, is similar to *C. trigonifolius* in all vegetative characters (Engel & Glenny 2019), but the former has very distinctive androecia of heteroscyphoid type, with 3-8 pairs of ventricose bracts on leafless ventral branches that are hidden under the normal leaves, while male bracts of *C. trigonifolius* are relatively shortly ventricose at the base of large rounded flat lamina and are set in spikes at the end of normal leaved branches or main shoots, or inserted inside main shoot portions; androecia of heteroscyphoid type are lacking. Furthermore, *H. furcistipulus* is calcicolous since *C. trigonifolius* was found in ultramafic massifs.

Genus *Cryptolophocolea* L.Söderstr.

Cryptolophocolea explanata (Mitt.) Váňa & Crand.-Stotl. (Fig. 2)

Phytotaxa 202: 69 (Söderström *et al*. 2015). — *Lophocolea explanata* Mitt., *Flora Vitiensis*: 404 (Mitten 1871 [1873]). — *Chiloscyphus explanatus* (Mitt.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 414 (Engel & Schuster 1984 [1985]). — Type: **Samoa**. *Powell s.n.* (lecto-, selected by Váňa et Crandall-Stotler [in Söderström *et al*. 2015], NY[NY00965738], not seen; isolecto-, G[G00121761]!).

Further specimens examined. — **New Caledonia**. South Province, Mts. Koghis, in forest, V-VI.1905, *Etesse s.n.*, ex herb. E. G. Paris nr 13 (G s.n.).

Distribution in New Caledonia. — South Province. Known from a single collection in Mts Koghis by Etesse in 1905.

Total range. — Pacific Islands, occurs also in Samoa (type locality).

Description (based on the New Caledonian specimen)
Autoecious.

Habit
Plants medium sized, wet shoots up to 2.10 mm wide when flattened. Leaves obliquely spreading, convex to nearly explanate.

Leaves
In medium parts of stems, leaves 0.70-0.90 mm long, 0.45-0.65 mm wide at base, 0.20-0.25 at apex, long ovate to narrowly trapezoid when flattened, both margins nearly symmetrically convex above the base becoming nearly straight to slightly concave subapically, apices usually obliquely truncate, with a sharp tooth at both angles and rare additional short teeth on ventral margins, dorsal margins entire, decurrent, not connivent.

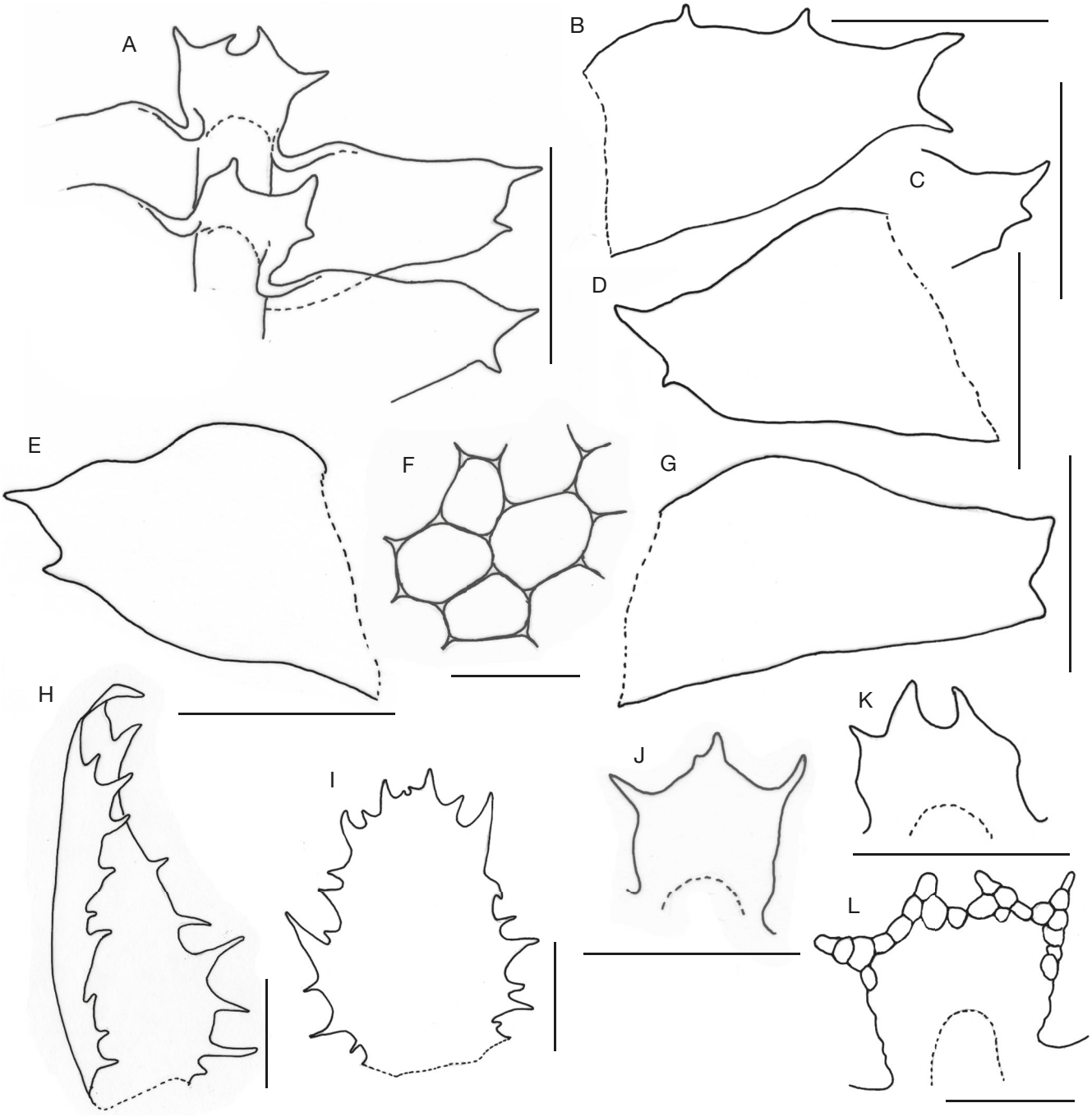

Fig. 2. — *Cryptolophocolea explanata* (Mitt.) Váňa & Crand.-Stotl.: **A**, shoot in ventral view; **B**, **D**, **E**, **G**, leaves; **C**, leaf apex; **F**, cells; **H**, female bract; **I**, female bracteole; **J**-**L**, underleaves. All drawn from the specimen *Etesse s.n.* at G (s.n.). Scale bars: A-E, G-K, 500 µm; L, 200 µm; F, 50 µm.

Cells
Leaf cells hexagonal, 24-36 µm wide, 24-50 µm long, thin walled, trigones small, acute.

Underleaves
Hardly wider than the stem, 0.30-0.40 mm, usually as wide as long, narrowly connate to the nearest leaves on both sides, rounded-quadrate to slightly obovate, bifid up to ¼ down with rather short triangular acuminate lobes and lunate sinus, margins convex, recurved near base, with one tooth on both sides, teeth shorter or like apical lobes.

Gametangia
Gynoecia terminal on normal-leaved branches or main shoots, bracts ovate lanceolate, asymmetric, 2.20 mm long, 0.90 mm wide, canaliculate, margins laciniate, bracteoles oblong, 1.60 mm long, 1.20 mm wide, margins laciniate; perianths subcylindrical, 3-carinate, keels broadly winged, ciliate along

the whole length, mouth densely laciniate; androecia in long spikes with more than 15 pairs of bracts, intercalary or terminal on normal leaved branches, bracts 1.00 mm long, 0.50 mm wide, smaller than the normal leaves and saccate at dorsal base, antheridia stalk biseriate.

Comments
Lophocolea explanata was reported from New Caledonia by Paris (1906) based on a specimen collected by Etesse. No voucher has been found in the herbarium of E. G. Paris at REN, but a duplicate is kept in G (see also Stephani's correspondence to Paris, 9.VII.1905 [Rennes 1 University Library]) matching the isolectotype of *L. explanata* in G and confirms the presence of this species in New Caledonia. Stephani (1906) described the species as being dioecious, likely owing to the absence of male shoots in the type, but the New Caledonian specimen is autoecious.

Cryptolophocolea subcostata (Steph.) Thouvenot (Fig. 3)

Cryptogamie, Bryologie 39 (3): 364 (Thouvenot *et al.* 2018). — *Lophocolea subcostata* Steph., *Species Hepaticarum* 6: 295 (Stephani 1922). — *Chiloscyphus subcostatus* (Steph.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 423 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. *Le Rat s.n.* (lecto-, here designated, G["In jugo Dogny, 1050 m", VII.1909, *L. Le Rat 424*, G00112445]!; isolecto-, REN[herb. E. G. Paris s.n.]).

Further specimens examined. — **New Caledonia**. South Province, ridge between the path to Dzumac and Mt. Ouin, 1100 m, 17.V.1951, *Hürlimann 2599* (PC[PC167677]); Païta, Humboldt massif, 1205 m, cloud forest, 30.IX.2008, *Thouvenot NC1799*; North Province, Hienghène, Panié massif, between Bwa Téan and Payolé, 1000 m, 9.X.2012, *Thouvenot NC1879*.

Distribution in New Caledonia. — Scattered in North and South Provinces, in cloud forest above 1000 m.

Total range. — Endemic.

Description
Autoecious.

Habit
Plants medium sized, moist shoots 3.00 mm wide.

Leaves
In medium parts of stems, leaves 0.90-1.00 mm long, 0.60-0.70 mm wide at bases, 0.30-0.40 mm at apices, obliquely spreading, dorsally convex, canaliculate, when flat long ovate, asymmetrical, ventral bases widened, dorsal margins nearly straight, apices acute, truncate or bilobate, with additional irregular sharp teeth at apices and ventral margins, dorsal margins entire or with a few smaller teeth, decurrent.

Cells
Leaf cells round, 25-35 µm wide, trigones large, basal cells larger.

Underleaves
Large, widely connate to the leaves on both sides, rounded, short bifid with connivent lobes and lunate sinus, margins sharply toothed with many long teeth like the apical lobes, disc 0.40-0.60 mm wide.

Gametangia
Gynoecia terminal on normal leaved branches, bracts much tongue like, canaliculate, margins unevenly ciliate-toothed, bracteoles shorter, margins ciliate-toothed; perianths subcylindrical, 3-carinate, keels broadly winged, ciliate along the whole length, mouth shortly trilobate, lobes oval, laciniate; androecia in long spikes, intercalary to subterminal on leaved branches, bracts like the vegetative leaves but smaller and dorsally saccate at base.

Comments
As mentioned by Thouvenot *et al.* (2018), this species is separated from the two additional *Cryptolophocolea* species reported from New Caledonia by leaves strongly canaliculate (separating it from *C. explanata* (Mitt.) Váňa & Crand.-Stotl.) and autoecious sexuality and short oval perianth lobes (separating it from *C. levieri* (Schiffn.) L. Söderstr.). From the closely related *C. costata* (Nees) L.Söderstr. it is separated mainly by the subtruncate to shortly trilobed perianth mouths, smaller size with leaves less than 2 mm long (vs 2-3 mm), rounded underleaves and dorsal leaf margins entire or with a few small teeth. As molecular evidence for a possible synonymy with the latter is lacking, *C. subcostata* is kept as a separate species.

Genus *Heteroscyphus* Schiffn.

Heteroscyphus argutus (Reinw., Blume & Nees) Schiffn. (Fig. 4)

Oesterreichische Botanische Zeitschrift 60: 172 (Schiffner 1910). — *Jungermannia arguta* Reinw., Blume & Nees, *Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum Exhibentia Ephemerides sive Observationes Historias et Experimenta* 12: 206 (Reinwardt *et al.* 1824). — *Chiloscyphus argutus* (Reinw., Blume & Nees) Nees, *Synopsis Hepaticarum*: 183 (Gottsche *et al.* 1845). — Type: **Java**. "In montibus Sadjra […] Iavae insulae, prope Rawayan…", *Blume s.n.* (G[G00280112]).

Chiloscyphus acutus Steph., *Species Hepaticarum* 6: 302 (Stephani 1922). — Type: **New Caledonia**. "*Lerat*" *s.n.* (lecto-, here designated, G["Île des Pins, Forêt de Condo", V.1909, *L. Le Rat 44*, G00069505]!; isolecto-, REN[herb. E. G. Paris]!; syn-, G["Île des Pins, Grotte d'Aoupéna", V.1909, *L. Le Rat 72*, G00282946]!) **syn. nov.**

Further specimens examined. — **New Caledonia**. South Province, Farino, Grandes Fougères Nature Park, Houé river, 430 m, 24.IX.2008, *Thouvenot NC435*; 370 m, 16.IX.2016, *Thouvenot NC2450*; La Foa, Mts. Koghis, 500 m, IV.2013, *Coulerie COU143*; Mt. Dogny, 540 m, 9.V.2015, *Metoyer MET061*; Mt. Dzumac, IV.1907, *Le Rat s.n.* as "*Chiloscyphus jackii*" (REN[herb. E. G. Paris]); Mts. Koghis, on bark and rocks near stream, 1000 ft, forest, 21.IV.1914, *Compton 801* as *Chiloscyphus argutus* (BM[BM013409505]).

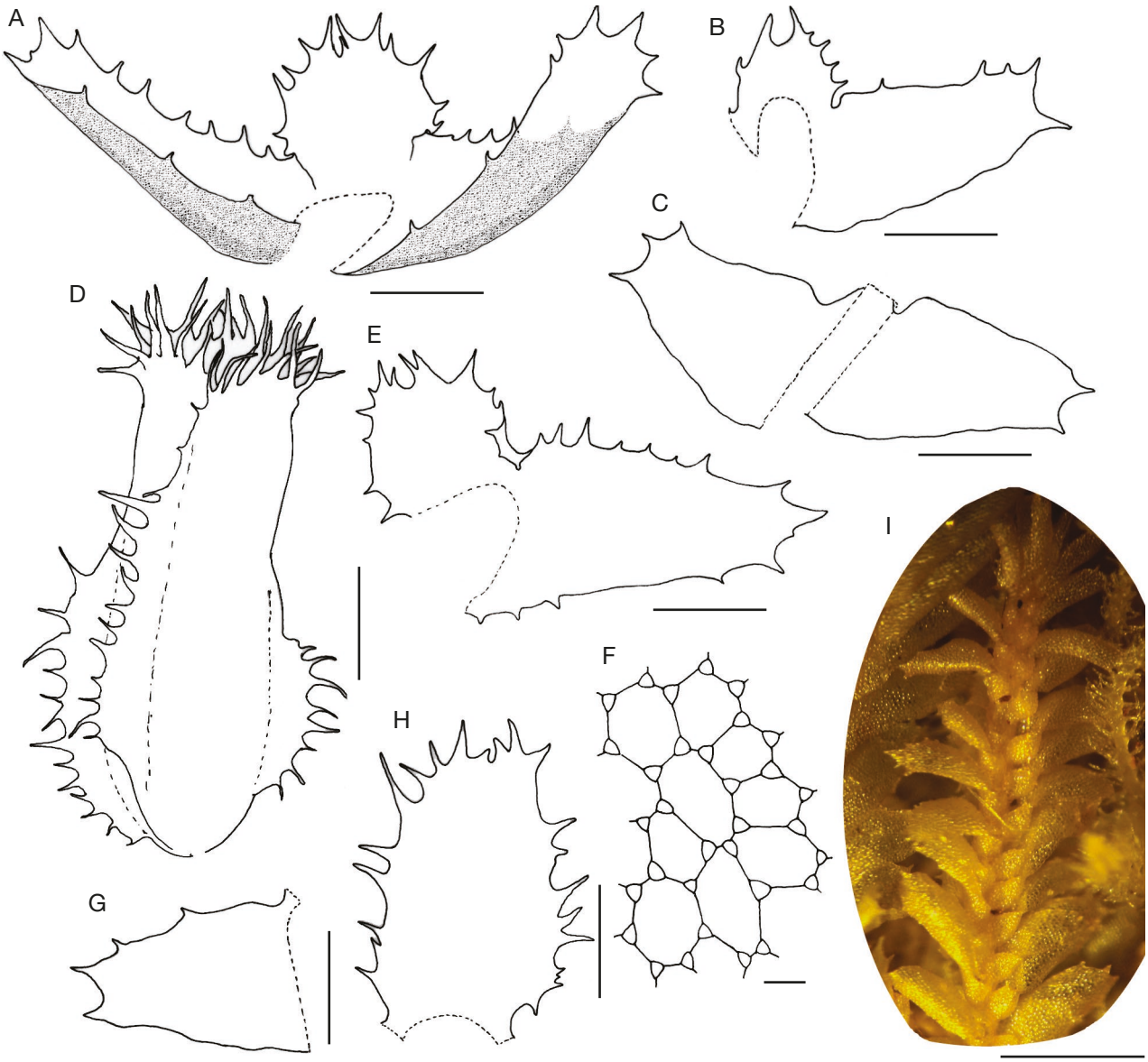

Fig. 3. — *Cryptolophocolea subcostata* (Steph.) Thouvenot: **A**, **B**, **E**, leaves and underleaves, ventral view; **C**, **G**, leaves; **D**, perianth; **F**, cells; **H**, female bracteole; **I**, androecium. All illustrated from *Hürlimann 2599a* (PC0167677). Scale bars: F, 20 µm; A-E, G, H, 500 µm; I, 1 mm.

Distribution in New Caledonia. — Frequent in North and South Provinces, including Isle of Pines, in moist conditions on ground, dead wood, trees or tree ferns, collected between 300-1200 m.

Total range. — Southern Asia, Indonesia, Oceania, Australasia, Africa.

DESCRIPTION

Based on the lectotype of *Chiloscyphus acutus*. Further descriptions and illustrations in Piippo (1985).

Dioecious.

Habit

Plants medium, wet shoots 1.50-2.50 mm wide; leaves alternate to subopposite, dorsally obliquely assurgent in a wide angle *c*. 130°, spreading at a right angle when flattened.

Leaves

Ovate-oblong, 1.20-1.40 mm long, 1.00-1.20 mm wide at bases, 0.60-0.80 mm below apices, apices widely rounded, with usually four linear teeth, up to eight uniseriate cells long, the upper ones acute to narrowly rounded, sometimes with one or two additional teeth, lateral margins naked but usually with one subapical tooth on both dorsal and ventral sides and the ventral often with a tooth more.

Cells

Leaf cells hexagonal, their size progressively increasing up to down, (20-)25-35 µm wide, cell walls evenly a little thick, without trigones.

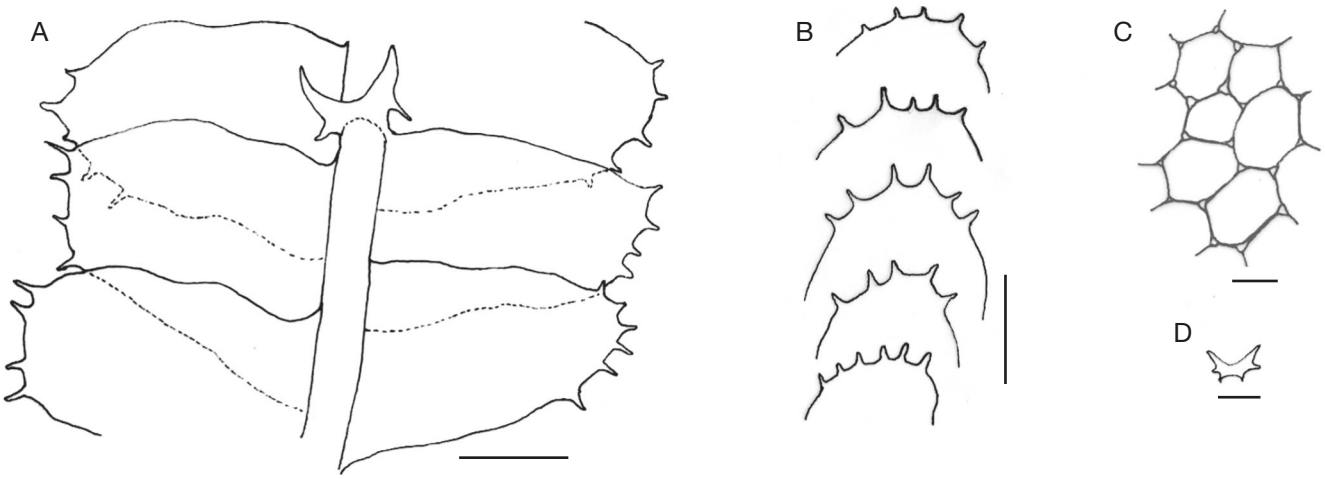

Fig. 4. — *Heteroscyphus argutus* (Reinw., Blume & Nees) Schiffn.: **A**, portion of shoot in ventral view; **B**, leaf apices; **C**, cells; **D**, underleaf. All drawn from the lectotype of *Chiloscyphus acutus* Steph. (G00069505). Scale bars: A, B, 500 µm; C, 20 µm; D, 200 µm.

Underleaves
Free on both sides or unilaterally narrowly connate to the nearest leaf, overall dimensions 0.40-0.50 mm long, 0.80-1.00 mm wide, disc transversally elongate, narrow, 0.10-0.15 mm wide, 0.40 mm long, sinus wide, flat or shallowly convex, bifid with lobes widely spreading, curved frontward, horn like, narrowly triangular at base, evenly acuminate, ending in linear points, lateral margins short, each one with a linear segment backward turned.

Gametangia
At the end of very abbreviated leafless branches; gynoecia with bracts and bracteoles unevenly toothed, perianths cyathiform, deeply 3-lobate, lobes spinose-toothed; androecia in long narrow spikes made of 3-9 pairs of bracts, bracts deeply bifid with narrow segments ending in 4-6 uniseriate cells.

Comments
Based on Stephani's diagnoses and drawings, *Chiloscyphus acutus* is separated from *C. argutus* by the leaf apices, which are acute instead of truncate. In the type specimens, however, the leaf apices are truncate to convex, rarely acute, with 4-6 short teeth like *Heteroscyphus argutus*. All other features are identical.

Both specimens of *Chiloscyphus acutus* in G were collected by Mrs Louise Le Rat on Île des Pins and sent by E. G. Paris to Stephani for identification. One of them, collected in Condo Forest, was annotated "*n.sp.*", "*original*" and "*cum flore sterili*" by Stephani, and can therefore be selected as the lectotype. The second, collected in Aoupéna cove, was first identified by Paris as *Plagiochila*; Stephani subsequently added the name *Chiloscyphus acutus*. As it was collected in a nearby locality at the same date by the same collector, it may reasonably be regarded as a syntype of *C. acutus*.

Heteroscyphus aselliformis
(Reinw., Blume & Nees) Schiffn.
(Fig. 5)

Oesterreichische Botanische Zeitschrift 60: 172 (Schiffner 1910). — *Jungermannia aselliformis* Reinw., Blume & Nees, *Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum Exhibentia Ephemerides sive Observationes Historias et Experimenta* 12: 412 (Reinwardt *et al.* 1824). — *Chiloscyphus aselliformis* (Reinw., Blume & Nees) Nees, *Synopsis Hepaticarum*: 176 (Gottsche *et al.* 1845). — Type: **Java**. *Blume s.n.*, not seen.

Chiloscyphus theriotii Steph., *Species Hepaticarum* 6: 316 (Stephani 1922). — Type: **New Caledonia**. *Franc s.n.* (lecto-, here designated, G["Mts. Koghis, 1/11/1909", *Franc s.n.*, hb. Theriot 169, G00069428]!; isolecto-, PC[as *Chiloscyphus aselliformis*, PC0767992]!).

Further specimens examined. — **New Caledonia**. North Province, Pouébo, Diahoué, Tooliwök pass, on bark in rain forest, 700 m, 21.IX.2019, *Thouvenot NC2827*; Mandjélia, on a tree fern base, 701 m, 14.IX.2019, *Thouvenot NC2896* (PC[PC0779855]); South Province, Mts. Koghis, Mt. Bouo ridge, 700 m, 20.IV.1951, *Guillaumin et Baumann-Bodenheim 12670* (PC[PC0767993]); Mts. Koghis, Mt. Moné, south side, 750 m, 27.VII.1951, *Hürlimann 2779* (PC[PC0767988]); Nouméa, along the pathway from the Koghis lodge towards Mt. Bouo, epiphyte, *c.* 850 m, *F. Müller NC277*; Yaté, Rivière Bleue Provincial Park, Pourina trail, 480 m, on bark in an open wet forest, 20.IX.2016, *Thouvenot NC2482*; Mts. Koghis, 1.XI.1909, *Franc s.n.*, det. Stephani as "*Chiloscyphus hebridensis*" (G, PC[PC0767992]).
Papua New Guinea. Morobe Prov., Cromwell Mts., *c.* 2250 m, 20.VI.1981, *Koponen 31350*, det. S. Piippo (PC[PC0767989]).
Java. Res. Pasoeroean, 1200 m, 04.VI.1930, *Verdoorn 19*, det. W.E. Nicholson (PC[PC0767990]).

Distribution in New Caledonia. — Frequent in North and South Provinces on tree trunks and fern tree rhizomes in rainforests and mesophilous forests at medium elevations (collected between 300-750 m).

Total range. — Southeast Asia, Indonesia, Melanesia.

Description
Dioecious.

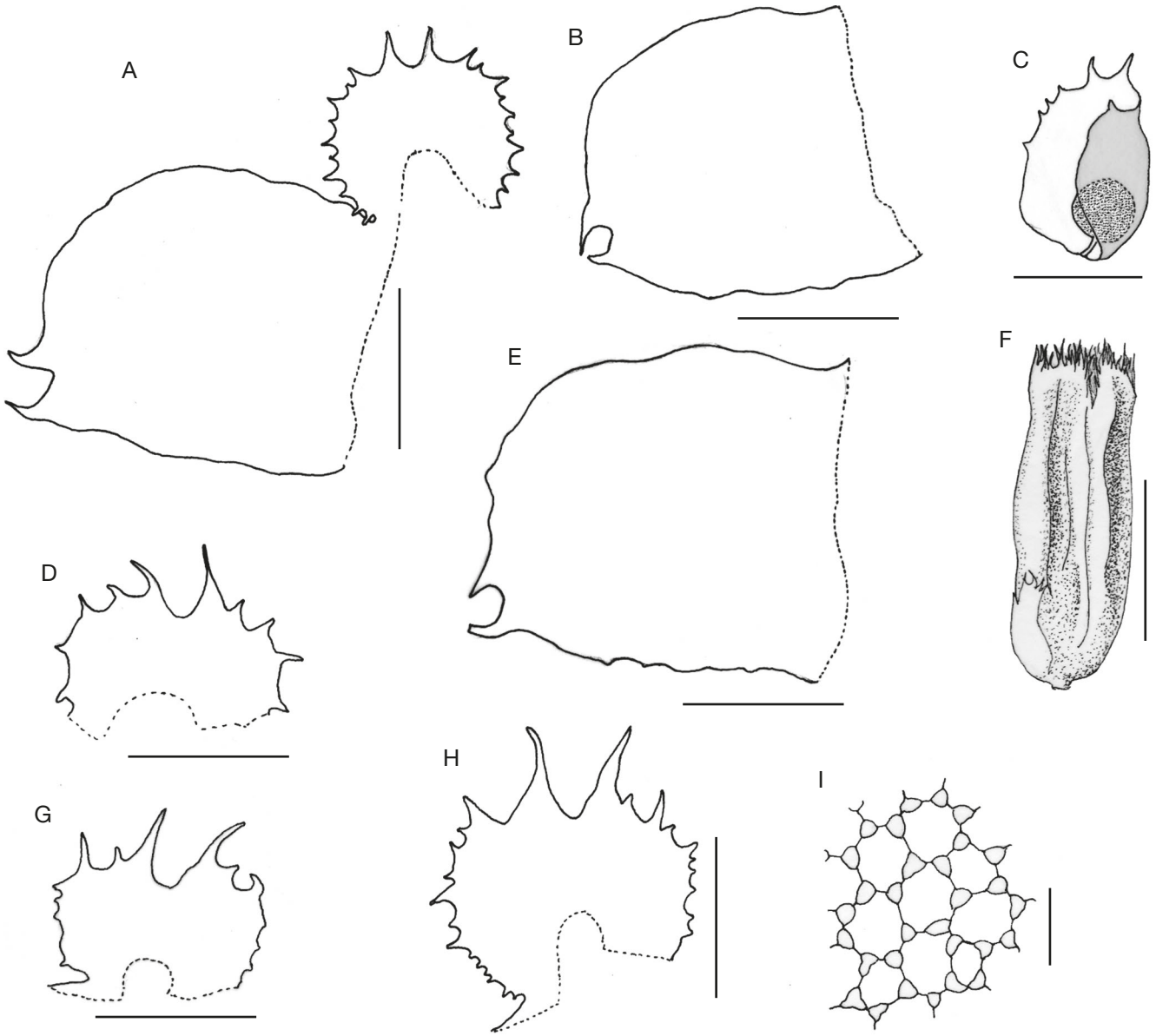

Fig. 5. — *Heteroscyphus aselliformis* (Reinw., Blume & Nees) Schiffn.: **A**, leaf and underleaf; **B**, **E**, leaves; **C**, male bract with antheridium; **D**, **G**, **H**, underleaves; **F**, perianth; **I**, cells. All except **F** (from *Guillaumin et Baumann-Bodenheim 12670* [PC0767993]) drawn from the following types of *Chiloscyphus theriotii* Steph.: **A**-**D**, **H**, from PC0767992; **E**, **G**, **I**, from G00069428. Scale bars: A, B, D-H, 1 mm; C, 500 µm; I, 50 µm.

Habit

Plants medium to large, soft textured, 4-5 mm wide when flattened; leaves dorsally assurgent, concave, widely imbricate, subopposite, dorsal leaf margins confluent, lateral-intercalary branches sparse, flagelliform branches occasional to frequent.

Leaves

Leaf shapes variable with normal leaves typically 1.25-2.00 mm long, 1.25-2.50 mm wide, asymmetrically quadrate-rounded, ventral margins rounded, dorsal margins nearly straight, apices asymmetrical, shortly bifid, sinus lunate, shifted toward the dorsal margin, two short triangular lobes erect to connivent, acute to acuminate, ending in long piliform apices, fragile, often broken and absent, sometimes with one additional subapical lobe, both lateral margins entire or the ventral sparsely toothed, leaf variations involve smaller size and symmetry, then the overall shape is oval, and margin ornamentation varying from 0 to +/- 5 small teeth, one celled, or with a few piliform processes.

Cells

30-50 µm, cell walls thin with large trigones at most contiguous.

Underleaves

Large, 0.80-1.70 mm wide, rounded to slightly reniform, shortly bifid, sinus lunate, lobes erect, narrowly triangular acuminate, apices piliform, lateral margins with many small teeth, sometimes with 1-2 subapical additional long teeth, lobe-like.

Gametangia
At the end of short leafless branches, lateral-intercalary; gynoecia with two innermost pairs of bracts and bracteoles, free, margins fimbriate all around, bracteoles 2.0 mm long, 1.30 mm wide, deeply bifid, bracts 2.00 mm long, 2.50 wide, 3(-4)-fid, perianth cyathiform to subcylindrical, 2.00 mm long, split to mid length in three lobes toothed-fimbriate; androecia in short spikes of one or two pairs of bracts, bracts cochleariform, margins minutely toothed with two sharper teeth at apices, antheridia stalks bi-seriate.

Comments
Heteroscyphus aselliformis is a very variable species (Stephani 1907) and has been described under several names, depending on their geographic origin, i.e., as *Chiloscyphus theriotii* in New Caledonia. Some of the specimens from New Caledonia, including the type material of *C. theriotii*, are rather stable with a large size, leaves 3.25 mm long and 2.5 wide, oblong-rounded, asymmetrically bifid with apices shifted toward the dorsal margins which is loosely recurved (vs tightly so, or duplicate), ventral leaf margins eventually with a short tooth beneath the apex, underleaves connate to both nearest leaves by a medium to narrow band, wide rounded, apices bifid, lobes narrowly triangular acute to acuminate, margins evenly and sharply denticulate all around. Other New Caledonian collections, however, and specimens from other countries, are more variable. Specimens from Papua New Guinea, for example, are smaller and with entire underleaf margins while those from Java seem to be intermediate in size and with crenulate underleaf margins.

In the field, *H. aselliiformis* resembles *H. confertus* and *H. giganteus* by its pale colour, light green to brownish, large size and leaves dorsally assurgent, somewhat cochleariform. It differs from those two species by its longer and sharper leaf lobes, and the presence of additional sharp teeth on the leaf margins. Furthermore, the rounded to reniform underleaves, which are bifid with narrowly triangular erect lobes and lateral margins copiously denticulate, differ from those of *H. giganteus* which has laciniate underleaf margins, and from those of *H. confertus* which has widely triangular underleaf lobes. In addition, the latter species is smaller. The species also resembles *H. hebridensis* and some New Caledonian specimens of *H. aselliformis* collected by Franc (G, PC) were misidentified as *H. hebridensis* by Stephani. *Heteroscyhus hebridensis*, however, has rather widely triangular ovate leaves, more strongly laciniate underleaves and small to inconspicuous trigones.

Heteroscyphus assurgentissimus
J.J.Engel, Thouvenot & Frank Müll.
(Fig. 6)

Nova Hedwigia 113: 67 (Engel *et al*. 2021). — Type: **New Caledonia**. South Province, Parc Provincial de la Rivière Bleue, *c*. 200-380 m, lowland rain forest, on a rockface, 5.IX.2001, *Müller NC327* (holo-, DR; iso-, F, hb. Thouvenot).

Distribution in New Caledonia. — Only known from the type locality in South Province.

Total range. — Endemic.

description
Further description and illustrations in Engel *et al*. (2021).
Dioecious.

Habit
Plants rigid, up to 5 mm wide when flattened, the shoot tips sharply dorsally assurgent; ventral-intercalary branching frequent; stems narrow for plant size, 0.20-0.30 mm wide; leaves subopposite, stiffly dorsally assurgent, often forming a gentle bow-like arch, the adaxial face of opposing leaves facing one another and forming a deep narrow channel; leaves closely imbricate, dorsally connate and forming an elevated, laminar lip to *c*. 4 cells wide; leaves moderately convex in dorsal sector, moderately abaxially concave in ventral sector.

Leaves
1.50-2.50 mm long, 0.90-1.30 mm wide at widest point, elongate ovate-trapezoid to lingulate, distinctly narrowed toward the apex, moderately to distinctly dilated in ventral-basal sector; apex bifid to 0.05-0.10, the lobes divergent, occasionally parallel, the ventral lobe often larger than the dorsal, the dorsal lobe at times reduced to a small tooth or lacking, the lobes narrowly acute to acuminate, the sinus mostly lunate, occasionally narrowly rounded; lamina margins entire.

Cells
30-47 µm wide, 37-57 µm long, somewhat larger near leaf bases, median leaf cells with strong secondary thickenings of the radial walls, each thickening interrupted by a single, large, clearly defined pit, the wall thickenings converging at the cell junctures to form massive nodose trigones.

Underleaves
2.3-3.5 times the stem width when flattened, connate with the leaves on both sides, connate portion 3-6 cells wide, imbricate, stoutly ovate to subreniform, 0.80-1.30 mm long, 0.80-1.10 mm wide; apex 2-4-lobed, the median pair of lobes often larger, the lobes ± parallel, acute-apiculate to acuminate, entire or with a tooth toward the outer margin, lamina margin on each side with 1-5 small teeth.

Gametangia
Gynoecia not seen; androecia small for plant size, hidden by leaves in dorsal aspect, on abbreviated, determinate, ventral-intercalary branches, the androecia foliose, with 2-5 pairs of bracts, the bracts strongly dorsally assurgent, suberect, similar to leaves in shape and form except the bracts are more concave and the apex is notably more narrowed, the apex bidented, the base concave ventricose, the dorsal pocket more strongly inflated, with a several-celled tooth distally; the antheridia stalk biseriate; bracteole stoutly ovale, bifid to *c*. 0.5, the lamina margins each with a small tooth.

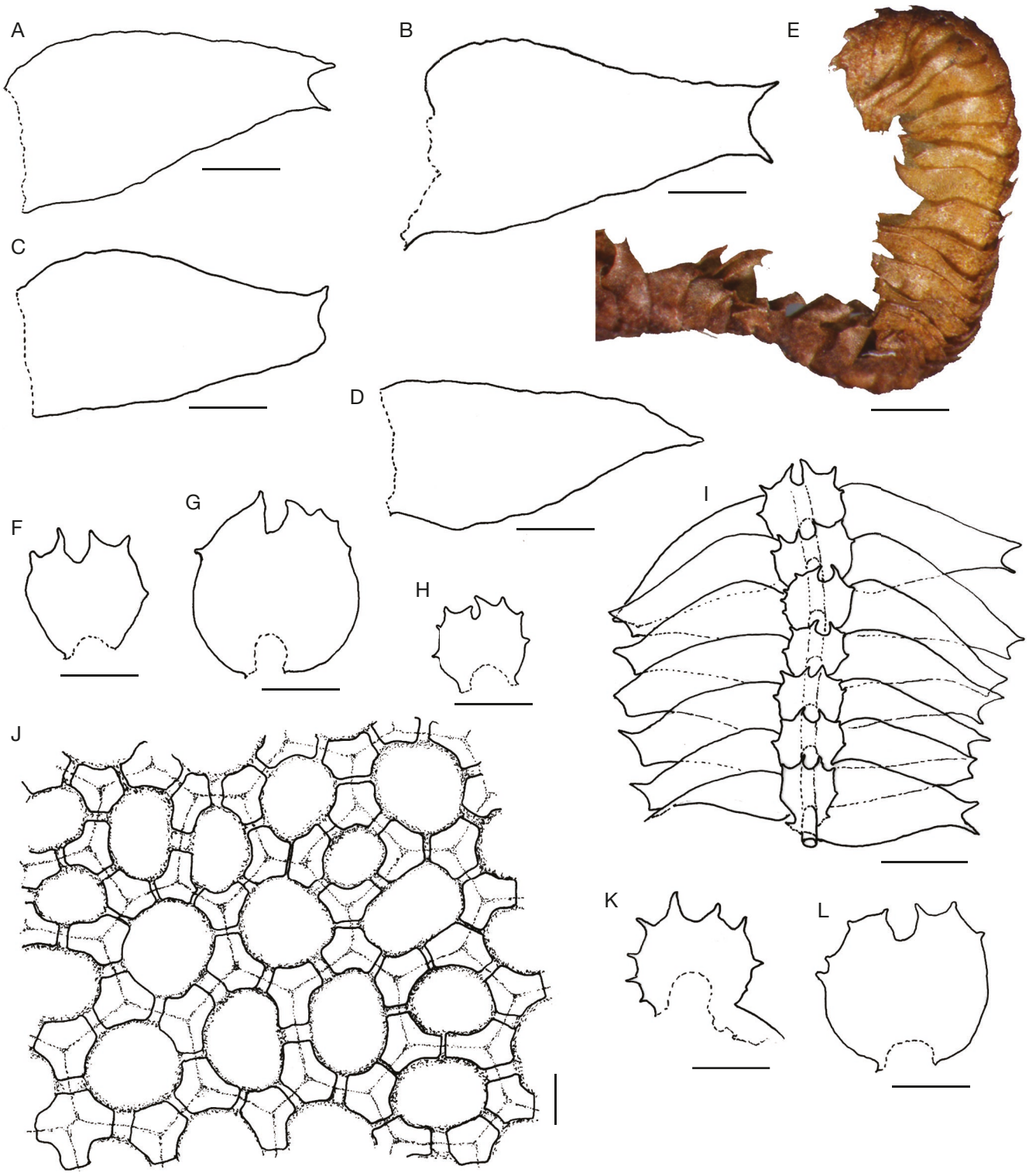

FIG. 6. — *Heteroscyphus assurgentissimus* J.J.Engel, Thouvenot & Frank Müll.: **A-D**, leaves; **E**, shoot habit in dry condition, lateral view; **F-H**, **K**, **L**, underleaves; **I**, shoot portion, ventral view; **J**, leaf cells. All illustrated from the holotype. Scale bars: A-D, F-H, K, L, 500 µm; E, I, 1 mm; J, 20 µm.

COMMENTS

Heteroscyphus assurgentissimus clearly stands out by: 1) dorsally assurgent leaves and shoot apices; 2) strictly ventral-intercalary branching; 3) ovate trapezoid to lingulate, bifid leaves; and 4) massive trigones extending into strongly thickened cell walls narrowly pitted. It could be regarded as close to *Cryptolophocolea explanata* by the leaf and underleaf shapes, but the latter species can be easily separated from *H. assurgentissimus* by its complanate habit, thin-walled cells without trigones and gametangia on elongate shoots.

Heteroscyphus caledonicus (Steph.) Schiffn. (Fig. 7)

Oesterreichische Botanische Zeitschrift 60: 172 (Schiffner 1910). — *Chiloscyphus caledonicus* Steph., *Species Hepaticarum* 3: 216 (Stephani 1907). — Type: **New Caledonia**. *Deplanche s.n.* (holo-, G[G00069500]!).

Further specimens examined. — **New Caledonia**. South Province, Mé Areimbo, X.1909, *L. Le Rat 341* (G); Mts. Koghis, in forest, 300 m, 4.IV.1909, *Franc s.n.* (G); North Province, Touho, Massif des Lèvres, Tipelei upper valley, on sedimentary rocks, 315 m, 12.X.2012, *Thouvenot NC2426* (PC[PC0712113]).

Distribution in New Caledonia. — Reported from South Province according to the labels of historic collections, but recently found only in North Province, in remote places of the north-eastern coastal massifs, at low elevations.

Total range. — Endemic.

Description

Dioecious.

Habit

Plants fragile, minute to medium sized, very variable in width, usually up to 3.00 mm, but many shoots less than 1 mm wide; leaves subopposite, horizontally spreading at right angle, slightly imbricate to contiguous, dorsally free, the homologous leaves separated by a strip of 3-4 epidermal cells on the dorsal midline of the stem; stems 0.15-0.20 mm wide.

Leaves

1.10-1.40 mm long, 0.85-1.20 mm wide, rectangular to oblong, apices truncate to widely triangular, with a spinose tooth on each three angles, teeth at most 3 cells long, dorsal and ventral margins entire.

Cells

Leaf cells hexagonal, 60-70 µm long, 40-50 µm wide, longer near bases, without trigones or trigones small and acute.

Underleaves

Inserted in an inverted U, narrowly decurrent on one or both sides, sometimes narrowly connate to the ventral bases of the nearest leaves, otherwise free and set away from the corresponding leaves to the middle of the next ones; underleaves wider than long, 0.30-0.40 mm long, 0.40-0.60 mm wide, usually 1-2 times the stem width, bifid rarely trifid, discs narrowly transverse, only two cells high at sinus insertion, lobes linear, above 2-celled bases or not, erect, sinus widely lunate or flat, lateral margins with one to three linear segments, lobes and segments fragile, often broken, sometimes furcate.

Gametangia

Gynoecia at the end of short leafless lateral-intercalary branches, bracts asymmetrically bifid, laciniate-toothed, bracteoles symmetrically bifid up to mid length, margins toothed; perianths cyathiform, deeply trilobed, lobes ovate with laciniate-toothed margins; androecia not seen.

Comments

Heteroscyphus caledonicus can be distinguished from the variable *H. grandiflorus* by: 1) leaves mainly oblong-rectangular instead of ovate; 2) leaves contiguous or narrowly overlapping instead of imbricate; 3) apical teeth spinose, shorter, not ending in piliform tips; and 4) cells with small trigones, if any.

The type in G is sterile and scanty, but fresh material collected by the author contained gynoecia, which are described here for the first time and are similar to those of *Heteroscyphus* and *Chiloscyphus*. The species is provisionally maintained in *Heteroscyphus* pending the discovery of androecia. Like *H. etesseanus* and *H. cornutistipulus* (see below) as well as further *Heteroscyphus* species in Australasia (Engel 2015), *H. caledonicus* lacks typical vegetative characters of *Heteroscyphus* such as connate underleaves, large trigones and opposite leaves.

Heteroscyphus coalitus (Hook.) Schiffn. (Fig. 8)

Oesterreichische Botanische Zeitschrift 60: 172 (Schiffner 1910). — *Chiloscyphus coalitus* (Hook.) Dumort., *Recueil d'Observations sur les Jungermanniacées* 1: 19 (Dumortier 1835). — *Jungermannia coalita* Hook., *Musci Exotici* 2: tab. 123 (Hooker 1820). — Type: **New Zealand**. Dusky Bay, *A. Menzies s.n.* (G[G00283086]!).

Chiloscyphus confertifolius Steph., *Species Hepaticarum* 6: 304 (Stephani 1922). — Type: **New Caledonia**. *Lerat s.n.* (lecto-, here designated, G["Nov. Caledon. Inter Farino et Table Unio. 07/1909", *Le Rat 95*, G00069493]!) **syn. nov.**

Lophocolea latistipula Steph., *Species Hepaticarum* 6: 281 (Stephani 1922). — *Chiloscyphus latistipulus* (Steph.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 418 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. *Franc s.n.* (lecto-, here designated, G["*Lophocolea latistipa* (sic) n.sp., Nlle Calédonie, forêt de Tao, 600 à 800 m", I.1910, *Franc s.n.*, G00121768]!) **syn. nov.**

Chiloscyphus latistipus Steph., *Species Hepaticarum* 6: 309 (Stephani 1922). — Type: **New Caledonia**. *Lerat s.n.* (lecto-, here designated, G["Nova Caledonia, Me Areimbo. s.d., *Dna L. Le Rat 171*, mit Balantiopsis, mit Lepidozia", G00069461]!; isolecto-, REN[herb. E. G. Paris, s.n.]!) **syn. nov.**

Chiloscyphus similis Steph., *Revue bryologique* 35: 28 (Paris 1908), non *Chiloscyphus similis* Steph., *Kongliga Svenska Vetenskaps Academiens Handlingar*, Ny Följd 46: 56 (Stephani 1911). — *Chiloscyphus subsimilis* Steph., *Species Hepaticarum* 6: 314 (Stephani 1922), nom. illeg. — Type: **New Caledonia**. *Lerat s.n.* (lecto-, here designated, G["*Chiloscyphus subsimilis*. Nov. Caledon. Sine schedule", 1907, *Le Rat 195*, G00069431]!) **syn. nov.**

Chiloscyphus francanus Steph., *Species Hepaticarum* 6: 306 (Stephani 1922). — Type: **New Caledonia**. *Franc s.n.* (lecto-, here designated, G["Mt. Dzumac, 900 m, tronc d'arbre", 1.XI.1907, *Franc s.n.*, G00283066]!; syn-, G["Nlle Calédonie, Mts. Koghis, versant ouest, 300 m, bords d'un torrent", 20.X.1907, *Franc s.n.*, G00069483, G0069484! s.l., s.d., *Franc s.n.*, G00283067]!; isolecto-, PC[PC0101950]!; isosyn-, PC[PC101948, PC0101949]!) **syn. nov.**

Further specimens examined. — **New Caledonia**. South Province, Sarraméa, Dogny plateau, on ground in rain forest, 650 m, 24.X.2019, *Thouvenot NC2602* (PC[PC0779853]); Yaté, Dzumac

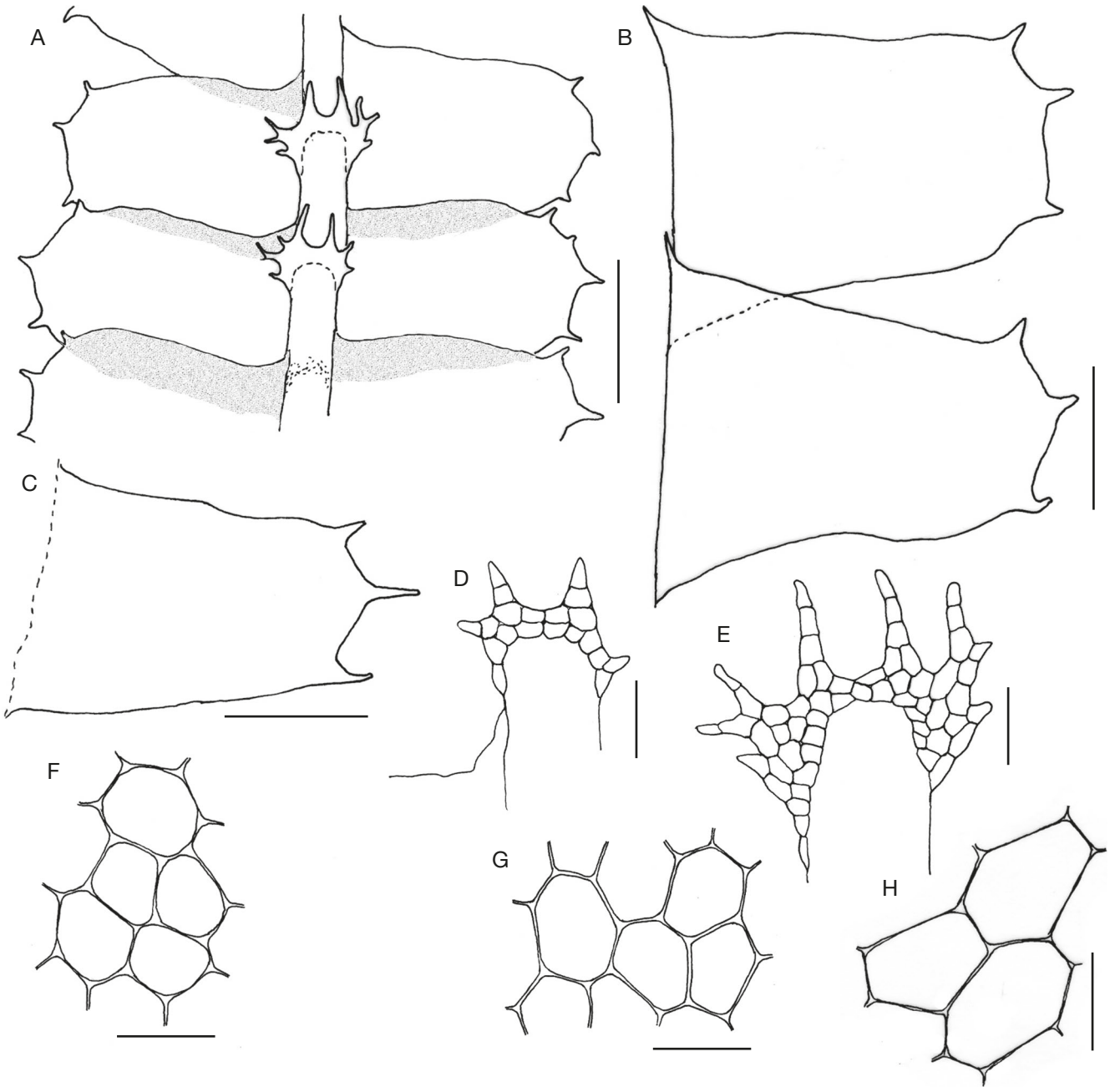

Fig. 7. — *Heteroscyphus caledonicus* (Steph.) Schiffn.: **A**, shoot portion, ventral view; **B**, two adjacent leaves, dorsal view; **C**, leaf; **D**, **E**, underleaves; **F**, cells from upper third of leaf; **G**, cells from median part; **H**, cells from lower part. **A**, **D**-**G**, drawn from *Thouvenot NC2426*; **B**, **C**, **H**, from the lectotype of *Chiloscyphus caledonicus* Steph. (G00069500). Scale bars: A-C, 500 µm; D, E, 100 µm; F-H, 50 µm.

massif, on ground in rain forest, 900 m, 26.X.2012, *Thouvenot NC2392*; North Province, Poindimié, Amoa valley, Tipwadabwé, on damp rock in a creek, 163 m, 13.X.2019, *Thouvenot NC2726*; South Province, Mé Amméri, 700 m, 30.IX.1950, *Guillaumin & Baum. Bod. 9150*, det. Hürlimann, as *Chiloscyphus francanus* (G[G045946]); "Mts. Koghis, forêt", *Franc s.n.* as *Chiloscyphus similis* (*sensu* 1908) (PC[PC0167662], G s.n.); "in jugo Dogny 1040 m", VII.1909, *L. Le Rat s.n.* as *Chiloscyphus latistipus* (G s.n.); "in jugo Dogny", X.1909, *L. Le Rat s.n.* as *Chiloscyphus latistipus* (PC[PC0101941, PC0150605]); "Mts. Koghis", 1.X.1909, *Franc s.n.* as *Chiloscyphus latistipus* (G s.n.).
Chiloscyphus similis (*sensu* Stephani 1911): **Chili**. Fuegia, *Scottsberg s.n.* (G[G00069415]).

Distribution in New Caledonia. — Frequent in rain forest and creek banks in both provinces of Grande Terre, collected from 150 to 1150 m, on soils or rocks, occasionally at the base of trees.

Total range. — South-East Asia, Indonesia, Melanesia, Australasia, (Argentina?).

Description

Dioecious.

Habit

Plants large with shoots 2.50-4.00 mm wide.

Leaves
Spreading at nearly right angle, longitudinally convex, oval-oblong to subrectangular, 1.30-1.60 mm long, 1.00-1.60 mm wide at bases, 0.50-0.80 mm at apices, usually as wide as long at base, not dorsally confluent, margins entire, truncate apices straight to slightly convex, with a single tooth at both angles, teeth acuminate to linear, acute, 3-6 uniseriate cells long above and 0-2 biseriate ranks at base.

Cells
Median leaf cells hexagonal, somewhat elongate, 30-60 µm long, 30-75 µm wide, trigones acute, small to inconspicuous.

Underleaves
Reniform, 2-3 times the stem width, 0.20-0.50 mm long, 0.70-1.20 mm wide, inserted on the stem in a deep sinus and connate to both adjacent leaves by a very wide band of cells, the apical margin widely convex with 4-6 straight teeth, sublinear acute, the innermost erect, the lateral spreading, like the leaf ones.

Gametangia
Gynoecia at the end of short leafless ventral lateral branches, bracts small, rounded, 2-toothed, perianths 1 mm long, cupulate with trilobate mouth, lobes rounded, toothed, surface mammillose; androecia not seen.

Comments
Heteroscyphis coalitus is morphologically highly variable and a large number of forms and varieties have been described in this species (Tropicos 2021). According to Piippo (1985), the species especially varies in the shape of the underleaves and their connation to the leaves. As it is a species widely distributed, it is not surprising that there are so many names for this taxon.

The original materiel of *Chiloscyphus confertifolius* at G is limited to a single packet handwritten by Stephani which is therefore selected as the lectotype. Regarding *Lophocolea latistipula*, two specimens are kept as types at G, both collected by Franc in the same locality. The specimen with the mark "*n.sp.*" is selected despite the orthographic error "*latistipa*" which may not lead to confusion, since the epithet *latistipus* is in fact assigned to *Chiloscyphus latistipus* with a type collected by Mrs L. Le Rat. In addition, the drawing by Stephani matches with this specimen. In contrast, a second specimen labelled *Lophocolea latistipula* in G (G00112472, duplicate PC0102424) turned to be *Chiloscyphus longifissus* Steph. (see below).

Among the specimens marked as types of *Chiloscyphus latistipus* at G, the specimen G00069461 is selected as lectotype since it contains the collecting number (171) and the annotation "*n.sp.*" in a letter from Stephani to E. G. Paris dated 31 March 1910 (Rennes1 University Library). Furthermore, "*original*" is written on the label in the author's handwriting. In contrast, the specimens kept at PC (PC0101941 and PC0150605) are in packets with the handwriting of E. G. Paris without any annotation by Stephani, so that they cannot be considered with certainty as parts of the original material.

The name *Chiloscyphus similis* was given to two different type specimens a few years apart by Stephani. In 1908, a New Caledonian specimen collected by Le Rat was validly published under this name in *Revue bryologique* and the original materiel can be identified with the number 195 according to a letter to E. G. Paris dated 2 January 1908 (Rennes 1 University Library). But, in 1911, Stephani described another *C. similis* based on a voucher collected by Scottsberg from Tierra del Fuego. The drawing and protologue show a very different plant, confirmed by the examination of the corresponding specimen from Tierra del Fuego kept at G. No New Caledonian specimen labelled *C. similis* and matching the diagnosis published in 1908 has been found at G, REN or PC. On another hand, in 1922, Stephani published *Chiloscyphus subsimilis* based on a type specimen kept at G and marked with the same number (195) than *C. similis* (1908), according to the correspondence from Stephani to E. G. Paris. Consequently, *C. subsimilis* is an illegitimate name, superfluous against *C. similis* (1908) (*International Code of Nomenclature*, art. 52.1, Turland *et al.* 2018; Loiseau *et al.* 2019), which was validly published with an identified type, while *C. similis* (1911) is invalid as a later homonym. Fortunately, *C. similis* (1911) from Tierra de Fuego is furthermore synonym of *Heteroscyphus valdiviensis* (Mont.) Schiffner (Fulford 1976).

A lot of duplicates of the original material used by Stephani for *Chiloscyphus francanus* were examined, raising the opportunity to recognise a set of syntypes. But a further specimen kept at PC as an isosyntype (PC0101947), cannot be a type since it was collected one year later than the specimens kept at G and lacks annotation by Stephani.

Heteroscyphus confertus (Steph.) Thouvenot
(Fig. 9)

Cryptogamie, Bryologie 39 (3): 365 (Thouvenot *et al.* 2018). — *Chiloscyphus confertus* Steph., *Species Hepaticarum* 6: 305 (Stephani 1922). — Type: **New Caledonia**. *Franc s.n.* (lecto-, here designated, G["Mts. Koghis, 600 m", 1.XI.1909, *Franc 210*, G00069492]!; syn-, PC["Mts. Koghis, 300 m", 1911, *Franc s.n.*, PC0101951]!).

Heteroscyphus rotundiphyllus (H.A.Mill.) Thouvenot, *Cryptogamie, Bryologie* 39 (3): 365 (Thouvenot *et al.* 2018). — *Chiloscyphus rotundifolius* Steph., *Species Hepaticarum* 6: 313 (Stephani 1922), nom. illeg. — *Chiloscyphus rotundiphyllus* H.A.Mill., *Phytologia* 47: 321 (Miller 1981). — Type: **New Caledonia**. "*Lerat*" *s.n.* (lecto-, here designated, G[New Caledonia, "Dent de St Vincent, VII 1909", *Le Rat 189* (herb. Thériot), G00069432]!) **syn. nov.**

Further specimens examined. — **New Caledonia**. North Province, Hienghène, Ouaième Rocks, on twigs in mountain scrubland, on metamorphic bed rock, 982 m, 22.IX.2019, *Thouvenot NC3285*; South Province, "near Nouméa", s.d., *Le Rat s.n.* (PC[PC0167665]); Yaté, Rivière Bleue natural Park, Pourina trail, on bark in a wet forest clearing, 670-695 m, 20.IX.2016, *Thouvenot NC2477*; Païta, Mont Mou, on twigs in cloud forest, 1219 m, 17.IX.2016, *Thouvenot NC1971*; Humboldt massif, along the trail to the hut, on bark in cloud forest, 1205 m, 30.IX.2008, *Thouvenot NC1832*; *NC1851*.

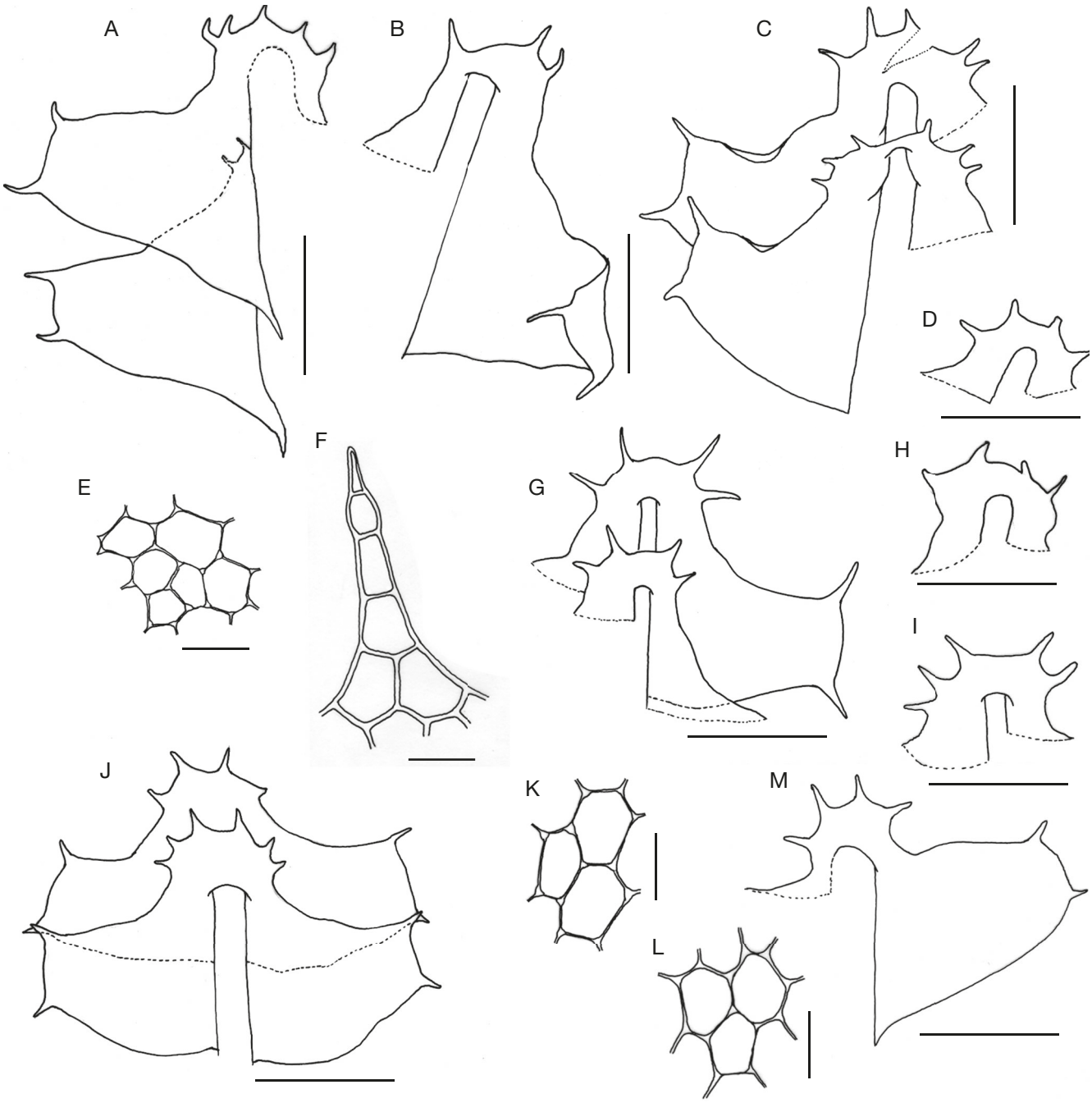

Fig. 8. — *Heteroscyphus coalitus* (Hook.) Schiffn.: **A**, leaves and underleaf, dorsal view; **B**, **C**, **G**, **J**, **M**, leaves and underleaves, ventral view; **D**, **H**, **I**, underleaves; **E**, **K**, **L**, leaf cells; **F**, tooth at leaf apex. **A**, **B**, **D**, **H**, **E**, drawn from the isotype of *Jungermannia coalita* Hook. (G00283086); **C**, **G**, **I**, from the syntype of *Chiloscyphus francanus* Steph. (G00283067); **J**, **K**, from a specimen *Franc s.n.* of *Chiloscyphus similis* Steph. (PC0167662); **F**, **L**, **M**, from the lectotype of *Chiloscyphus subsimilis* Steph. (G00069431). Scale bars: A-D, G-J, M, 1 mm; E, F, K, L, 50 µm.

Distribution in New Caledonia. — Scattered in both provinces of the main island, Grande Terre, collected from 300 to 1200 m, where it grows usually on barks in wet scrublands and open forests, more rarely on rocks in creek banks.

Total range. — Endemic

Description

Dioecious.

Habit

Plants large, shoots 3.50-4.00 mm wide when flattened, soft and fragile; shoots as a whole convex in ventral view and dorsally canaliculate, at most tube like and the ventral leaf faces exposed with conspicuous underleaves; leaves dorsally assurgent, undulate from back to front with the antical half convex, facing the corresponding antical half of the opposite leaf and the postical half concave, leaves densely imbricate,

subopposite, the dorsal margins of opposite leaves confluent on stem back.

Leaves
Orbicular, symmetrical, up to 2.50 mm as wide as long, apices shortly bifid, at times entire, sinus lunate, lobes erect to connivent, triangular acuminate, margins entire, crenulate or minutely toothed.

Cells
Leaf cells rounded hexagonal, 25-50 µm wide, with medium to large bulging trigones, becoming longer towards bases.

Underleaves
Large, up to 5 times the stem width, widely connate to the nearest leaves on both sides, rounded to slightly reniform, 0.70-1.40 mm as wide as long, 1/10-1/3 bifid, sinus obtuse to right angled, lobes triangular acuminate to lanceolate-linear, both margins with few to numerous small teeth.

Gametangia
At the end of short leafless lateral-intercalary branches; gynoecia with bracts lobate, toothed, half long as the perianth, bracteoles small, toothed, perianths cyathiform, 3.00 mm long, 1.70-2.50 mm wide, with 5-6 rounded plicae, upper parts lobate, margins toothed-ciliate, calyptrae small, 0.6-0.7 times the perianth length; androecia in curved spikes, small, 2-4 pairs of bracts, bracts oval with retuse apices and 1-2 unicellular teeth, margins with a few slime papillae, antheridium stalk cells two ranked.

Comments
Stephani (1922) published *Chiloscyphus confertus* and *C. rotundifolius* with nearly the same description. Checking the type specimens at G, it was not possible to find clear distinctive features and the differences between the corresponding drawings by Stephani (icones nr 001925 and 001978) are parts of the variability in leaf and underleaf marginal ornamentations. Fresh specimens also show variations in leaf apices, leaf and underleaf ornamentations in the same plants so that they could be equally assigned to both species. As a result, they are considered as synonyms. As both names were published at the same date and as the name *Chiloscyphus rotundifolius* was illegitimate (Turland *et al*. 2018: art 11.4), *H. confertus* is the correct name.

This species can be separated from other New Caledonian species with orbicular leaves, such as *Heteroscyphus aselliformis* and *H. kanakensis*, by the homomallous shoots. In addition, *H. aselliformis* is readily separated from *H. confertus* by asymmetrical leaves and leaf apices with two long filiform lobes, and *H. kanakensis* by stronger texture (not fragile), smaller plant size with shoots up to 3 mm wide and leaves to 1.6 mm long, and by the entire or crenulate leaf margins and rounded apices. It also shares many features with *Heteroscyphus menziesii* (Mitt.) J.J.Engel, from New Zealand, but the latter is a smaller species, the leaves have a conspicuous lip like connation at back, leaf apices are 2-toothed with sublinear short teeth instead of clearly bifid, and the underleaf lobes are thinner and forward directed. A specimen of *H. confertus* collected in New Caledonia by Le Rat and kept in PC (PC0167665) is a doubtful type, contrary to the assumption of Thouvenot *et al*. (2018), since the locality differs from that of the type in G. Moreover, the date of collecting is lacking.

Heteroscyphus cornutistipulus
(Steph.) Thouvenot, comb. nov.
(Fig. 10)

Chiloscyphus cornutistipulus Steph., *Species Hepaticarum* 6: 303 (Stephani 1922). — Type: **New Caledonia**. *Franc s.n.* (lecto-, here designated, G["Nlle Calédonie, Mts. Koghis", 1.XI.1909, *Franc 166*, G00069490]!).

Further specimen examined. — **New Caledonia**. South Province, Sarraméa, Dogny, 855 m, on dead wood in wet forest, 26.IX.2016, *Thouvenot NC3283* (PC[PC0779841]).

Distribution in New Caledonia. — Only known from scattered localities in South Province, on dead wood in wet forest at medium elevation.

Total range. — Endemic.

Description
Dioecious.

Habit
Plants medium sized, branching lateral-intercalary; wet shoots 3.50-4.00 mm wide, somewhat complanate, with leaves alternate, horizontally spreading, slightly convex, antical margins free, separated by 2 cortical cell files, shortly decurrent on the stem.

Leaves
1.60-2.20 mm long, 1.20-2.00 mm wide, oval to oblong, slightly longer than wide, apices entire to slightly retuse, widely rounded, margins entire, hardly crenulate.

Cells
Median leaf cells rounded-hexagonal 40-80 µm wide, with thin walls and small to medium acute trigones up to 9 µm wide.

Underleaves
Narrowly to conspicuously connate on single or both sides to the closest leaves, connation 1-6 cells wide, underleaves 3-5 times as wide as the stem, bifid, lobes narrowly triangular, set wide apart, sinus lunate, disc transversely elongate, 1-2 short teeth on both lateral margins.

Gametangia
Androecia and gynoecia on short leafless lateral branches; androecia in spikes made of 6 pairs of bracts very smaller than the normal leaves and inflated; female bracts not seen, female bracteoles 1/3-1/2 bifid, with 1 tooth on both sides; perianths cyathiform, 2.20 mm long, 1.20 mm wide, 3-plicate, plicae rounded, mouth wide, lobate-laciniate, margins roughly toothed; calyptrae 2/3 shorter than the perianths.

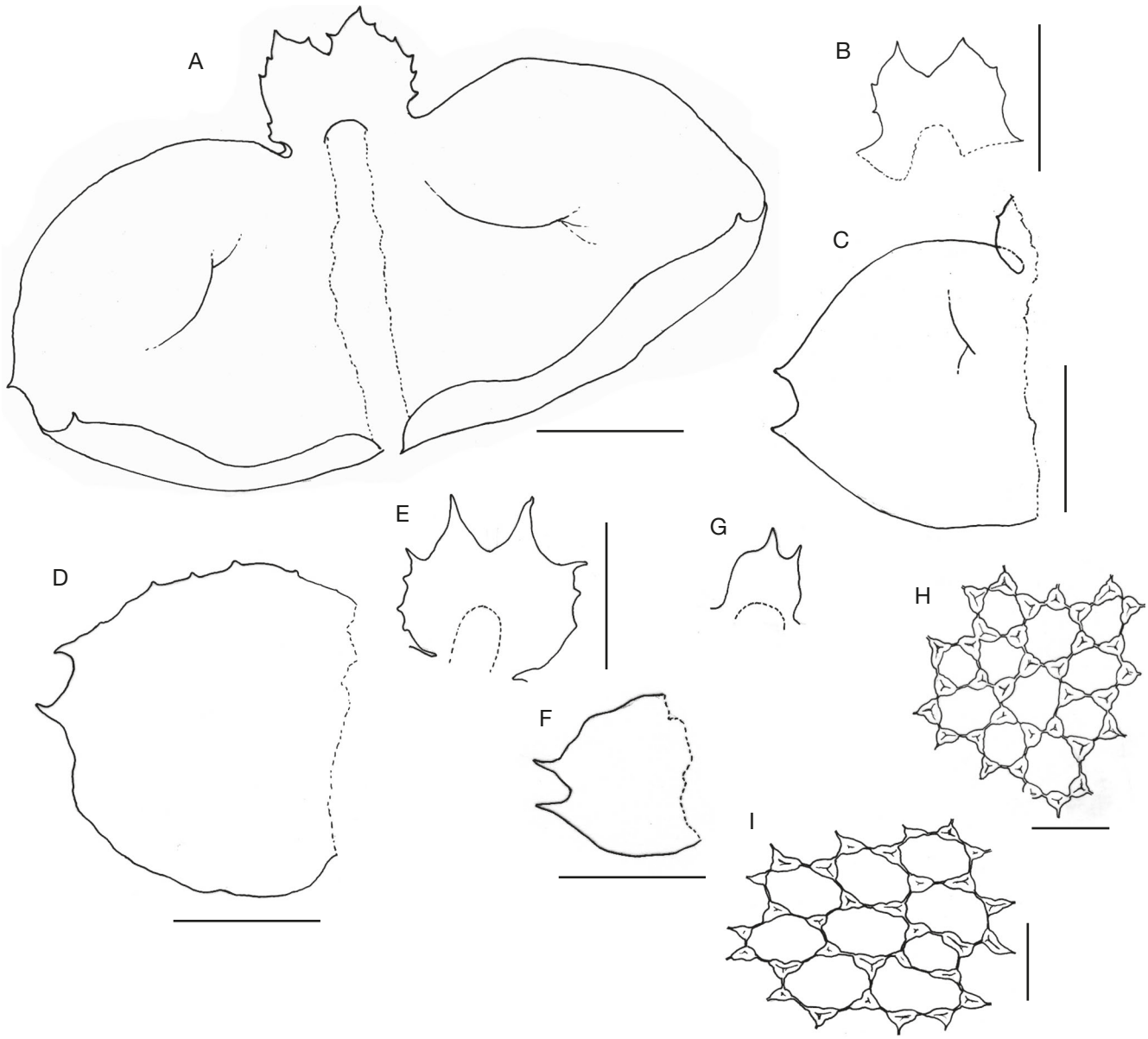

Fig. 9. — *Heteroscyphus confertus* (Steph.) Thouvenot: **A**, shoot portion, ventral view; **B**, **E**, **G**, underleaves; **C**, **D**, **F**, leaves from different shoot segments. **A**, **H**, **I**, drawn from a syntype of *Chiloscyphus confertus* (PC0101951); **B**, **C**, from *Thouvenot NC2477*; **D**-**G**, from the lectotype of *Chiloscyphus rotundiphyllus* Steph. (G00069432). Scale bars: A-G, 1 mm; H, I, 50 µm.

Comments

The type specimen has no gametangium, although the packet is annotated "*c. per.*". A recently collected specimen has androecia and gynoecia (*Thouvenot NC3283*) and indicates that the species belongs in *Heteroscyphus*. The fertile plant has smaller trigones but is otherwise vegetatively identical to the type of *Chiloscyphus cornutistipulus*. Like in *H. caledonicus* (see under that species), some vegetative characters of *H. cornutistipulus* (Steph.) Thouvenot, comb. nov. are chiloscyphoid, such as the alternate leaves and the narrow connation of the underleaves.

Heteroscyphus cornutistipulus (Steph.) Thouvenot, comb. nov. is close to *Chiloscyphus trigonifolius* and *H. succulentus*, but *C. trigonifolius* is easily separated from *H. cornutistipulus* (Steph.) Thouvenot, comb. nov. by its smaller size with shoots 1.5-2 mm, strongly involute leaves when dry and the ovate-triangular leaf shape. Furthermore, the androecia are in spikes on normal-leaved shoots, male bracts being quite similar to the normal leaves. *Heteroscyphus succulentus* differs by its larger size, subopposite leaves, underleaves margins long laciniate instead of short toothed, bulging leaf cells without trigones, and crenulate leaf margins.

Heteroscyphus deplanchei (Steph.) Schiffn. (Fig. 11)

Oesterreichische Botanische Zeitschrift 60: 172 (Schiffner 1910). — *Chiloscyphus deplanchei* Steph., *Species Hepaticarum* 3: 203

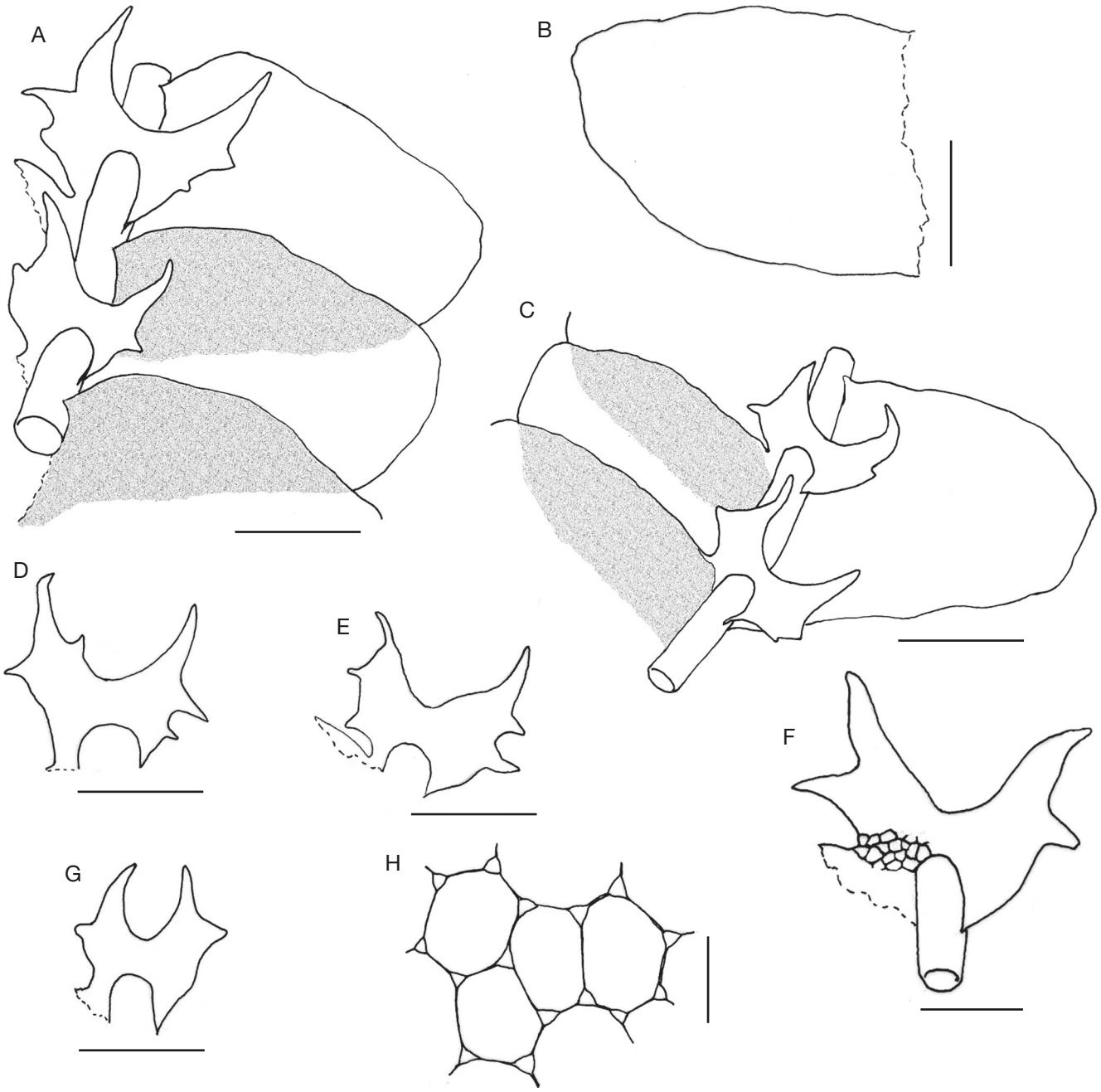

Fig. 10. — *Heteroscyphus cornutistipulus* (Steph.) Thouvenot, comb. nov.: **A**, **C**, shoot portions, ventral view; **B**, leaf; **D**-**G**, underleaves; **H**, mid-leaf cells. All drawn from the lectotype of *Chiloscyphus cornutistipulus* Steph. (G00069490). Scale bars: A-E, G, 500 µm; F, 500 µm; H, 50 µm.

(Stephani 1907). — Type: **New Caledonia**. *Deplanche s.n.* (holo-, G[G00069487]!).

Lophocolea heteromorphis Steph., *Species Hepaticarum* 6: 275 (Stephani 1922). — *Chiloscyphus heteromorphus* (Steph.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 416 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. "*Lerat*" *s.n.* (holo-, G["*Lophocolea heteroformis* (sic) n.sp., Dent de St Vincent, juillet 1909", *Le Rat s.n.*, G00112505]!) **syn. nov.**

Further specimens examined. — **New Caledonia**.North Province, bank of the upper Diahot, on siliceous sand, 430 m, 31.VIII.1951, *Hürlimann 2901* (G); Hienghène, Pwé Hwa Wéc river, on rocks in creek bank, 630 m, 22.IX.2019, *Thouvenot NC2773* (PC[PC0779850]); South Province, Dumbéa, Pic des Sources, s.d., *Le Rat 265a* (G); Mt. Mou, VII.1904, *Le Rat s.n.* (G); Pourina valley affluent, 150 m, on dead branch in mesophilous forest, 4.VI.1951, *Hürlimann 2655* (GOET); Yaté, Wé Toa, on stump bark in rain forest, 500 m, 8.IX.2019, *Thouvenot NC2852* (PC[PC0779849]); Plaine des Lacs, on rocks in lowland wet forest, 260 m, 6.X.2016, *Thouvenot NC2441*; Pic du Grand Kaori, on rocks covered with humus in lowland wet forest, 480 m, 4.X.2016, *Thouvenot NC2433*; Lac Chakéké, on damp soil in creek bank, 425 m, 4.X.2019, *Thouvenot NC2729*; "Rivière Bleue, forêt vallicole, épixyle", 160 m, 15.V.1970, *Schmid 148* as "*Chiloscyphus physanthus*" (PC[PC0146342]); Mont Dore, Mouirange, on dead wood in rain forest, 550 m, 16.IX.2019, *Thouvenot NC2818*; Rivière Blanche, Rivière Bleue Natural Park, sentier des Cochons, 556 m, 17.IX.2019, *Thouvenot NC2859*; *MacKee 30813* as "*Chiloscyphus caledonicus*" (PC[PC0737581]).

Fig. 11. — *Heteroscyphus deplanchei* (Steph.) Schiffn.: **A**, shoot portion, ventral view; **B**, leaf cells; **C**, **K**, leaf apices diversity; **D**, leaf; **E**, shoot portion, dorsal view; **F**, female bract; **G**, androecium, dorsal view; **H**, pair of male bracts and bracteole, dorsal view; **I**, leaf and underleaf; **J**, perianth open with calyptra (**ca**). **A**, **B**, drawn from the holotype of *Chiloscyphus deplanchei* Steph. (G00069487); **C**-**F**, **J**, from *Thouvenot NC2852*; **G**, **H**, from *Thouvenot NC2773*; **I**, **K**, from the type of *Lophocolea heteromorphis* Steph. (G00112505). Scale bars: A, C-F, I-K, 1 mm; B, 50 µm; G, 400 µm; H, 200 µm.

Distribution in New Caledonia. — Fairly frequent in the ultramafic massif of South Province, rare in siliceous massifs of North Province, at low to medium elevation (collected from 150 to 1000 m) on dead wood or tree stumps in rain forest.

Total range. — Endemic.

Description

Dioecious.

Habit
Large plants, shoots 3.00-5.00 mm wide, usually single, lateral-intercalary branching rare; leaves firms, obliquely assurgent dorsally, canaliculate-convex, spreading at right angle to the stem, subopposite, reaching the dorsal mid-line of the stem and usually confluent.

Stem
300 µm wide, with 60-100 homogeneous thin-walled cells on transverse section.

Leaves
Mostly ovate-lingulate, wider at bases, 1.80-2.70 mm long, 1.20-2.00 mm wide at base, margins entire as well as the apices that are widely rounded to obliquely truncate to retuse with rounded angles, in some secondary shoots a few or many leaves may be emarginate to shortly bifid with 1-2 acute short lobes.

Cells
Leaf cells 40-60 µm wide, thin walled with strong nodulose trigones, not confluent.

Underleaves
Reniform, 8-10 times wider than the stem, 0.80-1.50 mm long, 1.80-2.50 mm wide, connate on both sides to the ventral bases of the nearest leaves, apices bifid to quadrifid, lobes narrowly acuminate from triangular bases, sinus widely lunate, margins long toothed-laciniate all around, teeth narrowly acuminate, at times furcate.

Gametangia
Androecia and gynoecia at the apices of very short lateral-intercalary leafless branches; androecia small, up to 1 mm long, in spikes made of four pairs of bracts, bracts inflate concave with truncate apices, 3-toothed, 400 µm long, 300 µm wide in situ, bracteoles shortly bifid, 250 µm as wide as long; gynoecia with two series of female bracts and bracteoles, more or less similar, obovate in outline, apices lobate, more or less deeply incised, margins toothed to laciniate, bracts 3.00 mm long, 2.50 mm wide, bracteoles smaller, 2.25 mm long, 2.00 mm wide, perianths cyathiform, without plicae or shallowly plicate in upper part, 3.50 mm long, 2.80 mm wide, mouth deeply laciniate, calyptrae very shorter than the perianths.

Comments
Stephani (1907) described *Chiloscyphus deplanchei* with leaf apices "*truncato-rotundo vel emarginatulo*". The scarce shoots of the holotype at G fit this description, but examination of additional material shows that this character is rather variable. The largest forms have leaves with essentially entire, rounded apices, and strongly laciniate underleaves with the apical lobes hardly distinguishable from the lateral processes. But mostly, the plants have long shoot portions with acute or shortly bifid leaf apices and other portions, mainly terminal, with entire, rounded leaves. In rare cases almost all leaves are acute or bifid, with a few entire, rounded leaves being restricted to the shoot apices. Later, Stephani (1922) describes *Lophocolea heteromorphis* with leaves "*inaequaliter bifida vel solum apiculata*". The type specimen seen at G shows mostly such leaves but leaves with entire rounded apices occur on some shoots. Underleaves may be smaller, less wide and less divided, but here too there are underleaves like in *Chiloscyphus deplanchei*. In fact, all other features are very similar: habit, shoot width, stem anatomy, cell size and shape, gametangia and most of the underleaf characters. As the leaf apex shape is the only diverging character, varying along a continuum between two extreme patterns represented by *Chiloscyphus deplanchei* and *Lophocolea heteromorphis*, it can be asserted that they represent variants of the same species.

Heteroscyphus deplanchei superficially looks like *H. succulentus* (Gottsche) Schiffn. (see below), which has a similar leaf shape, but the latter can be distinguished by the fleshy, translucent, dorsally free leaves with a more lax areolation, and underleaves long toothed rather than laciniate and the cells without trigones. Furthermore, the male bracts of *H. succulentus* are rounded truncate and the perianth is 3-plicate with a toothed mouth (Piippo 1985). *Heteroscyphus deplanchei* might also be confused with *H. supinopsis*. For the distinctive characters, see below the relevant paragraph.

Although Stephani described the gynoecia, the type material in G is sterile. The above account of the gametangia, which contains the first description of the androecia, is based on material collected by the author in 2019.

Heteroscyphus diestianus (Sande Lac.) Piippo
(Fig. 12)

Acta Botanica Fennica 131: 165 (Piippo 1985). — *Chiloscyphus diestianus* Sande Lac. in Miquel, *Annales Musei Botanici Lugduno-Batavi* 1: 296 (Sande Lacoste 1864). — Type: **Indonesia**. Banca, in m. Maras, 2000'; *van Diest s.n.*, not seen.

Specimen examined. — **New Caledonia**. South Province, Mont Humboldt, *c.* 1600 m, 21.VIII.2003, *Müller NC803* (DR and author's private herbarium).

Distribution in New Caledonia. — Only found in South Province at the highest elevation.

Total range. — Also occurring in Borneo, Indonesia, Malaysia and Papua New Guinea (Piippo 1993).

Description
Based on the New Caledonian specimen. Further descriptions and illustrations in Piippo (1993).

Habit
Plants fleshy, rather swollen, medium sized, shoots 3.00 mm wide, usually single, lateral-intercalary branching rare; leaves subopposite, thin, imbricate, dorsally obliquely assurgent at angle of ± 45°, laterally spreading at right angle to the stem, the dorsal segments convex, the ventral strongly concave, dorsal margins not reaching the mid-line of the stem, not fused to the opposite leaf margin, the dorsal bases not decurrent.

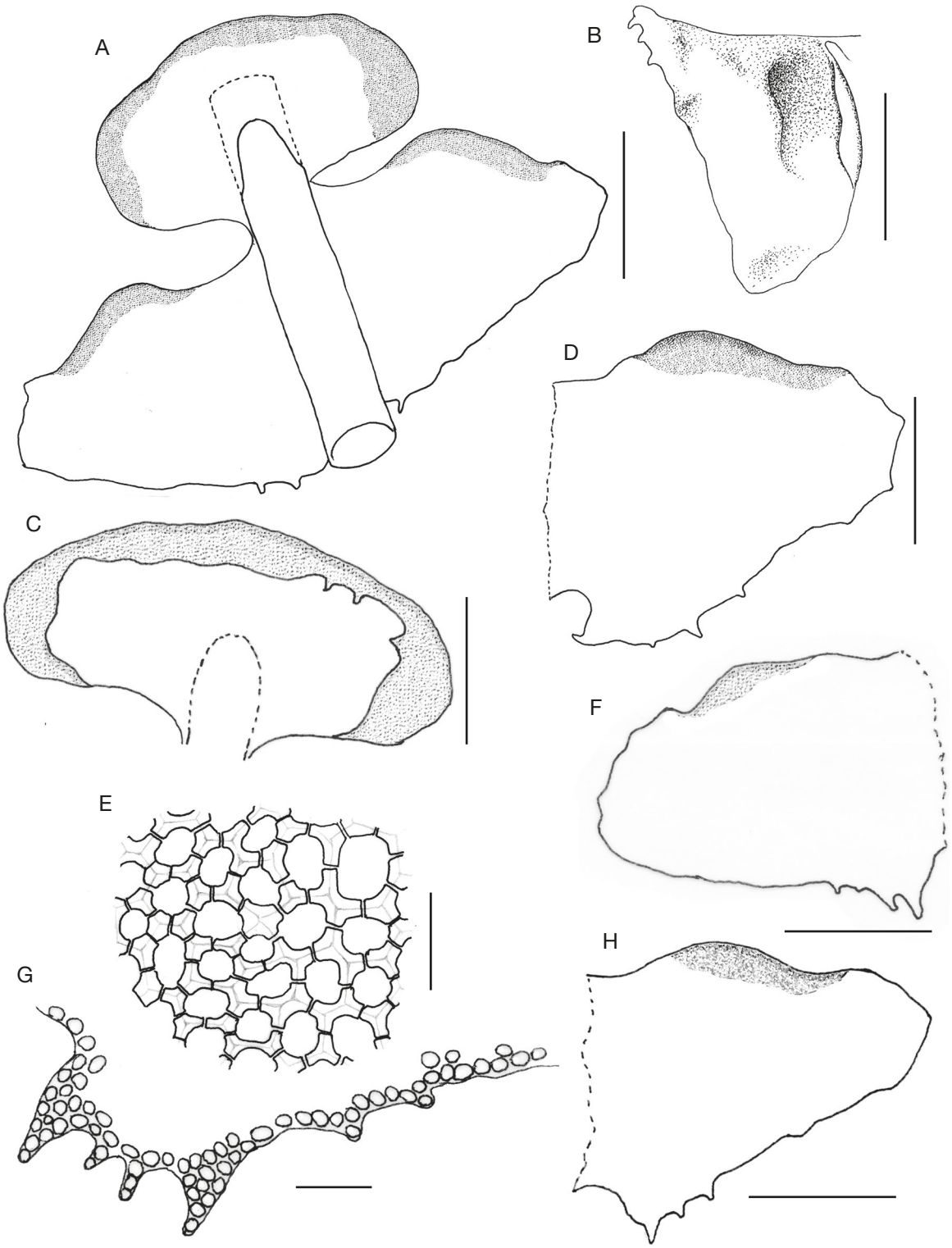

FIG. 12. — *Heteroscyphus diestianus* (Sande Lac.) Piippo: **A**, shoot portion, ventral view; **B**, dorsal face of leaf, with reflexed ventral margin; **C**, underleaf, adaxial face (dorsal view); **D**, **F**, **H**, leaves, ventral view; **E**, cells; **G**, appendices in basal segment of dorsal leaf margin. All drawn from *Müller NC803*. Scale bars: A-D, F, H, 500 µm; E, 50 µm; G, 100 µm.

Leaves

Ovate, 1.20-1.40 mm long, 0.90-1.20 mm wide at bases, 0.45-0.60 mm wide below apices, dorsal bases expanded, usually toothed, dorsal margins nearly right above the bases, entire or with a few teeth near base, ventral margins entire, arched and recurved in part making a conspicuous concavity on dorsal surface, apices rounded, often sinuous to angulate, apical margin entire; teeth small to conspicuous, from linear,

1-3 cells long, to triangular, 2-3 cells wide at base, 4-5 cells long, the teeth cells rounded.

Cells
Leaf cells rounded to oval, 33-60 µm long, 25-37 µm wide, very thick-walled with one pit on each side, trigones fused to the walls, marginal cells smaller, cells often bulging.

Underleaves
Inserted in a deep sinus, 5-9 times wider than the stems, widely reniform, 0.55-0.80 mm long, 1.10-1.80 mm wide, very narrowly connate on both sides to the nearest leaves, free margins abaxially recurved giving a swollen appearance to the underleaves, apices essentially entire but somewhat undulate, with a few remote teeth or none, teeth like on the leaves but smaller.

Gametangia
Not seen.

Comments
Heteroscyphus diestianus is easily recognized by the large swollen underleaves, widely reniform, as wide as the leaves, the teeth restricted to the base of leaf dorsal margins and the strongly thickened cell walls. Its presence in New Caledonia is documented by a single specimen collected in 2003, in the vicinity of one of the highest summits of the country.

Heteroscyphus etesseanus
(Steph.) Thouvenot, comb. nov.
(Fig. 13)

Chiloscyphus etesseanus Steph., *Species Hepaticarum* 3: 217 (Stephani 1906). — Type: **New Caledonia**. *Etesse s.n.* (lecto-, here designated, G["ex Herb. E. G. Paris, Nova Caledonia, in ditione Noumeana, 1904", *Etesse 12*, G00061024]!).

Further specimen examined. — **New Caledonia**. North Province, Poindimié, Amoa valley, Tipwadabwé, on rocks in wet mesophilous forest, 163 m, 13.X.2019, *Thouvenot NC2752* (PC[PC0779851]).

Distribution in New Caledonia. — Hitherto only known from North Province, rarely collected on rocks at low altitude (160-250 m) in wet forest with tall trees. The mention "Nouméa" on the label of the type specimen is not reliable since Etesse's specimens were not precisely located and were commonly labelled as having originated from the capital of New Caledonia. In fact, his bryophyte gatherings were made along the Tipindjé river in North Province (Morat 2010), about 30 km from the locality of the recent collection.

Total range. — Endemic to North Province, on the north-eastern versant of the central range.

Description
Dioecious.

Habit
Plants small, wet shoots 1.60 mm wide, stems rigid, leaves horizontally spreading, slightly convex, contiguous, alternate.

Leaves
Rectangular, 0.60 mm long, 0.50 mm wide, apices truncate, concave, both distal angles triangular acute, usually with a short linear tooth three cells long, some leaves pseudo-trilobate, sometimes with a further tooth, apical or subapical on the ventral margin, margins otherwise entire.

Cells
Leaf cells hexagonal, 24-40 µm wide, firm walled without trigone.

Underleaves
Small, hardly wider than the stem, obconical, free on both sides, deeply bifid, the discs sometimes strongly reduced, lobes divergent, setaceous, sinus variable, V-like or lunate or nearly flat, both lateral margins with a single tooth at most, small to linear.

Gametangia
On short leafless, lateral-intercalary branches; gynoecia with laciniate bracts, bifid bracteoles with a single small tooth on both lateral margins; perianths about 1.5 mm hight, campanulate, deeply trilobate, lobes laciniate-toothed, calyptrae very shorter than the perianths; androecia in spikes of up to six pairs of bracts.

Comments
Some vegetative features of the species such as the alternate leaves, the leaf cells without trigones and the small, free underleaves are suggestive of *Chiloscyphus*. But the spicate androecia on abbreviated ventral branches are typical of the genus *Heteroscyphus*. Recent studies on *Heteroscyphus* in Australasia treat species with similar vegetative features and highlight the importance of androecia and perianth types to discriminating these two genera (e.g. Engel & He 2010; Engel 2013, 2015). These studies warrant the transfer of *Chiloscyphus etesseanus* to *Heteroscyphus*.

Heteroscyphus etesseanus (Steph.) Thouvenot, comb. nov. is superficially similar to *H. argutus*, but the latter species can be easily distinguished from *H. etesseanus* (Steph.) Thouvenot, comb. nov. by its larger size and the rounded instead of retuse leaf apices with at least four teeth.

Heteroscyphus giganteus (Steph.) Hürl.
(Fig. 14)

Bauhinia 12: 114 (Hürlimann 1998). — *Chiloscyphus giganteus* Steph., *Species Hepaticarum* 6: 307 (Stephani 1922). — Type: **New Caledonia**. *Franc s.n.* (lecto-, here designated, G["Mt. Mou, 1200 m", 1.XI.1908, *Franc s.n.*, G00069481]!; isolecto-, G[G00283069]!).

Chiloscyphus giganteus fo. *minor* Herzog, *Arkiv för Botanik*, n.s. 3 (3): 46 (Herzog 1953). — Type: **New Caledonia**. 8.VII.1949, *Selling B126 p.p.* (holo-, S).

Further specimens examined. — **New Caledonia**. North Province, Hienghène, Ouaième rocks, on trunks in mountain shrubland, 854 m, 22.IX.2019, *Thouvenot NC2798*; South Province, Mont Dore, Prony, Baie du Carénage, 16.XI.1950, *Guillaumin 8579a*

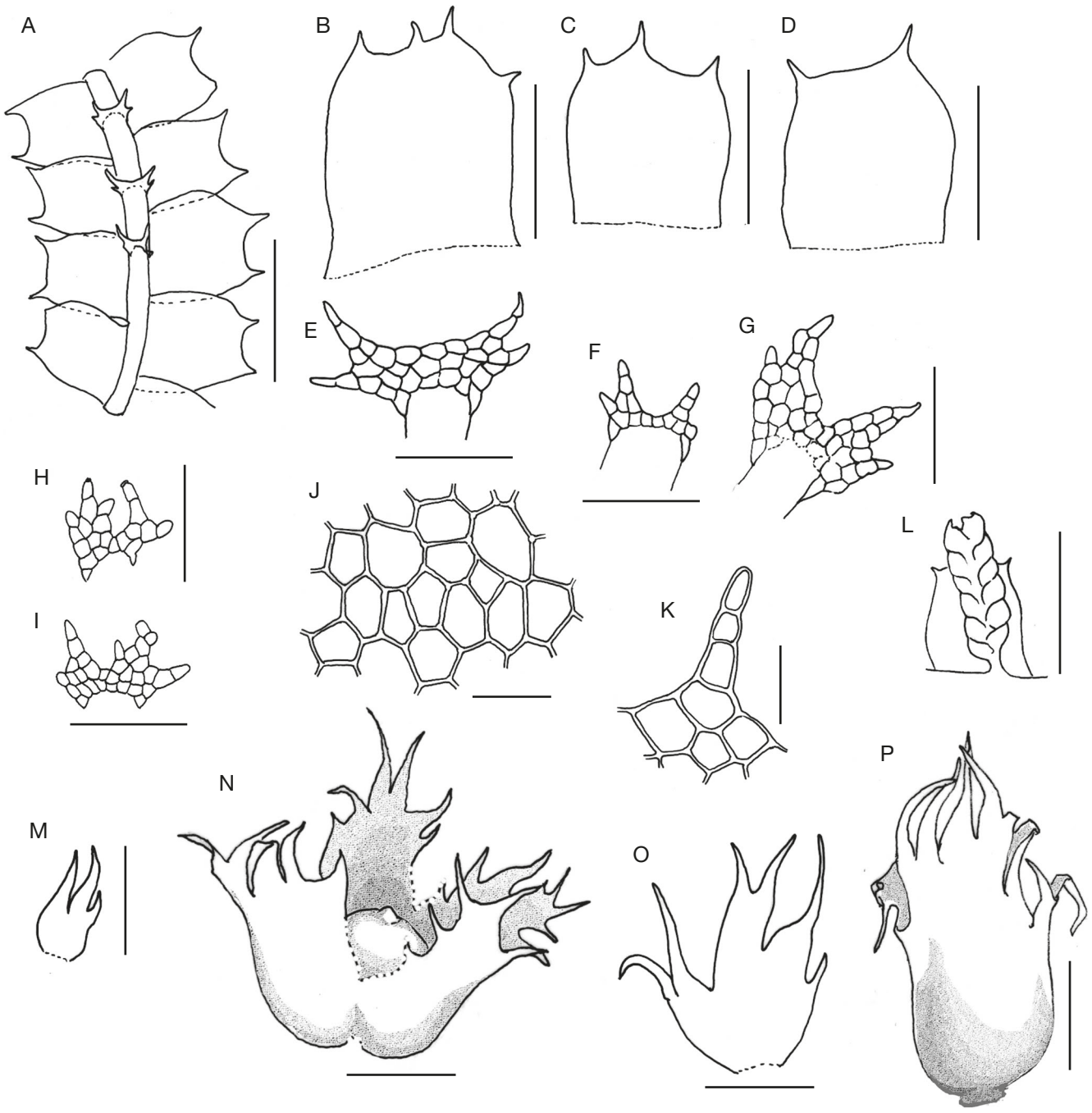

Fig. 13. — *Heteroscyphus etesseanus* (Steph.) Thouvenot, comb. nov.: **A**, shoot portion, ventral view; **B**-**D**, leaves; **E**-**I**, underleaves; **J**, median leaf cells; **K**, tooth at leaf apex; **L**, androecium; **M**, female bracteole; **N**, perianth tearing showing the inserted calyptra; **O**, female bract; **P**, perianth. **A**, **L**, **M**-**P**, drawn from the lectotype of *Chiloscyphus etesseanus* Steph. (G00061024); **B**-**D**, **K**, from *Thouvenot NC2752*; **E**-**J**, from *Thouvenot NC2753*. Scale bars: A, L, 1 mm; B-D, M-P, 500 µm; E-I, 200 µm; J, K, 50 µm.

(GOET); Yaté, Forêt du Mois de Mai, 235 m, 23.X.2012, *Thouvenot NC1008*; Yaté, Goro, 200-310 m, 31.III.2016, *Metoyer 122*; Yaté, Pic du Grand Kaori, on bark, 472 m, 4.X.2016, *Thouvenot 2435* (PC[PC0779852]); Bouloupari, Mt. Do, on bark, 960 m, 15.IX.2016, *Thouvenot NC2470*.

Distribution in New Caledonia. — Frequently found in South Province, rarer in North Province, at low to medium altitudes (collected from 0 to 1250 m), *Heteroscyphus giganteus* grows on barks in various vegetation types, from photo-xerophilous to cloud forests, primary or secondary mountain scrublands, gallery forests.

Total range. — Endemic.

Description

Dioecious.

Habit

Plants light green, large, fragile, 4.00 mm wide in fresh condition, 6.00-7.00 mm when flattened, simple or sparsely furcate, branching lateral-intercalary, leaves subopposite, dor-

sally assurgent, longitudinally undulate with the ventral half concave and the dorsal convex, thus the shoots are swollen.

Leaves
Large, rounded, more than 3.00 mm wide, margins entire, apices emarginate with short lunate sinus and two short lobes triangular to rounded.

Cells
Leaf cells 30-56 µm wide, thin walled, hexagonal with rounded lumina and large truncate trigones.

Underleaves
Reniform, 1.00-1.60 mm long, 1.00-2.00 mm wide, bilaterally connate to the nearest leaves, deeply bifid, the lobes lanceolate, simple or furcate, widely divergent, lateral margins usually with at last two long narrow teeth or laciniae.

Gametangia
At the end of very short leafless lateral shoots; gynoecia 2.75 mm long, involucres strongly inflate, bracts 2.00 mm long, 1.75 mm wide, ovate in outline, deeply and asymmetrically bifid, margins coarsely toothed, teeth large and triangular, bracteoles 2.00 mm long, 1.50 mm wide symmetrically bifid, sinus half-length deep, lateral margins coarsely toothed, young perianths cyathiform, deeply multifid, lobes ovate-triangular sparsely and coarsely toothed. Androecia in curved spikes, made of about 5 pairs of bracts.

Comments
This species is easily separated from all other New Caledonian Lophocoleaceae by the combination of the following characters: 1) large shoots, 6-7 mm wide; 2) large leaves rounded concave and dorsally assurgent so that the shoots seem inflate; 3) margins entire; 4) apices emarginate with small lunate sinus; 5) leaf cells with large truncate trigones; and 6) underleaves bifid with lobes widely divergent, and 2-3 laciniae on each lateral margin. Fresh fertile specimen shows the dioecious condition and allows to describe the gynoecium. *Heteroscyphus giganteus* superficially looks like *H. aselliformis* and *H. confertus*; to distinguish characters see under these species. The size of *C. giganteus* fo. *minor* is like in *H. confertus*, but underleaves and trigones match those of *C. giganteus*. Consequently, it is not necessary to separate this form.

Heteroscyphus grandiflorus (Steph.) Hürl.
(Fig. 15)

Bauhinia 12: 114 (Hürlimann 1998). — *Chiloscyphus grandiflorus* Steph., *Species Hepaticarum* 6: 307 (Stephani 1922). — Type: **New Caledonia**. *Lerat s.n.* (lecto-, here designated, G["Original", *Lerat 265-03*, G00069506]!; syn-, G[Pic des Sources, "moitié", *Le Rat 259*, G00283070!, Mt. Mou, VII.1909, *Le Rat 133*, G00283071]!; isosyn-, REN[Mt. Mou, VII.1909, *Le Rat s.n.*, herb. E. G. Paris]!).

Chiloscyphus grandiflorus var. *latifolius* Herzog, *Arkiv för Botanik*, n.s. 3 (3): 49 (Herzog 1953). — Type: **New Caledonia**. N.branch of Yaté River, 400 m., 8.VII.1949, *Selling B12* (holo-, S) **syn. nov.**

Chiloscyphus quadricilius Steph., *Species Hepaticarum* 6: 312 (Stephani 1922). — Type: **New Caledonia**. "*Lerat*" *s.n.* (lecto-, here designated, G["Nova Caledonia", s.l., s.d., *Lerat 21*, G00283105]!) **syn. nov.**

Further specimens examined. — **New Caledonia**. North Province, Poindimié, Tango plateau, Napapwa, on the ground in rain forest, 467 m, 20.IX.2019, *Thouvenot NC2895*; South Province, Bouloupari, Mt. Do, on peridotite rocks in cloud forest, 995 m, 25.X.2012, *Thouvenot NC752*; Paita, Dzumac massif, on rocks in mesophilous forest, 915 m, 18.IX.2008, *Thouvenot NC331*; Yaté, Nooti, on laterite rock, in photo-xerophyte forest, 443 m, 5.X.2019, *Thouvenot NC2750*; Yaté road, col des deux Tétons, 24.VII. 2014, *Métoyer NC1686* (NOU); *MET027* (NOU); Yaté road, col des deux Tétons, 3.XII.2014, *Métoyer NC1687* (NOU); *NC1688* (NOU); *MET055* (NOU); *MET056* (NOU).

Distribution in New Caledonia. — One of the most frequent species of Lophocoleaceae in both provinces of Grande Terre, *Heteroscyphus grandiflorus* grows in usually wet conditions on the ground where it occupies a range of substrates, including bare soil, humus, plant debris, dead wood, rock, etc. at low to medium elevations (collected from sea level to 1000 m).

Total range. — Endemic.

Description
Dioecious.

Habit
Variable (see comments); plants medium to large, light green to red-brown or olive-brown, wet shoots 2.00-4.00(-5.00) mm wide, leaves subopposite, densely imbricate, dorsally free, when dry dorsally concave to canaliculate, patent at 60-90° angle.

Leaves
The most typical leaves are 1.00-2.00 mm long, 0.80-2.00 mm wide at base, widely oval-ovate, apices rounded to widely triangular, usually with 3 long cilia made of 3-6 uniseriate elongate cells narrower from base to tip, ventral margins with 0-3(-4) cilia identical to the apical ones.

Cells
Leaf cells 37-65 µm long, 32-42 µm wide, trigones medium to large, rounded to truncate.

Underleaves
Connate with the ventral bases of both nearest leaves, the most typical underleaves transversely elongate, 2-4 times wider than the stem, discs 0.35-0.50 mm high, 0.60-1.00 mm wide, apices bifid-quadrifid, sinus lunate, lobes narrowly linear lanceolate, single or furcate, lateral margins with one to several long narrow teeth sometimes furcate, at most the entire margins appearing laciniate all around, minor forms with only four apical teeth or two apical and one small marginal on both sides.

Gametangia
On short lateral-intercalary branches lacking normal vegetative leaves, rarely with one pair of small vegetative leaves at base; gynoecia with bracts large, lobate-laciniate, bracteoles smaller, deeply bifid and laciniate; perianths cyathiform, 3.00 mm long, 2.00 mm wide, deeply lobate-laciniate at

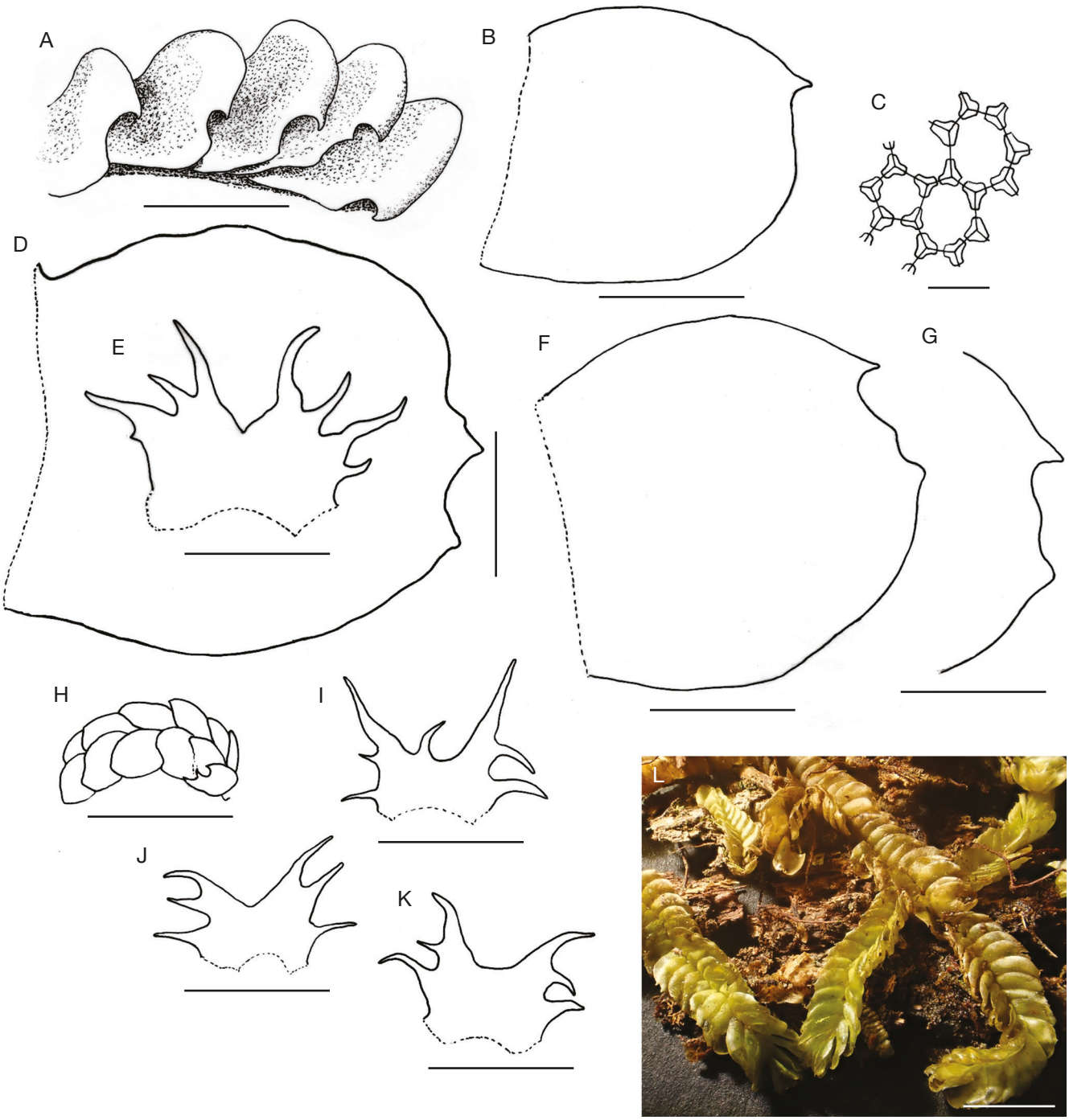

Fig. 14. — *Heteroscyphus giganteus* (Steph.) Hürl.: **A**, shoot portion, lateral view; **B**, **D**, **F**, **G**, leaves; **C**, leaf cells; **E**, **I**-**K**, underleaves; **H**, androecium, dorsal view; **I**, habit, dorsal view. **A**, **B**, **H**-**J**, drawn from *Coulerie 196*; **C**-**E**, from the lectotype of *Chiloscyphus giganteus* Steph. (G00069481); **F**, **G**, **K**, from *Thouvenot NC1008*; **L**, photo from *Thouvenot NC2823*. Scale bars: A, B, D-K, 1 mm; C, 50 µm; L, 5 mm.

mouth; androecia in short spikes, 0.40 mm long, with 2-5 pairs of bracts cochleariform-canaliculate, toothed-ciliate, bracteoles shortly bifid with a few unicellular teeth, antheridium stalk three ranked.

Comments

As underlined for many species of the genus, this frequent species has variable looks, mainly in leaf and underleaf ornamentations, even in the same plant, so that some specimens might be thought to belong to different species or distinct varieties. Usually, main shoots have the largest leaves, with many cilia around the margins and underleaves with two apical lobes often furcate and lateral margins lobate ciliate, whereas, on the secondary branches, leaf margins may be naked except the apical three cilia and underleaf cilia may be simple; minimal forms of underleaves have only two apical cilia and one

short cilia on both margins. But, in all observed specimens, the overall leaf shape and areolation are constant despite the size and ornamentation diversity, except the single sample from semi-aquatic habitat with oblong-oval leaves, usually biciliate leaf apices, olive brown colour (*Thouvenot NC2894*). Other characters varying case to case are colour, from light green to red brown or olive green, leaf cell trigones truncate to rounded, underleaf cell trigones which may be like the leaf ones to nearly absent. The well-developed populations include usually a large morphological variability. But we are often faced with quite homogeneous populations with a peculiar set of characteristics raising the question of the variety status. Notably, the variety *latifolius* defined by Herzog from differences in leaf size and number of leaf segments falls in synonymy to the typical forms since such characters can be observed in some shoots of the types kept at G: the observed variability in the leaf base width ranges from 0.70 to 1.00 mm and ornamentation from 3 to 8 fringe segments. This is a frequent character in Lophocoleaceae where secondary shoots and ultimate branches exhibit less process numbers and smaller sizes than primary stems. Old primary parts may be destroyed or broken and inconspicuous in some type specimen so that it could give rise to different diagnoses. At the other end, populations might be gathered into a variety "*minor*" when the following forms of morphological characters are evenly expressed: leaves without marginal processes except the three, rarely two, apical ones, underleaves of the less developed type, hardly twice as wide as the stem, 2-4-fid, lobes short linear, one short tooth on both margins (e.g. *Metoyer NC1687*, *Thouvenot NC2895*). Some were collected in peculiar habitats, namely very shaded, semi-aquatics or disturbed habitats. In the latter cases, the author hypothesise they could be mats of secondary shoots regenerating from broken stems, since it was sometimes possible to find a few old shoot segments with typical wide laciniate underleaves.

Among the two type specimens of *Chiloscyphus quadricilius* kept at G, only number G00283105 matches the Stephani's protologue and, therefore, is selected as the lectotype. The selection of the specimen G00069435 "sur les arbres, 1905, *Le Rat 302*" as a type specimen of *C. quadricilius fide* Bonner (1963: 767) is not supported by the observation of its morphological characters since leaf apices are widely rounded with four small apiculate teeth at leaf apices and small bifid underleaves with only one marginal tooth on both margins, so that it differs highly from the diagnose and drawing of Stephani and turns to be *Heteroscyphus argutus*. The type specimen of *Chiloscyphus quadricilius* here selected is sterile, but the vegetative and male characters are convenient for a transfer into the genus *Heteroscyphus*, underleaves widely connate on both side with the neighbouring leaves, leaves subopposite, leaf cells with large bulging trigones, androecia at the end of short leafless lateral branches. Furthermore, the features described by Stephani together with our observation on the type perfectly match *Heteroscyphus grandiflorus*, even if Stephani states the leaf cells are lacking trigones. In the type specimen, the cells show large nodulous trigones.

For the distinction from *Heteroscyphus caledonicus*, see under this species.

The antheridium characters have not been published by Stephani in his diagnosis of *Chiloscyphus grandiflorus*. It can newly be described from vouchers of recently collected male shoots (e.g. *Metoyer NC1688*, *Thouvenot NC2750*).

Heteroscyphus kanakensis Thouvenot & Engel (Fig. 16)

Nova Hedwigia 112: 166, 1-2 (Thouvenot & Engel 2021). — Type: **New Caledonia**. South Province, Yaté, Rivière Bleue Natural Park, La Tranchée, on tree bark in river side, ultramafic massif, 200 m, 19.X.2016, *Thouvenot NC2487* (holo-, PC[PC0779856]; iso-, F, hb. Thouvenot).

Further specimens examined. — **New Caledonia**. North Province, Pouébo, Diahoué, on wet rocks in the creek Wé Wayat, 400 m, 21.IX.2019, *Thouvenot NC2771*; *NC2829*; Touho, Pombei, Tiwaka valley, on rocks in high bush of *Melaleuca quinquenervia* (Cav.) S.T.Blake and *Gymnostomum* sp., volcano-sedimentary massif, 415 m, 12.X.2016, *Thouvenot NC2488* (para-, NOU, F); South Province, Lac Chakéké, on silt-laden deposits on barks along a temporary creek, in gallery forest, 411 m, 4.X.2019, *Thouvenot NC2727* (para-, PC[PC0779848], F, hb. Thouvenot).

Distribution in New Caledonia. — In a few localities at low altitudes in North and South Province, from 200 to 400 m. It grows on various substrates, barks, rocks, or silt laden deposits on trunks along creeks and was found in wet forest in sedimentary massif as well as gallery forest inside ultramafic scrubland.

Total range. — Endemic.

Description

Further description and illustrations in Thouvenot & Engel (2021).

Dioecious.

Habit

Plants rather rigid, fragile, pale green, pale brown in older sectors, somewhat water repellent, the shoots to 3 mm wide when flattened; stems narrow for plant size; leaves subopposite, typically obliquely dorsally assurgent (the basal sector of dorsal half angling upward at *c.* 45° from stem and never facing dorsal base of opposing leaf), the leaves densely imbricate, free dorsally; leaves somewhat longitudinally undulate in dorsal aspect, moderately convex in dorsal sector, moderately abaxially concave in ventral sector, the concave ventral sector overlayed by the convex dorsal half of the leaf immediately above.

Leaves

Subsymmetrical, up to 1.60 mm long, ovate and up to *c.* 1.3 times longer than wide; apex broadly rounded, entire; margins broadly and ± evenly arched, entire to faintly crenulate, the dorsal margin not decurrent.

Cells

Leaf cells with nodulose trigones separated by narrow, thin-walled places, the trigones sometimes confluent, the median

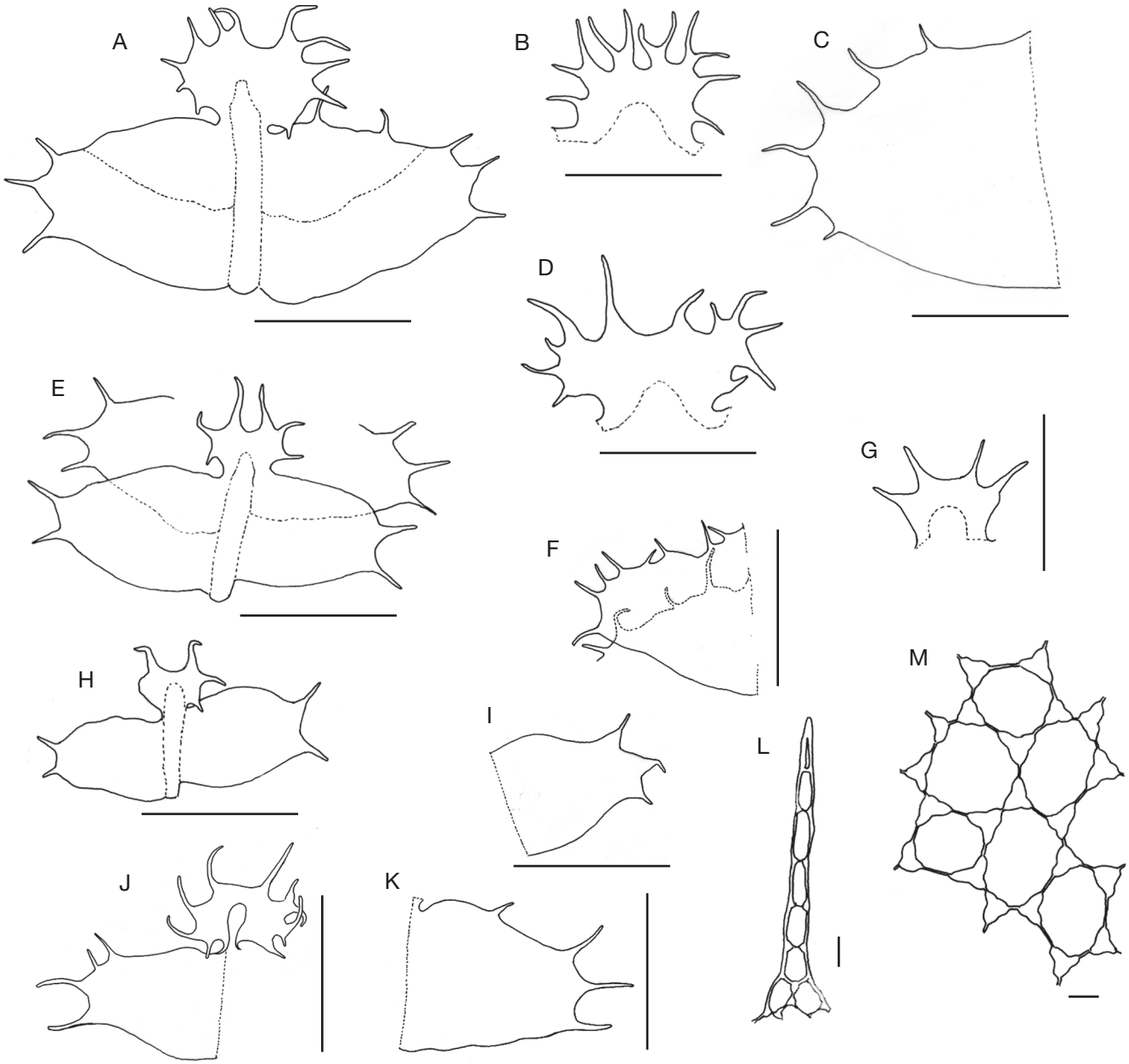

Fig. 15. — *Heteroscyphus grandiflorus* (Steph.) Hürl.: **A**, **E**, **H**, shoot portions from different parts of a single specimen; **B**, **D**, **G**, underleaves; **C**, **I**, **K**, leaves; **F**, ventral margins of two adjacent leaves showing their imbrication; **J**, leaf and underleaf; **L**, cilia from leaf apex; **M**, cells. **A**, **E**, **H**, drawn from the specimen *Thouvenot NC2745*; **B**, from *Thouvenot NC1486*; **C**, **D**, from *Thouvenot NC0752*; **F**, from the syntype of *Chiloscyphus grandiflorus* Steph. (G00283070); **G**, from *Thouvenot NC2895*; **I**, **J**, from the lectotype of *Chiloscyphus grandiflorus* (G00069506); **K**, from the syntype of *Chiloscyphus grandiflorus* (G00283071); **L**, **M**, from *Thouvenot NC2750*. Scale bars: A-K, 1 mm; L, M, 20 µm.

leaf cells uneven in size, 8-12 µm wide, 10-20 µm long, somewhat larger near the base; surface with a granular, scurffy appearance throughout.

Underleaves

4-5 times the stem width when flattened, symmetrically connate with the leaves on both sides, the connate portion 1-3 cells wide; underleaves imbricate, rotund to oblate, 0.50-0.80 mm long, 0.50-0.90 mm wide, usually 1.15 times wider than long; apex bifid to *c*. 0.35, the lobes ± parallel to weakly divergent, widely triangular, acute to stoutly acuminate, the sinus narrowly to widely rounded; lamina margins on both sides with a large tooth, the lamina margins otherwise entire or with 1-2(3), smaller, accessory teeth below.

Gametangia

Gynoecia on short lateral-intercalary, leafless branches; bracts deeply laciniate-lobed, the margins toothed toward the base; bracteole deeply bifid, the margins sparsely laciniate or toothed; perianths seen only in juvenile state, cyathiform, eplicate, the mouth lobulate, the lobules ending in a uniseriate row and with small teeth below; androecia small for plant size,

nearly hidden by leaves in dorsal aspect, fully exposed in ventral aspect, on abbreviated, determinate, lateral-intercalary branches, the androecia usually strongly arched, with 2-8 pairs of bracts, the bracts dorsally convex, strongly ventricose, half-spherical-helmet shaped, the dorsal pocket scarcely defined, the inflated upper faces of the bracts elevated above the level of the axis so that the spike is furrowed, the apices rounded to retuse, entire, the margins sparingly crenulate by projections of a single cell, with slime papillae few to numerous; bracteoles oblong, short bifid, the margins entire, rarely with a small tooth, with slime papillae few to numerous; antheridial stalk biseriate.

Comments

Heteroscyphus kanakensis superficially resembles *H. menziesii* (Mitt.) J.J.Engel described from New Zealand (Engel & Glenny 2019). They share many characters, among them: 1) a habit with light colour, medium size 2-3 mm wide when flattened, canaliculate shoots with subopposite leaves more or less assurgent; 2) rounded leaves densely imbricate, longitudinally undulate; 3) large trigones, cells bulging so that the leaf surfaces are bumpy; 4) bifid rounded underleaves, relatively large, connate on both sides with the nearest leaves. However, *Heteroscyphus kanakensis* is characterized by: 1) rather rigid shoots; 2) leaves obliquely assurgent, the dorsal insertion of both opposite leaves separated by one file of stem cells; 3) leaf margins and apices entire; 4) underleaves 4-5 times the stem, with two triangular acute teeth at apices and 1-3 smaller teeth on both lateral margins; and 5) androecia longer, in arched spikes of 2-8 pairs of bracts, conspicuous in ventral view. In contrast, typical forms of *H. menziesii* has soft and spongy shoots, leaves vertically assurgent, the dorsal base facing the dorsal base of the opposite leaf, dorsal leaf margins conspicuously connate by way of a laminar strip several cells wide, leaf apices 2-toothed, underleaves up to 3 times the stem width, margins with many dentiform or ciliiform teeth, androecia shorter with 1-2 pairs of bracts, hidden in both ventral and dorsal views (Engel & Glenny 2019).

For differences from the similar species *Heteroscyphus confertus*, see the comparison under that species.

Heteroscyphus parapilistipulus
(Thouvenot) Thouvenot, comb. nov.
(Fig. 17)

Chiloscyphus parapilistipulus Thouvenot, *Candollea* 75: 286, figs 1; 2 (Thouvenot & Price 2020). — Type: **New Caledonia**. South Province, La Foa, Dogny plateau, on wet rock in the creek Dogny, 918 m, *Thouvenot NC2451* (holo-, PC[PC0763751]!; iso-, author's private herbarium; para-, G[**New Caledonia**. "In jugo Dogny (1050 m)", VII.1909, *L. Le Rat s.n.*, G00051491!, G00051492!]; PC[PC0102406!, PC0150609!]; REN s.n.!).

Further specimens examined. — **New Caledonia**. North Province, St Paul, Pwâ Yogac river, on damp emerged rock in a creek bed, 438 m, 24.IX.2019, *Thouvenot NC2786*.

Distribution in New Caledonia. — Scattered in North and South Provinces, rarely collected.

Total range. — Endemic.

Description

Further description and illustrations in Thouvenot & Price (2020).

Dioecious.

Habit

Plants olive green, medium to large, shoots up to 4.5 mm wide; shoots often attenuated with leaves becoming progressively smaller toward shoot tops; branching latero-ventral; leaves spreading at a wide angle from the stem, slightly convex, alternate, not dorsally decurrent.

Leaves

Normal leaves 1.40-2.00 mm long, 0.90-1.50 mm wide, oval-oblong, transversally to obliquely truncate; apices usually concave with a single acute tooth at both distal angles, sometimes shallowly bifid with short lobes widely triangular, minutely apiculate, some leaves with rounded apices; lateral margins entire and smooth.

Cells

Leaf cells hexagonal, isodiametric to slightly elongate, 44-66 µm long, 25-52 µm wide, walls thin without trigone.

Underleaves

Small, not or hardly wider than the stem, overall oval, deeply bifid, disc wider than long, 3-4 cells high, insertion line semi-circular, lateral margins with a small obtuse tooth on both sides, sometimes linear, apices with sinus lunate, both lobes erect or crescent shaped, narrowly lanceolate acuminate to linear.

Gametangia

Gametangia of both sexes terminal on short leafless branches, lateral ventral; only juvenile gynoecia seen, bracts oval, 1.20-1.80 mm long, bifid, lobes ovate acute, a lanceolate segment usually developed on the upper part of a single lateral margin otherwise entire or with rare small teeth, bracteole deeply bifid, 1.50 mm long, lobes narrowly lanceolate, more or less convergent, margins entire, perianth 2.0-2.5 mm long, cyathiform, smooth, tri-lobate, lobes deeply laciniate; androecia in thin spikes of ± 6 pairs of ventricose bracts.

Comments

This plant resembles *Lophocolea convexula* (synonym: *L. pilistipula*, see below) but differs from the latter species by: 1) a larger size of shoots, leaves and cells; 2) the absence of trigones; 3) outer cell walls flat thus leaf margins smooth, not crenulate; 4) a dioecious condition; 5) gynoecia on very short branches without vegetative leaves; and 6) androecia in spikes of six pairs of bracts on ventral lateral abbreviated branches. Among the three syntypes of *L. pilistipula* Steph. at G, only the tiniest specimen, from Isle of Pines

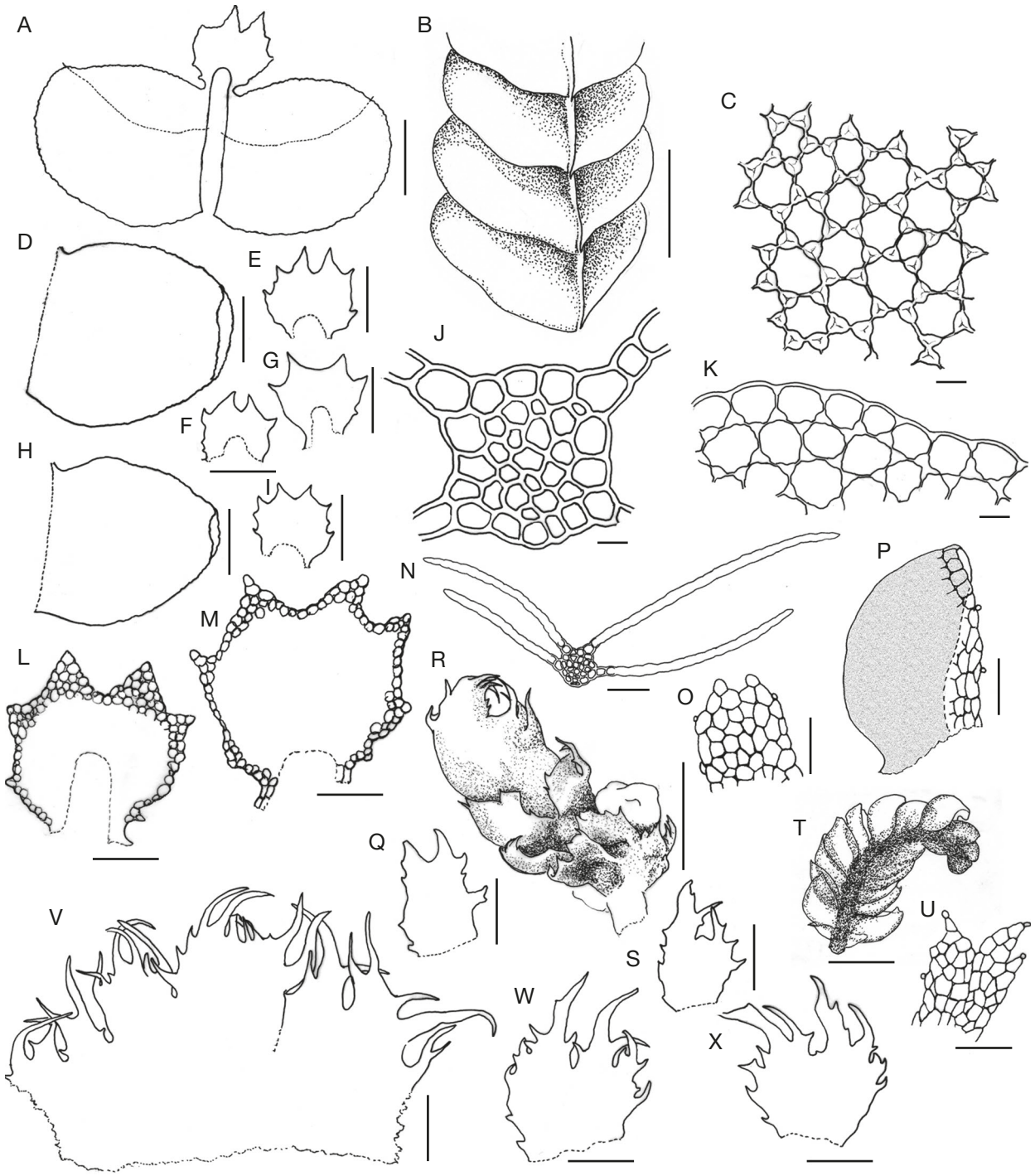

Fig. 16. — *Heteroscyphus kanakensis* Thouvenot & J.J.Engel: **A**, leaf pair and attached underleaf; **B**, portion of shoot (habit in dorsal view); **C**, median leaf cells; **D**, **H**, leaves; **E**-**G**, **I**, **L**, **M**, underleaves; **K**, marginal cells at leaf apex; **J**, stem transverse section; **O**, **U**, male bracteoles; **P**, male bract; **T**, androecium habit (ventral view); **N**, shoot transverse section showing dorsally assurgent antical part of leaves; **V**, top part of perianth (expanded); **Q**, **S**, female bracteoles; **R**, gynoecium habit (ventral view); **W**, **X**, female bracts. **A**, **F**, **L**, drawn from the paratype *Thouvenot NC2488*; **B**, **J**, **N**-**X**, from the holotype; **C**, **D**, **E**, **G**, **H**, **I**, **K**, **M**, from the paratype *Thouvenot NC2727*. Scale bars: A, D-I, Q, S, T, V-X, 500 µm; B, R, 1 mm; C, J, K, 20 µm; L, M, 200 µm; N-P, U, 100 µm.

(G00112487), matches the morphological features of this species. The other two, both from Dogny (G00051491 and G00051492) are sterile, have larger dimensions and belong to the new species *Heteroscyphus parapilistipulus* (Thouvenot) Thouvenot, comb. nov. with shoots being 3.00-4.50 mm wide, leaves 1.40-2.00 mm long and 0.90-1.50 mm wide near base, and cells 44-66 µm long and 33-50 µm wide. Furthermore, the leaf margins are smooth instead of crenulate. Duplicates of these collections are in PC. The initial placement of the species in *Chiloscyphus* was warranted by the discovery of a female plant (Thouvenot & Price 2020), but then, another specimen collected in North Province

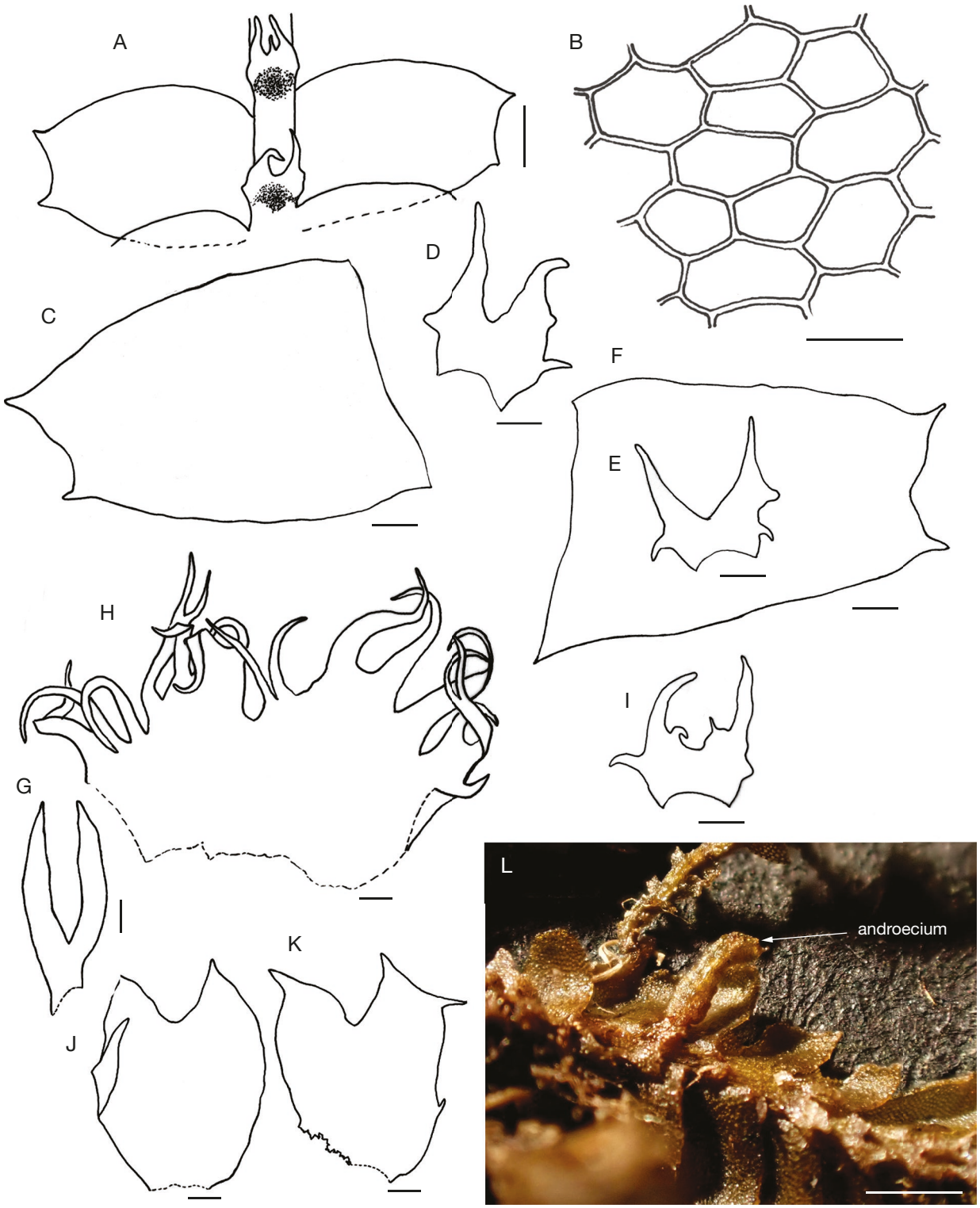

Fig. 17. — *Heteroscyphus parapilistipulus* (Thouvenot) Thouvenot, comb. nov.: **A**, shoot portion (ventral view); **B**, median leaf cells; **C**, **F**, leaves; **D**, **E**, **I**, underleaves; **G**, **H**, female bracts; **J**, female bracteole; **K**, top part of perianth (expanded). All drawn from the holotype. Scale bars: A, 400 µm; B, 50 µm; C-K, 200 µm; L, 1 mm.

(*Thouvenot NC2786*) has proven to be male, with a few old antheridia of heteroscyphoid type hidden amongst oldest parts of shoots. They consist of elongate spikes of six pairs of bracts at the end of short ventral lateral branches of limited growth, despite some vegetative leaves were seen at the end of a single spike. The combination of both sexual characters brings evidence for placing this species in the genus *Heteroscyphus*.

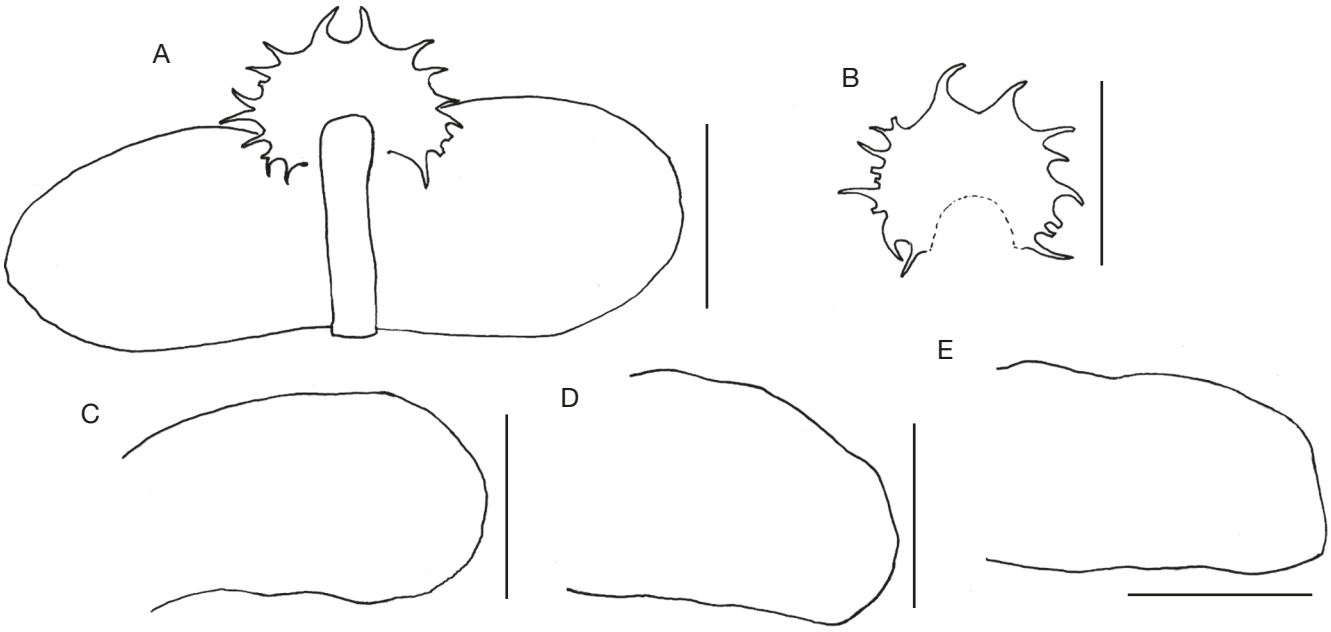

Fig. 18. — *Heteroscyphus splendens* (Lehm. & Lindenb.) Grolle: **A**, shoot portion, ventral view; **B**, underleaf; **C**-**E**, leaves. All drawn from the New Caledonian specimen *Hürlimann 2830* (GOET) of *Chiloscyphus decurrens* Nees. Scale bars: 1 mm.

Heteroscyphus splendens
(Lehm. & Lindenb.) Grolle
(Fig. 18)

Acta Botanica Fennica 125: 68 (Grolle & Piippo 1984). — *Jungermannia splendens* Lehm. & Lindenb., *Novarum et Minus Cognitarum Stirpium Pugillus* 4: 22 (Lehmann 1832). — Type: **India** ('India orientalis'). Wallich (lecto-, selected by Grolle [1984], S), not seen.

Chiloscyphus decurrens Nees, *Synopsis Hepaticarum*: 173 (Gottsche *et al.* 1845). — *Jungermannia decurrens* Reinw., Blume & Nees, *Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum Exhibentia Ephemerides sive Observationes Historias et Experimenta* 12: 206 (Reinwardt *et al.* 1824). — Type: **Java**. *Blume s.n.*, not seen.

Specimens examined. — **New Caledonia**. North Province, Poindimié, Amoa Valley, Twipadabwé, mixed with other liverworts on a rock in a river bank, volcano-sedimentary bedrocks, 211 m, 13.X.2019, *Thouvenot NC2730* (PC[PC0779854]); Hienghène, Pwé Hwa Wéc river, on rocks on creek bank, 630 m, 19.IX.2019, *Thouvenot NC2773*; Gomen road, east slope of Mt. Ignambi, 600 m, 16.VIII.1951, *Hürlimann 2830* as *Chiloscyphus decurrens* (GOET). **Java Occidental**. Priangan, Gede-Prangango, *c.* 2800 m, VIII.1930, *Verdoorn 2375* (PC[PC00035416]).

Distribution in New Caledonia. — In New Caledonia, this very distinctive species is only known from two localities in North Province.

Total range. — Paleotropical: from East Africa to Indonesia, Malaysia, Melanesia, South Pacific Islands (Hürlimann 1998).

Description

Based on the New Caledonian specimens. Further descriptions and illustrations in Piippo (1985).

Habit
Plants large, moist shoots *c.* 3.00 mm wide when flattened; leaves dorsally assurgent when dry, spreading when moist, subopposite, dorsal margins confluent.

Leaves
Oblong, *c.* 1.60 mm long, 1.40 mm wide at base, apices rounded-truncate, entire, ventral margins entire or with 1-2 small teeth near base, dorsal margin entire.

Cells
Median leaf cells 20-36 µm wide, lumina rounded to oval, trigones medium to large, acute.

Underleaves
Connate to the ventral margins of both nearest leaves, rounded to reniform, 0.80-1.00 mm long, 1.00-1.20 mm wide, 4.5 times the stem width, apices rounded, shortly bifid, lobes narrowly triangular, sinus narrow, margins spinose toothed to shortly ciliate all around.

Gametangia
Gynoecia at the end of short lateral-intercalary branches, perianths cyathiform; androecia not seen.

Comments

Heteroscyphus deplanchei and *H. supinopsis* superficially resemble *H. splendens* but can easily be separated from the latter by the ornamentation of the underleaf margins, which are strongly laciniate in *H. deplanchei* and more remotely toothed in *H. supinopsis* (see below).

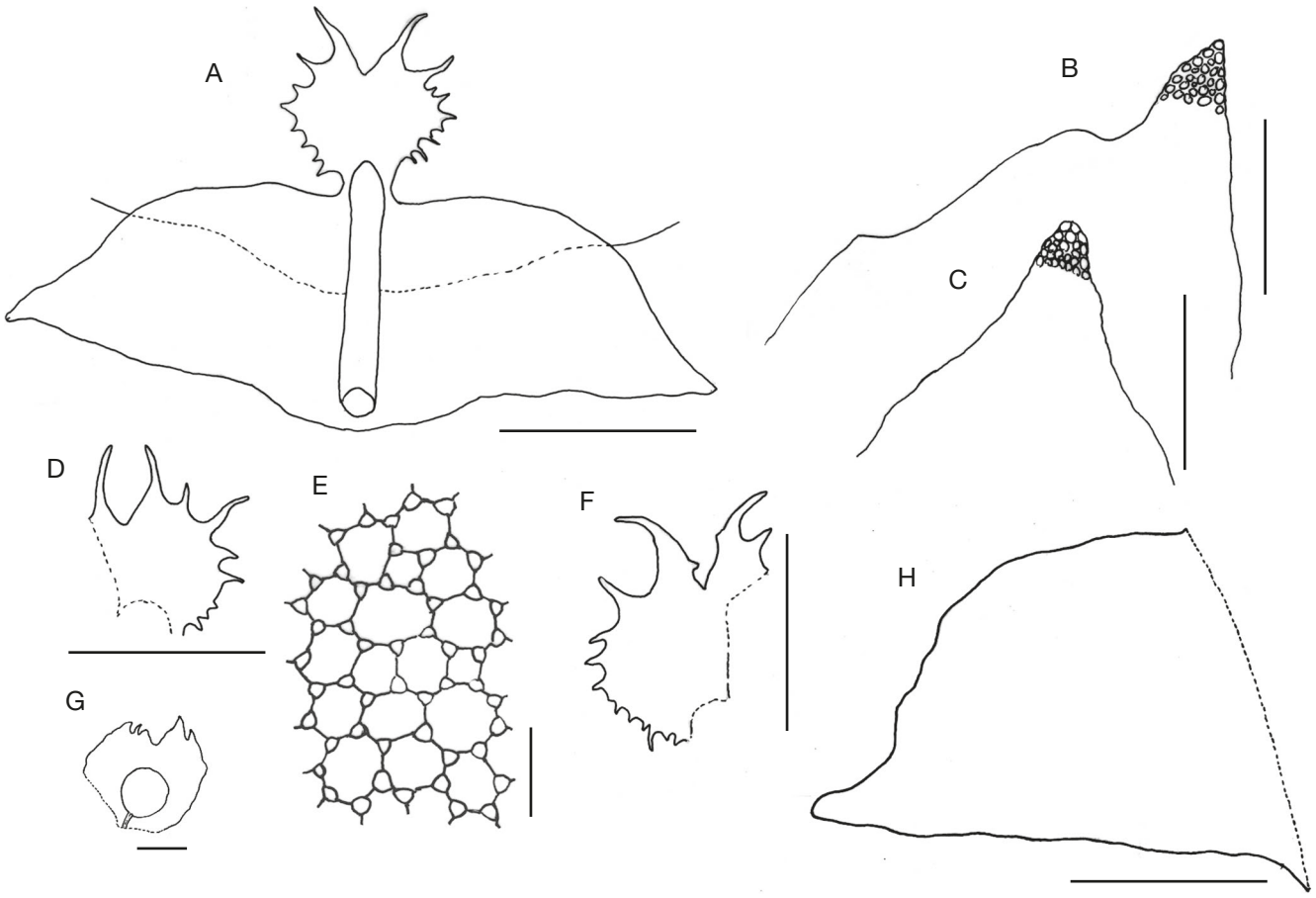

Fig. 19. — *Heteroscyphus subacuminatus* (Herzog) Thouvenot: **A**, shoot portion, ventral view; **B**, **C**, leaf apices; **D**, **F**, half underleaves; **E**, mid-leaf cells; **G**, male bract with antheridium; **H**, leaf. All drawn from *Thouvenot NC2740*. Scale bars: A, D, F, H, 1 mm; B, C, 500 µm; E, 50 µm; G, 200 µm.

Heteroscyphus subacuminatus
(Herzog) Thouvenot, comb. nov.
(Figs 19; 20)

Chiloscyphus subacuminatus Herzog, *Arkiv för Botanik*, n.s. 3 (3): 49 (Herzog 1953). — Type: **New Caledonia**. Slope above N. branch of the Yaté River, near the Forêt du Mois de Mai, 8.VII.1949, *Selling B144 p.p.*, not seen.

Specimen examined. — **New Caledonia**. North Province, Poindimié, Amoa valley, Tipwadabwé, on rocks along the trail when crossing a flooding creek, 211 m, 13.X.2019, *Thouvenot NC2740*.

Distribution in New Caledonia. — Rarely collected in both provinces of the main island, Grande Terre, at low elevation.

Total range. — Endemic.

Description
Dioecious.

Habit
Plants fragile, light olive green, brown in older parts, large shoots 3.50-4.50 mm wide, leaves subopposite, secund, dorsal margins conspicuously connate over the stem, dorsally assurgent at least in upper parts of the shoots, the lowest horizontally spreading.

Leaves
Leaf shape asymmetrically ovate acuminate, 2.00-2.50 mm long, 1.30-1.70 mm wide, ventral margins rounded in lower ⅔-¾, dorsal margin nearly right, apices widely acuminate, acute to narrowly rounded, rarely bifid, frequently broken (Fig. 20C, D).

Cells
Leaf cells hexagonal, 30-50 µm wide, walls thin with large subacute trigones, cell lumina round to ovate.

Underleaves
Narrowly connate to both nearest leaves, 0.75-1.00 mm long, 1.20-1.50 mm wide, the disc rounded with widely wedge-shaped bases, insertion in a deep sinus, apices ⅓ bifid, sinus narrowly lunate or acute, segments narrowly triangular, ending in piliform acumen, margins unevenly spinose-toothed all around.

Gametangia
Androecia at the end of very short lateral-intercalary branches lacking normal vegetative leaves, arranged in small spikes with up to 4 pairs of bracts, bracts very smaller than the vegetative leaves, imbricated, hemispheric, margins with a few short

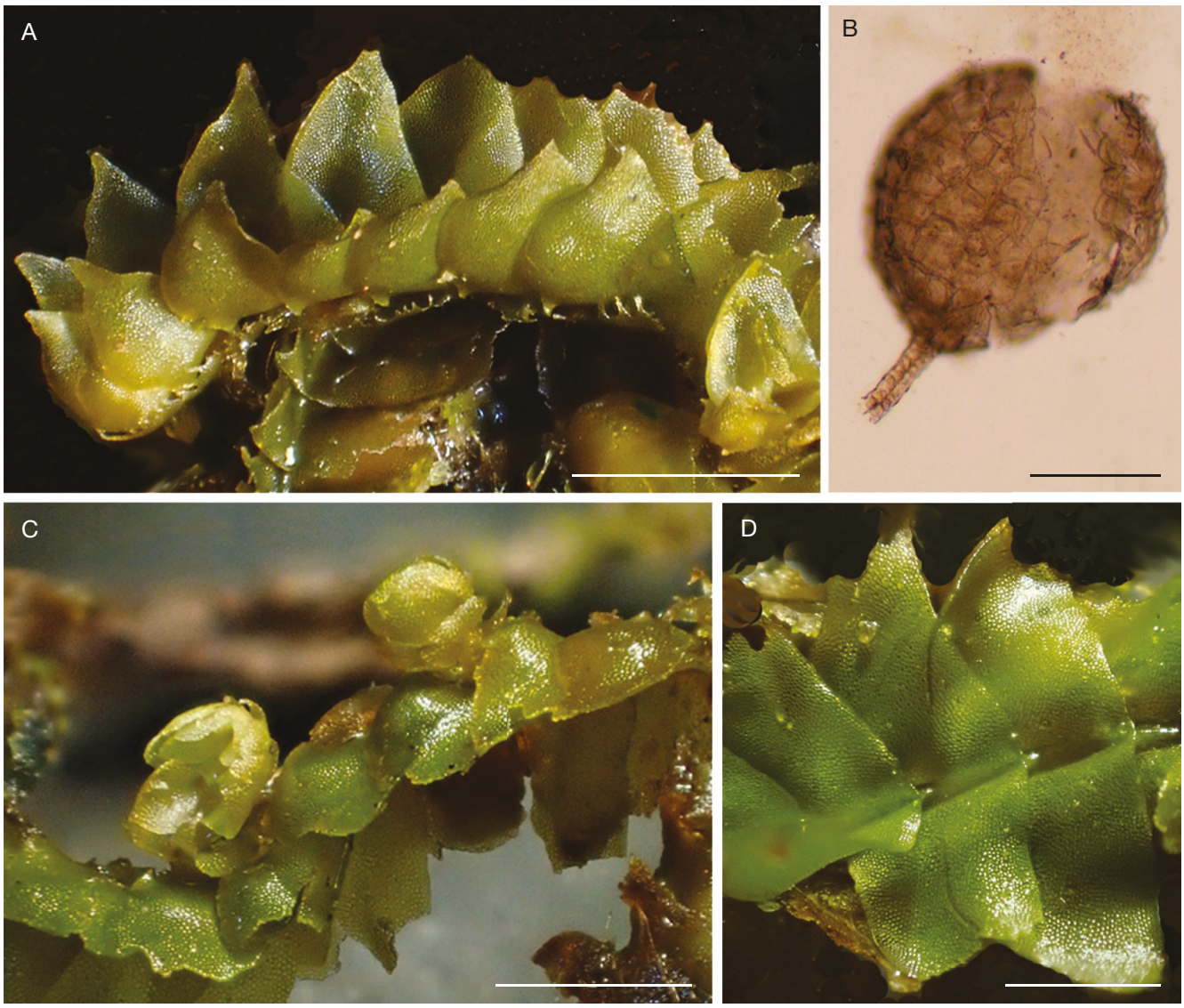

Fig. 20. — *Heteroscyphus subacuminatus* (Herzog) Thouvenot, comb. nov.: **A**, shoot in dorso-lateral view; **B**, antheridium; **C**, androecia on shoot portion, ventral view; **D**, shoot portion, dorsal view. All from *Thouvenot NC2740*. Scale bars: A, C, D, 1 mm; B, 100 µm.

teeth, bracteoles oblong-rectangular, shortly bifid, margins entire or with rare teeth, slime papillae rare to numerous on the margins and tooth apices of bracts and bracteoles, antheridia stalks biseriate; gynoecia not seen.

Comments

According to Herzog (1953), the type specimen of *Chiloscyphus subacuminatus* is sterile. The author collected male plants of the species in 2019, which showed the presence of androecia in short spikes on very short lateral branches and allowed the transfer of the species to *Heteroscyphus*. The transfer is also supported by the underleaves being connate with the nearest leaves on both sides, the subopposite, dorsally connate leaves, and the biseriate antheridial stalks.

Heteroscyphus succulentus (Gott.) Schiffn. (Fig. 21)

Oesterreichische Botanische Zeitschrift 60: 171 (Schiffner 1910). — *Chiloscyphus succulentus* Gött., *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 4: 574, 576 (Gottsche 1853). — Type: **Java**. *Zollinger 3513* ex parte (iso-, G[G00114825]!).

Specimens examined. — **New Caledonia**. North Province, Ouégoa, Diahot upper valley, 430 m, on siliceous sandy ground on the river-bank, 31.VIII.1951, *Hürlimann 2899a* (G); *2901* (G); Poindimié, Tipwadabwé, Amoa valley, 244 m, on dead wood in river side wet forest, in volcano-sedimentary bedrock, 13.X.2019, *Thouvenot NC3286* (PC[PC0779844]); South Province, Koghis, SE ridge of the Mt. Bouo, 830 m, on dead wood in mountain forest, 12.XI.1950, *Hürlimann 2088* (PC[PC0763233]).

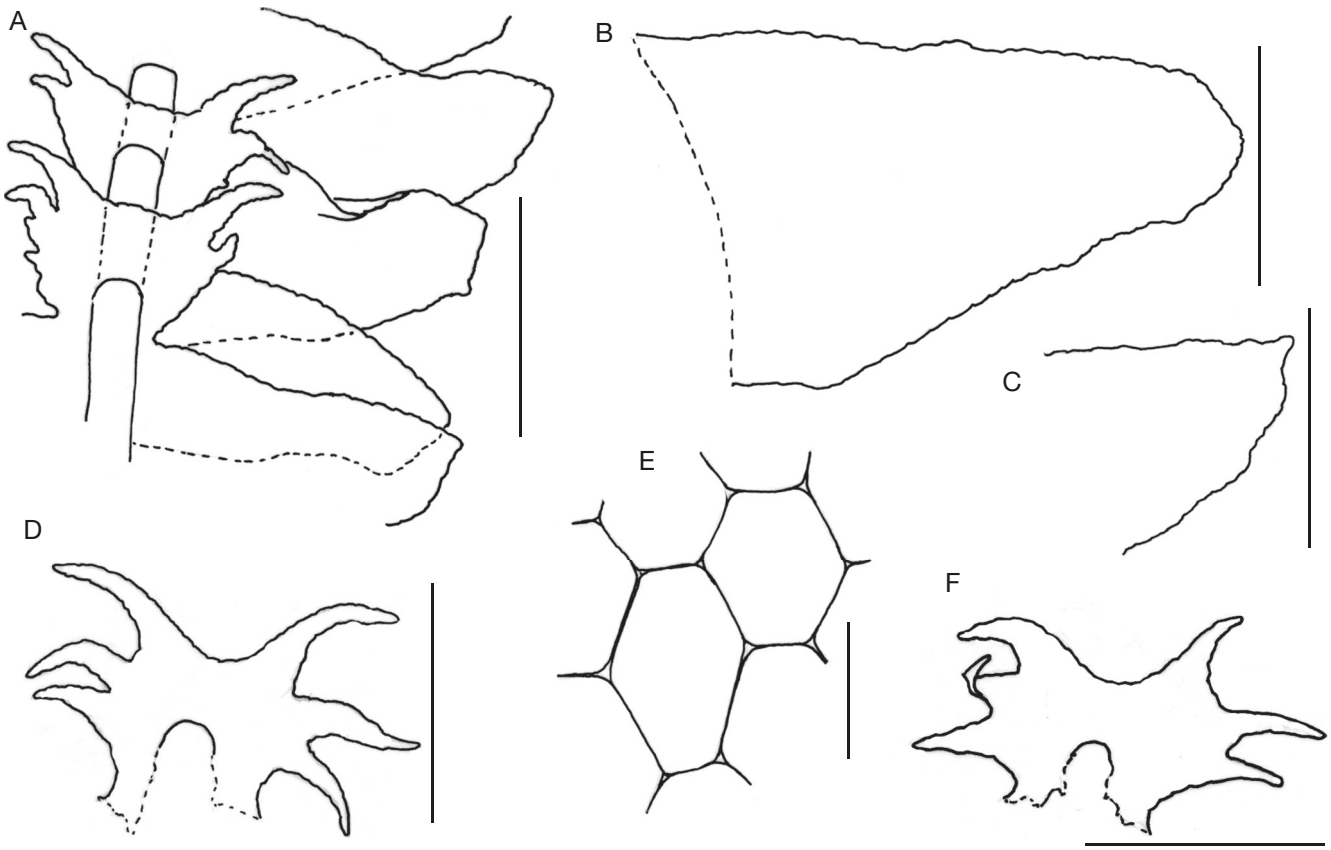

Fig. 21. — *Heteroscyphus succulentus* (Gottsche) Schiffn.: **A**, shoot portion, ventral view; **B**, leaf; **C**, atypical leaf apex; **D**, **F**, underleaves; **E**, leaf cells. All drawn from the isotype of *Chiloscyphus succulentus* Gött. (G00114825). Scale bars: A-D, F, 1 mm; E, 50 µm.

Distribution in New Caledonia. — New to New Caledonia, in North and South Province.

Total range. — Reported from Malaysia, Indonesia, Papua New Guinea and Tahiti (Piippo 1985, GBIF accessed 29 Sept. 2021).

Description

Habit

Plant large, light green, glossy, fleshy; shoots creeping, 4.00-4.50 mm wide, leaves subopposite, dorsally free and slightly decurrent, spreading, dorsally assurgent with a convex base, then somewhat secund.

Leaves

Thin, translucent, ovate-oblong to tongue-like, 1.80-2.00 mm long, 1.30-1.50 mm wide at bases, 0.60 wide at apices, typically with apices widely convex and entire, or truncate, with or without 1-celled teeth at angles, atypical leaves obliquely truncate or shortly bifid with triangular lobes separated by a wide sinus, obtuse or lunate; margin crenulate by the protruding bulging cells.

Cells

Hexagonal, 40-60 µm in upper half of the leaves, becoming elongate in basal part, up to 100 µm long, walls thin, without trigones, bulging so that leaf surface looks rough.

Underleaves

Narrowly connate to both nearest leaves, reniform in outline, 0.75-1.25 mm long, 1.25-2.50 mm wide, deeply bifid, lobes widely divergent, decurved, long lanceolate acuminate with linear apices, sinus widely lunate to flat, disc transversally rectangular, lateral margins with 2(-3) laciniae similar to the lobes; cells bulging.

Gametangia

Not seen.

Comments

Heteroscyphus succulentus looks superficially like *H. deplanchei* but can easily be distinguished by: 1) a fleshy appearance; 2) large, thin-walled, leaf cells without trigones; 3) dorsal margins of paired leaves not connate; and 4) the leaf surface appearing uneven and glossy because of the strongly bulging cells. For differences with *H. cornutistipulus* see above the relevant paragraph.

The species was never formally reported from New Caledonia, although Hürlimann collected a specimen in South Province in 1950 labelled *Heteroscyphus* cf. *succulentus* (PC, GOET, G) (unpublished). Parts of this material in PC and G were checked, together with further specimens, and the presence of this species in both provinces of the main island, Grande-Terre, can be confirmed. The whole range of the species in New Caledonia remains under-documented.

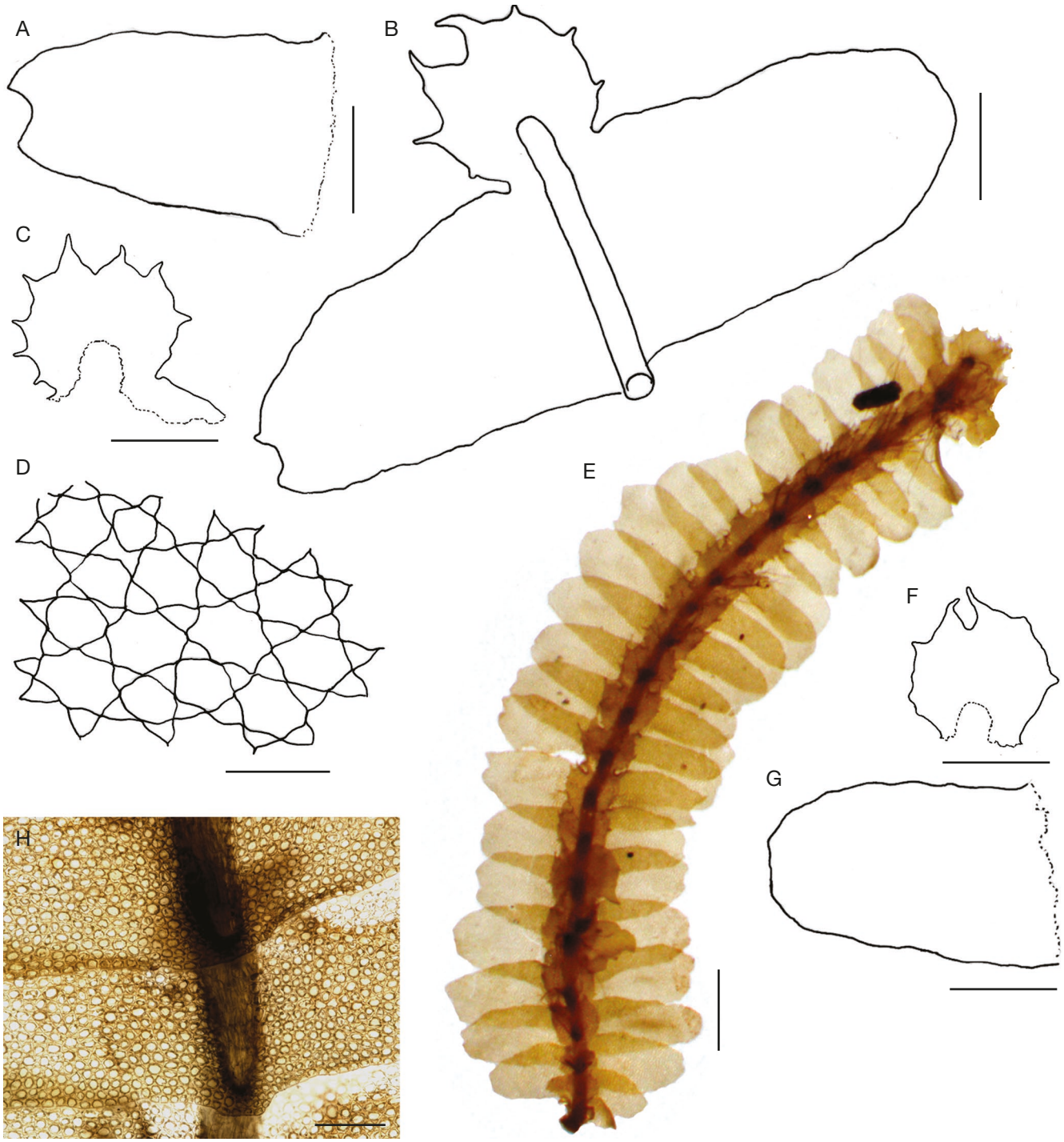

Fig. 22. — *Heteroscyphus supinopsis* J.J.Engel, Thouvenot & Frank Müll.: **A**, **G**, leaves; **B**, pair of leaves with associated underleaf, ventral view; **C**, **F**, underleaves; **D**, cells from leaf median portion; **E**, shoot portion, ventral view; **H**, dorsal leaf connation, dorsal view. All drawn from the holotype. Scale bars: A-C, F, G, 500 µm; D, 50 µm; E, 1 mm; H, 200 µm.

Heteroscyphus supinopsis
J.J.Engel, Thouvenot & Frank Müll.
(Fig. 22)

Nova Hedwigia 113: 62 (Engel *et al.* 2021). — Type: **New Caledonia**. South Province, Mt. Ouin, epiphytic in mossy forest, *c.* 900 m, 1.IX.2003, *Müller NC797* (holo-, DR; iso-, F, hb. Thouvenot).

Distribution in New Caledonia. — Only known from the type specimen in South Province.

Total range. — Endemic.

DESCRIPTION

Further description and illustrations in Engel *et al.* (2021).

Dioecious.

Habit
Plant medium sized, rather rigid, 2.8-3.8 mm wide when flattened; ventral intercalary branching infrequent; stem narrow for plant size, 0.15-0.20 mm wide; leaves subopposite, horizontal grading to obliquely dorsally assurgent, weakly to moderately convex in dorsal sector, moderately abaxially concave in ventral sector, loosely imbricate, the dorsal leaf bases connate and forming a laminar lip to *c*. 6 cells wide.

Leaves
1.30-1.80 mm long, 0.80-1.40 mm wide, subsymmetrical, mostly lingulate occasionally ovate to trapezoid, widest near the insertion; apex variable: broadly rounded to truncate, often retuse, sporadically short bilobed with lobe apices rounded to broadly acute, otherwise entire; margins straight or nearly so, entire.

Cells
25-35 µm wide, 30-40 µm long, somewhat larger near the base; in median portion of leaves with knot-like trigones that are separated by narrow, thin-walled places.

Underleaves
3.8-6.5 times the stem width, connate with the leaves on both sides, imbricate, stoutly ovate to subreniform, 0.6-0.9 mm long, 0.6-0.8 mm wide; apex bifid to (0.2)0.35-0.55, the lobes ± parallel to weakly divergent, acuminate from a broad base, entire or with a tooth toward base of outer margin; lamina 9-12 cells high and *c*. 2-5 times wider than long, the margins on each side with 1-5 dentiform to subciliiiform to occasionnaly laciniiform processes.

Gametangia
Gynoecia seen only in juvenile state, at the end of short leafless branches, lateral-intercalary, bracts ciliate to laciniate; androecia not seen.

Comments
Heteroscyphus supinopsis resembles *H. supinus* of New Zealand and Tasmania and *H. deplanche*i of New Caledonia. Like these species it is easily separated from other New Caledonian Lophocoleaceae by: 1) leaves usually lingulate with the apices and lateral margins entire; 2) cells with conspicuous trigones; 3) large underleaves wider than long with apices deeply bifid and margins armed with processes laciniate to dentiform. *Heteroscyphus supinopsis* is separated from the former by: 1) leaves distinctly connate dorsally; and 2) underleaves less deeply bifid (to 0.35-0.55 vs 0.8), underleaf discs longer (9-12 cells high at insertion vs 4-7) and less transversally elongate (2-5 times wider than long vs 7). It can be distinguished from the latter by: 1) its smaller size with shoots up to 3.8 mm when flattened vs 5 mm; 2) the absence of shoot segments with emarginate to bifid leaves; 3) shorter lateral processes on the underleaf margins, toothed to ciliate vs long laciniate; and 4) less robust stems with *c*. 40 cells in diameter vs up to 100.

Genus *Lophocolea* (Dumort.) Dumort.

Lophocolea bidentata (L.) Dumort
(Fig. 23)

Recueil d'Observations sur les Jungermanniacées 1: 17 (Dumortier 1835). — *Jungermannia bidentata* L., *Species Plantarum*: 1132 (Linnaeus 1753). — Type: **Great Britain**. *Zollinger 3613* (OXF), not seen.

Specimen examined. — **New Caledonia**. South Province, Humboldt Massif, 1200 m, on rocks, 30.IX.2008, *Thouvenot NC2490* (PC[PC0779842]).

Distribution in New Caledonia. — Newly reported, its distribution in New Caledonia is under-documented.

Total range. — Subcosmopolitan. In the austral Indo-Pacific region, *Lophocolea bidentata* is reported from the Mascarenes (Ah-Peng & Bardat 2005), Australia (McCarty 2006 as *Chiloscyphus latifolius* [Nees] J.J.Engel & R.M.Schust.), New Zealand (Glenny 1998 as *C. chlorophyllus* [Hook.f. & Taylor] Mitt.), Java (Söderström *et al*. 2010 as *C. coadnatus* [Hook f. & Taylor] Mitt.) and New Guinea (Piippo 1985).

Description
Based on the New Caledonian specimen.

Habit
Plant medium sized, in loose mats of interwoven stems with many branches, lateral-intercalary; main stems 0.20 mm wide, shoots complanate, main shoots 2.00-2.50 mm wide, branches variously narrower, sometimes strongly attenuated; leaves distichous, spreading at right angle, plane, contiguous to slightly imbricated, not connate dorsally, brownish in older main shoots.

Leaves
Ovate to oblong-rectangular, 1.20-1.40 mm long, 0.75-0.90 mm wide, margins smooth, entire, apices truncate, bilobed, lobes triangular at base with acute to piliform apices 1-3 cells long, sinus wide, lunate to right-angled, branch leaves contiguous to remote, smaller, with lobes narrower and piliform lobe apices longer.

Cells
Leaf cells rounded to oval, 25-30 µm x 25-45 µm, with small to large nodulous trigones.

Underleaves
Deeply bifid, disc small, 3 cells high at mid-insertion, 0.15-0.20 mm long, 0.20-0.25 mm wide, lobes narrowly lanceolate-linear, piliform apices 3-7 cells long, overall size 0.35-0.50 mm long, 0.40-0.60 mm wide, circa 2 times the stem width, not connate to the ventral margins of the leaves.

Gametangia
Not seen.

Comments
This species is newly reported from New Caledonia. Its wide range might be further extended since several austral species have already turned to be synonyms (see above total range) and many countries of the Pacific region are still understudied.

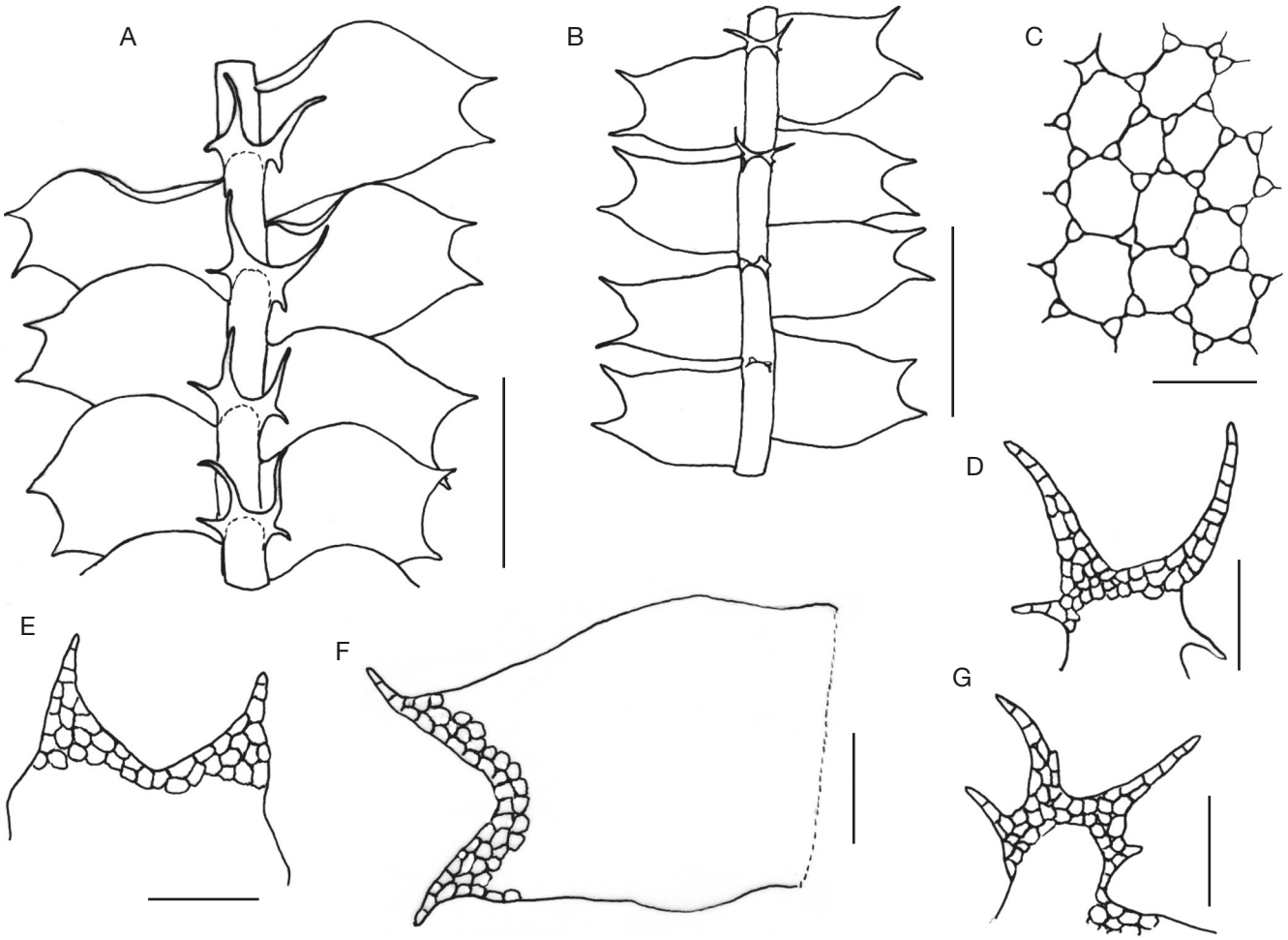

Fig. 23. — *Lophocolea bidentata* (L.) Dumort.: **A**, main shoot, ventral view; **B**, secondary shoot, ventral view; **C**, leaf cells; **D**, **G**, underleaves; **E**, leaf apex; **F**, leaf. All drawn from *Thouvenot NC2490*. Scale bars: A, B, 1 mm; D-G, 200 µm; C, 50 µm.

The New Caledonian specimen is sterile and shows a large variation in shoot width. It somewhat differs from typical *L. bidentata* only in the small to medium-sized trigones. The material differs from *L. bispinosa*, a New Zealand species which has similar overall shape and conspicuous trigones but possesses heterogeneous areolation with larger cells scattered inside the lamina and along the margins. Furthermore, the latter species has a deeper sinus between longer piliform lobes and leaf margins with ciliate processes.

The rarity of *Lophocolea bidentata* in New Caledonia could be linked to the ecological conditions since it was found in one of the highest localities of the island where it grows with *Cryptolophocolea subcostata* (Steph.) Thouvenot, *Telaranea bisetula* (Steph.) E.O.Campb., *Trichocolea pluma* (Reinw., Blume & Nees) Mont. and *Cheilolejeunea trapezia* (Nees) R.M.Schust. & Kachroo.

Lophocolea caledonica Steph.
(Fig. 24)

Species Hepaticarum 6: 267 (Stephani 1922). — *Chiloscyphus leratii* J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 418 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. "*Lerat*" *s.n.* (lecto-, here designated, G["prope summo Mt. Mou", XI.1908, *Le Rat 210*, G00112967]!; isolecto-, REN[herb. E. G. Paris]!).

Further specimen examined. — **New Caledonia**. South Province, Païta, Humboldt massif, on the trail toward the hut, on rock in cloud forest, 30.IX.2008, *Thouvenot NC3338*.

Distribution in New Caledonia. — *Lophocolea caledonica* was found at highest elevations in the peridotite massifs of South Province, only known from the type specimen and a single recent collection.

Total range. — Endemic.

Description
Dioecious.

Habit
Plant small, shoots 1.50 mm wide, leaves narrowly imbricate, spreading, alternate, dorsally free.

Leaves
Widely oval to oblong, 0.70-0.80 mm long, 0.50-0.60 mm wide, apices usually truncate to retuse, the margins densely

spinose-toothed around apices and distal parts of ventral and dorsal margins, both leaf surfaces smooth.

Cells
Leaf cells small, 16-20 µm, with conspicuous nodulose trigones.

Underleaves
Narrowly decurrent on one side but free from connation with the leaves, obconical, apices deeply bifid with lunate sinuses, lobes triangular lanceolate, lobes and lateral margins with teeth like the leaves.

Gametangia
Androecia at the end of normal leafy shoots or abbreviated leafless branches, ventral-lateral, with 3-5 pairs of bracts, rectangular, spinose-toothed at apices, the bases of the dorsal margins recurved and saccate; gynoecia at the end of normal leafy shoots, 2 pairs of bracts similar in shape to normal vegetative leaves but larger, 1.10 mm long, 0.60 mm wide; bracteoles smaller, 0.50-0.70 mm long, 0.35-0.40 mm wide, ovate, ½ or more bifid, sinus narrow, lobes oblong to lanceolate, often divided in secondary lobes, the upper margins toothed-laciniate; perianth elongate, basal half cylindrical, upper half trigone, not winged, mouth trilobed, sinus depth ⅓ the length of the whole perianth, lobes oval to lanceolate, subdivided by several deep cuts, margins sharply and densely toothed, the surface of the perianth sparsely bristled with short spikes, usually 1 (-2) cell long.

Comments
Lophocolea caledonica is a very distinct, elegant species with all leaves and underleaves finely spinose-toothed. Unfortunately, the type specimen is sterile as underlined by Stephani (1922). In the herbarium of E. G. Paris (REN), the author found part of the original specimen examined by Stephani with well-developed gametangia. The position of the gynoecia at the end of normal leafy shoots confirms its assignment to *Lophocolea*, together with vegetative characters, i.e., underleaves free, bifid, leaf apices emarginate. This species resembles the Australasian species of the *Lophocolea* section *Microlophocolea* Spruce (Engel 2010 as *Chiloscyphus* subg. *Microlophocolea*) especially *L. muricata* (Lehm.) Nees (see below). They share: 1) sizes of shoots, leaves, underleaves and cells; 2) leaf and underleaf shapes; and 3) margin ornamentations. *Lophocolea caledonica* differs from all the Australasian species of this section in the leaves smooth on both faces instead of armed with numerous conspicuous teeth on one or both surfaces.

Lophocolea convexula Mitt.
(Figs 25; 26)

Flora Vitiensis: 405 (Mitten 1871 [1873]). — Chiloscyphus convexulus (Mitt.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 413 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. Isle of Pines, *Strange s.n.* (holo-, NY[NY00965719!]).

Lophocolea kurzii Sande Lac., *Annales Musei Botanici Lugduno-Batavi* 1: 296 (1864). — *Chiloscyphus kurzii* (Sande Lac.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 417 (Engel & Schuster 1984 [1985]). — Type: **Java**. Tjiliwong valley, Bogor, 800', *Kurz s.n.* (holo-, L[L0060979, *fide* Kitagawa in sched. 1970]!) **syn. nov.**

Lophocolea fragillima Steph., *Species Hepaticarum* 6: 273 (Stephani 1922). — *Chiloscyphus fragillimus* (Steph.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 415 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. "*Lerat*" *s.n.* (lecto-, here designated, G["Lerat, Herb. Thériot", G00112413]!) **syn. nov.**

Lophocolea parva Steph., *Species Hepaticarum* 6: 287 (Stephani 1922). — *Chiloscyphus parvus* (Steph.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 420 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. Franc (lecto-, here designated, G["Nova Caledonia, 1906", *Franc s.n.*, "Herbier Lacouture", G00061334!]; isolecto-, PC[PC0102407!, PC0102408!]) **syn. nov.**

Lophocolea papulimarginata H.A.Miller, *Phytologia* 47: 323 (Miller 1981). — *Lophocolea papulosa* Steph., nom. illeg. *Species Hepaticarum* 6: 286 (Stephani 1922). — *Chiloscyphus papulimarginatus* (H.Mill.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 420 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. "*Lerat*" *s.n.* (lecto-, here designated, G["Ad arbores in summo Mt. Mou (1224 m)", I.1906, *Le Rat 44*, G00112490!]; isolecto-, REN[herb. E. G. Paris]!; syn-, G[Pic des Sources, s.d., *Le Rat 237*, G00051485!, Mt. Dzumac, IV.1907, *Le Rat 225*, G00051484!, *idem*, *Le Rat 232*, G00051487!, "Île des Pins, Forêt de Uapan", V.1909, *L. Le Rat 68*, G00051486!], isosyn-, REN["Île des Pins", V.1909, *L. Le Rat s.n.*, herb. E. G. Paris]!) **syn. nov.**

Lophocolea pilistipula Steph., *Species Hepaticarum* 6: 288 (Stephani 1922). — *Chiloscyphus pilistipulus* (Steph.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 421 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. "*Lerat*" *s.n.* (lecto-, here designated, G["Île des Pins, forêt de Watchia, à la baie de Oupe", V.1909, *L. Le Rat 55*, G00112487]!; isolecto-, REN[herb. E. G. Paris]!) **syn. nov.**

Further specimens examined. — **India**. Shambaganur, II.1932, *Foreau 3075* as *Lophocolea kurzii* (PC[PC0167666]).
Java. "Ad *Arengae sacchariferae* truncos in agro Buitenzorgensis", 250 m, 18.VI.1908, *Schiffner 696* as *Lophocolea kurzii* (PC[PC0763155]).
New Caledonia. South Province, Sarraméa, on the treck from Sarraméa to the Dogny Plateau, epiphyte, *c.* 170 m, 5.IX.2003, *F.Müller NC799* (DR); Nouméa, Tina, border between dry forest and mangrove, 0-2 m, 24.IX.2012, *Thouvenot NC2395*; Farino, Grandes-Fougères Natural Park, Creek Houé, on dead wood in a mesophylous forest, 370 m, 22.IX.2016, *Thouvenot NC2448*; Mont Dore, Demazures forest, on dead wood in wet forest, 330-420 m, 28.IX.2016, *Thouvenot NC2466*; Mont Dore, Yahoué, on trunk in the mesophilous forest along the river, 122 m, 10.X.2019, *Thouvenot NC2756*; North Province, Pouhembout, Forêt Plate, near Ouendé Falls, 300 m, road embankment, 7.IX.2003, *F.Müller NC815*; South Province, Mt. Dzumac, IV.1907, *Le Rat s.n.* as *Lophocolea papulosa* (G[G00051484, G00051487]); Pic des Sources, *Le Rat s.n.* "fragments" as *Lophocolea papulosa* (G[G00051485]); "Île des Pins, forêt de Wapan", V.1909, *L. Le Rat s.n.* as *Lophocolea papulosa* (G[G00051486]); Nouméa, Ouen Toro, 28.VIII.1950, *Hürlimann 2038a* as *Lophocolea papulosa* (PC[PC0167657]); Mé Aoui, 500 m, 8.II.1951, *Guillaumin & Baumann-Bodenheim 10375* as *Lophocolea papulosa* (PC[PC0167656], GOET); Boulari, 200 m, 23.VII. 1950, *Hürlimann 2015* as *Lophocolea parva* (G[G060814]); *Hürlimann 2017* as *Lophocolea parva* (G[G060826]); ex herbarium Bonati, *Franc s.n.* determinavit Stephani as *Lophocolea fragillima* (PC[PC0167654]); North Province, "ad radices Mt. Panié", II.1910, *Le Rat s.n.* "fragments" as *Lophocolea autoica* (G[G00128109]); South Province, Mts. Koghis, 21.IV.1914, *Compton 801* as "*Lophocolea levieri*" (BM[BM013409501, BM013409504]); Mt. Mou, on stone and

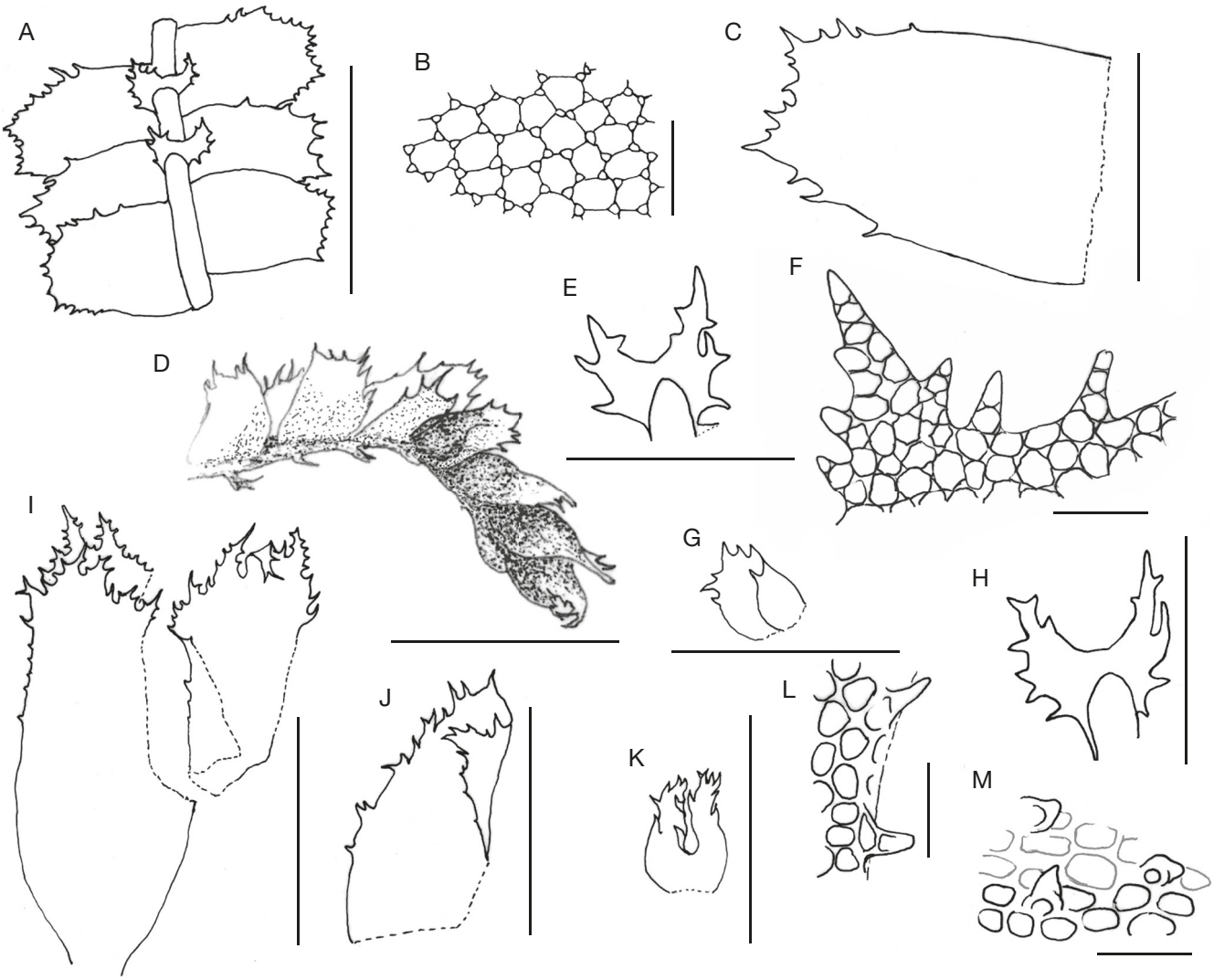

FIG. 24. — *Lophocolea caledonica* Steph.: **A**, shoot portion, ventral view; **B**, midleaf cells; **C**, leaf; **D**, androecium, lateral view; **E**, **H**, underleaves; **F**, leaf angle with teeth; **G**, male bract; **I**, perianth (torn); **J**, female bract; **K**, female bracteole; **L**, **M**, spines on the perianth surface. **A**, **E**, **H**, drawn from the lectotype (G00112967); **B**-**D**, **F**, **G**, **I**-**M**, from the isotype (REN). Scale bars: A, I-K, 1 mm; B, F, L, M, 50 µm; C-E, G, H, 0.5 mm.

mud in stream, 8.III.1914, *Compton 443* as "*Lophocolea levieri*" (BM[BM013409502]).

DISTRIBUTION IN NEW CALEDONIA. — The most frequent member of Lophocoleaceae at low altitude, in both provinces of the main island, including Isle of Pines; it grows on various substrates on the ground, rarer on barks of living trees, at low to medium elevations (collected from 0 to 900 m).

TOTAL RANGE. — Java (Söderström *et al.* 2010 as *Lophocolea kurzii*), Fiji (Söderström *et al.* 2011 as *Chiloscyphus parvus*), Malaysia (Chuah-Petiot 2011 as *Lophocolea kurzii*), Thailand (Lai *et al.* 2008 as *Lophocolea kurzii*).

DESCRIPTION

Paroecious, more rarely autoecious.

Habit

Plants small to medium, shoots 1.00-2.00 mm wide; leaves alternate, patent, dorsally assurgent, individually convex and secund, dorsally free; both terminal and lateral-intercalary branching present.

Leaves

Ovate-oblong, 0.55-1.00 mm long, 0.40-0.80 mm wide, leaf margins crenulate due to bulging marginal cells, leaf apices uneven on a same shoot, ranging from widely rounded or obtuse to retuse with widely concave sinus and rounded angles, possibly with one short acute tooth, other times leaf apices very shortly bifid with widely triangular lobes.

Cells

Hexagonal, 16-36 µm, thin-walled, trigones very small, acute, free walls bulging.

Underleaves

Small, free or very narrowly connate to one of the nearest leaves, 1-2 times the stem width, insertion in a deep sinus,

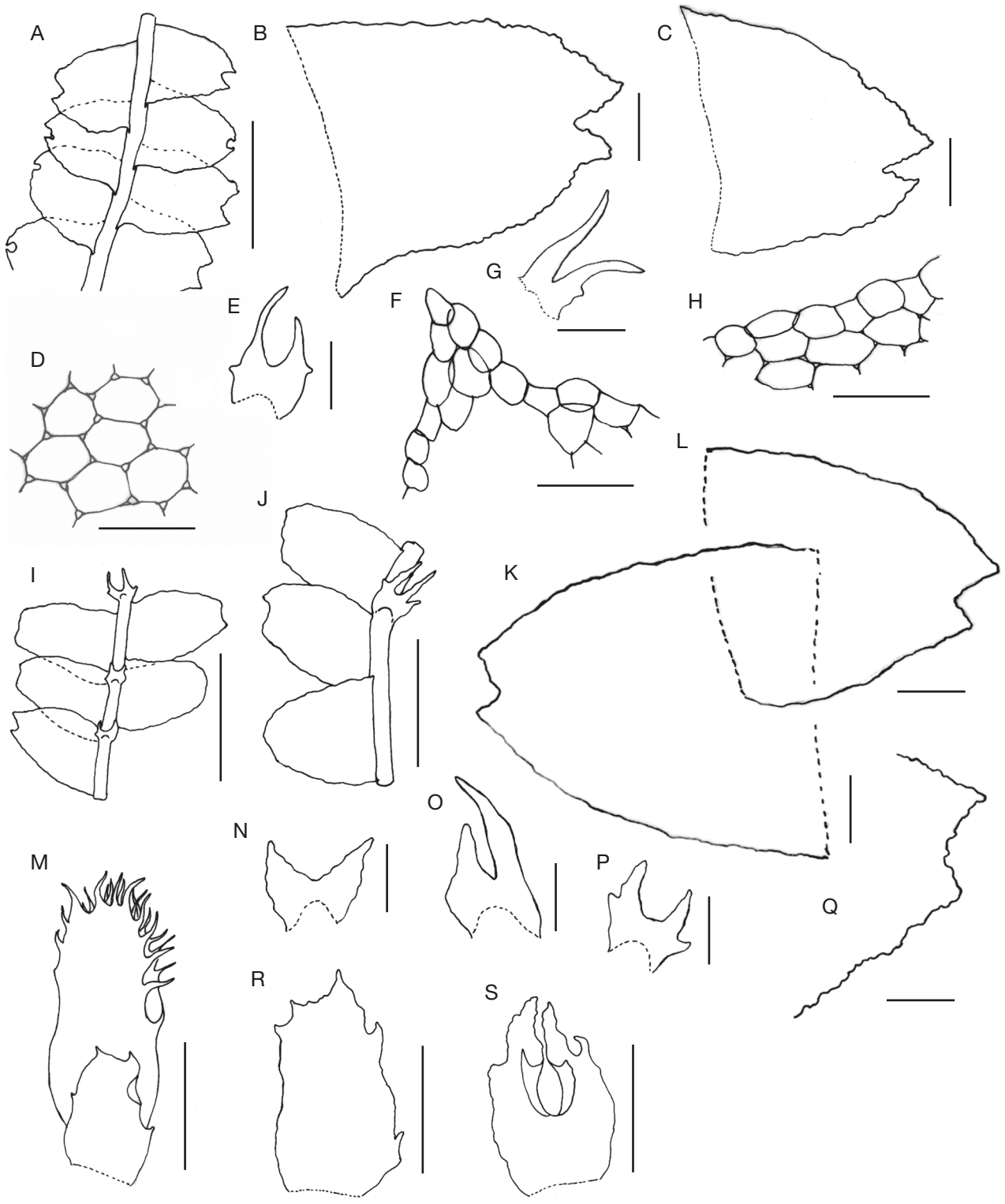

Fig. 25. — *Lophocolea convexula* Mitt.: **A**, shoot portion, dorsal view; **B**, **C**, **K**, **L**, leaves; **D**, median cells; **E**, **G**, **N**-**P**, underleaves; **F**, leaf lobe; **H**, marginal cells; **I**, **J**, shoot portions, ventral view; **M**, perianth with a bract; **Q**, leaf apex, strongly crenulate margin; **R**, female bract; **S**, female bracteole. **A**-**H**, drawn from the holotype of *Lophocolea kurzii* Sande Lac. (L0060979); **I**-**L**, **N**-**S**, from the lectotype of *Lophocolea fragillima* Steph. (G00112413); **M**, from the lectotype of *Lophocolea papulimarginata* H.A.Miller (G00112490). Scale bars: A, I, J, M, R, S, 1 mm; B, C, E, G, K, L, N-P, 200 µm; D, F, H, 50 µm; Q, 100 µm.

apices deeply bifid, lobes narrowly lanceolate, discs shorter than wide, lateral margins with a single short to filiform tooth on both sides, more rarely similar to the lobes, then with one more tooth.

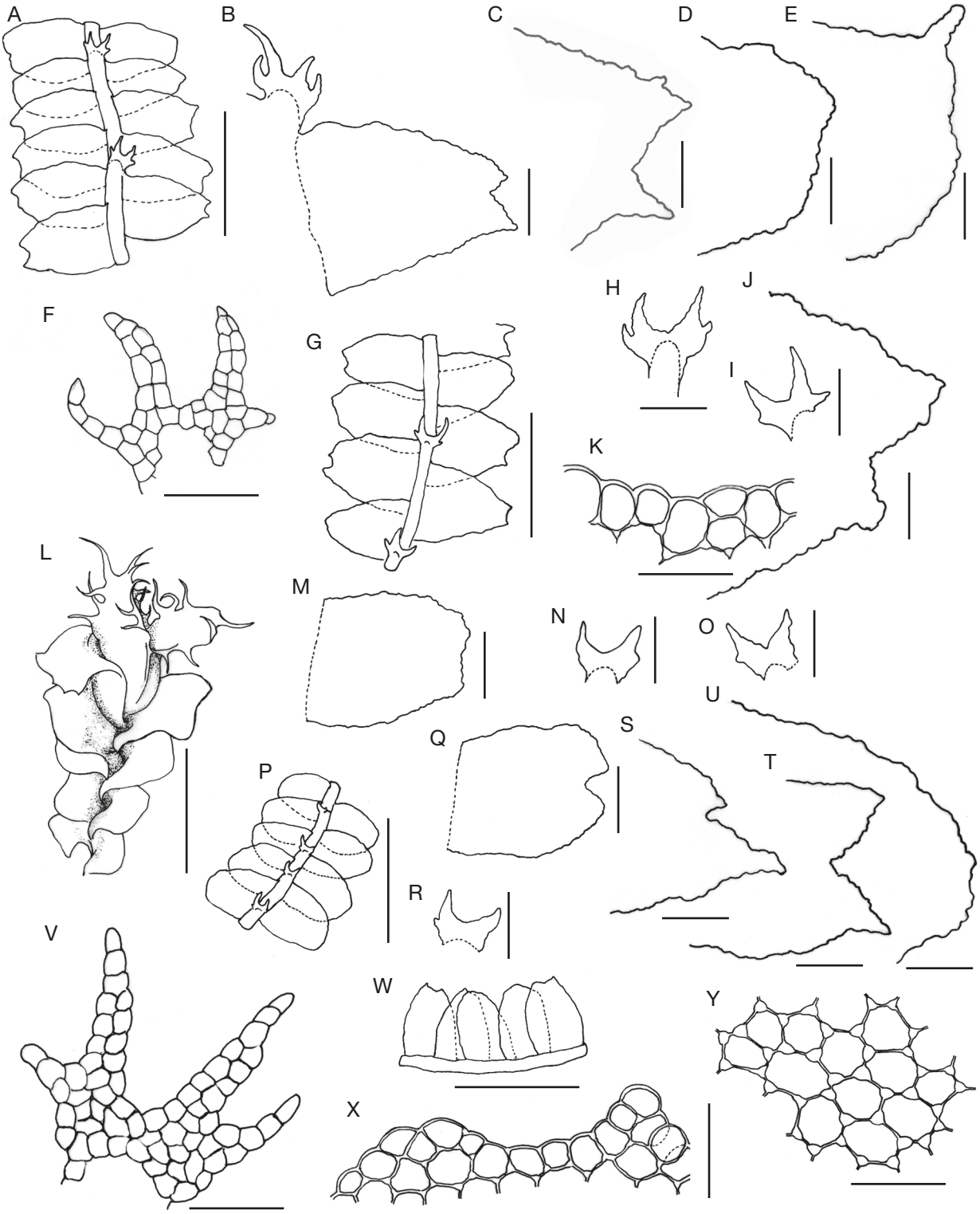

FIG. 26. — *Lophocolea convexula* Mitt.: **A**, **G**, **P**, shoot portion, ventral view; **B**, leaf and underleaf; **C**-**E**, **J**, **S**-**U**, leaf apices; **F**, **H**, **I**, **N**, **O**, **R**, **V**, underleaves; **K**, marginal cells; **L**, autoicous gametangia: perianth terminal with one pair of female bracts and four pairs of male bracts below, dorsal view; **M**, **Q**, leaves; **W**, adjacent leaves on stem; **X**, apex margin; **Y**, median cells. **A**-**F**, drawn from the lectotype of *Lophocolea pilistipula* Steph. (G00112487); **G**-**K**, from the lectotype of *L. papulimarginata* H.A.Miller (G00112490); **M**-**U**, from the lectotype of *Lophocolea parva* Steph. (G00061334); **L**, **V**-**Y**, from the isotype of *Lophocolea parva* (PC0102408). Scale bars: A, G, L, P, W, 1 mm; B, H, I, M-O, Q, R, 200 µm; C-F, J, S-V, 100 µm; K, X, Y, 50 µm.

Vegetative reproduction

Gemmae lacking, but regenerants occur on perianth mouth and bract margins in some specimens.

Gametangia

Gynoecia at the apices of main shoots or long branches with normal vegetative leaves, bracts oblong, variously and shortly

toothed, bracteoles bifid to the middle, lateral margins variously and shortly toothed; perianths oblong, 2-3 mm long, with cupulate-ovate base and trigone upper part, plicae narrow, acute, not winged, mouth deeply 3-fid to half the whole perianth length or more, the lobes narrowly ovate-triangular, strongly toothed to laciniate; androecia beneath the gynoecia, in series of 3-5 pairs of male bracts smaller than the female and saccate at dorsal base.

Comments

In addition to the plant described by Mitten as *Lophocolea convexula*, this group of taxa includes other New Caledonian plants described by Stephani (1922) as distinct species but very similar in most respects and similar to the South Asian *L. kurzii*. They share the following common features: 1) small size and dorsally convex secund leaves; 2) ovate leaves wider at base or at small distance above, decreasing to the apices in curve lines; 3) apices variable in a same shoot, typically entire or retuse, rarely or frequently shortly bifid with wide triangular lobes; 4) leaf margins crenulate; 5) underleaves small, hardly wider than the stems, deeply bifid, usually with one small tooth on both sides; 6) usually paroecious; and 7) perianths deeply 3-fid, triangular lobes sharply toothed or laciniate. As stressed by many authors (Sande Lacoste 1864; Schiffner 1900; Pearson 1922; Kitagawa 1973; Gradstein 2011) these plants look like *Lophocolea heterophylla* (Schrad.) Dumort., a species widely distributed in the Northern Hemisphere and very rare in the tropics where it has been reported from Cuba and ranges southwards to Brazil in the Southern Hemisphere (Gradstein & Pinheiro da Costa 2003). Besides this geographic separation, *L. heterophylla* may be distinguished by: 1) a leaf shape rather rectangular, not so decreasing to the apex; 2) some or many leaf apices bilobed, the lobes longer and sharper, separated by a deeper and wider sinus; 3) leaf margins entire, free cell walls flat; 4) perianths less deeply 3-fid, the lobes truncate, rounded to widely triangular, unevenly toothed; and 5) gemmae occasional and regenerants unknown. It would have been interesting to compare Brazilian material (not seen) with *L. convexula*. Schuster (1980) describes *L. heterophylla* subsp. *cladogyna* R.M.Schust., a subspecies with some specific characters of *L. convexula* namely the rounded leaves usually entire. But the subspecies of *L. heterophylla* usually produce gemmae, never regenerants (Paton 1999); in contrast, such cell clusters (regenerant) are found on leaves, bracts and perianth margins in some specimens of *L. convexula* collected in New Caledonia (e.g. *NC2756*), but gemmae have never been observed.

The holotype of *Lophocolea convexula* is fertile and shows paroecious sexual condition. As it is the earlier name among the many species described with this set of vegetative and sexual characters, we assume this name must be used for these plants in New Caledonia as well as in the Asian and South Pacific regions where *L. kurzii* was reported.

In New Caledonia, a single report of *Lophocolea kurzii* is from Paris (1908) based on a specimen collected by Le Rat in Loyalty Islands. This specimen is lacking in the herbarium of E. G. Paris (REN), but a lot of new species names, here considered as synonyms, were given by Stephani to the New Caledonian material sent by E. G. Paris, on the basis of different forms of characters, such as leaf and underleaf apices, cell width, leaf and perianth sizes. Careful examination shows that these characters are variable even in a same specimen. Consequently, Stephani invented new species which turned to be the same, when examined together. All the New Caledonian names, being published after the name of *L. convexula*, fall in synonymy with the latter, so that, the author assume that it might be more widely distributed in southern tropics.

The main differences seen in Stephani's diagnoses and drawings or found in the type material of the New Caledonian taxa concern the perianth shapes, oblong in *L. parva*, cupulate in *L. papulosa*, cyathiform in *L. convexula* and obovate-conical in *L. fragillima*. This aspect is difficult to evaluate on some old specimens, hardly fertile or with broken organs. However, all other gynoecial characters being similar or included in a short range of continuous variation, this diversity may be resumed in a length-width ratio ranging from 4 (*L. parva*), 3-2.5 (*L. fragillima*) to 2 (*L. papulosa*). The conservation requirements of old specimens, especially if they are types, prevent to provide sufficient data on size and ornamentation of the gynoecia and to assume a continuous variability in perianth shapes. However, the observed differences seem likely the result of various stages of maturity. In vegetative features, the main changes are the underleaves and leaf orientation. Underleaves are variable in a same specimen or even in a same shoot, the lobes being sometimes shorter without filiform apex, their orientation varying from erect incurved to spreading at an angle of 30-45°. Leaf arrangements are contiguous to slightly imbricate and obliquely patent in *L. fragillima*, or conspicuously imbricate and patent at right angle in *L. parva*, less conspicuously so in further species. However, dimensions are comparable in all the types and fresh specimens measured. Thus, morphological differences are insufficient to separate New Caledonian specimens as distinct taxa.

For lectotypification purpose of *Lophocolea pilistipula*, the specimen G00112487 from Pines Island is selected here since it perfectly matches the original description and belongs to the original materiel examined by Stephani as shown by the handwritten name and mentions "*n.sp.*" and "*c. per.*". The original description includes perianth characters and the selected lectotype is the single fertile specimen among the three type specimens kept at G. The remaining material at G, from Dogny, is sterile and larger in all the dimensions. They belong to another species described as *Heteroscyphus parapilistipulus* (see above). The original materials of *L. fragillima* and *L. parva* at G each comprise a single packet handwritten "*n.sp.*" by Stephani and are the only ones available for lectotypification. Among five packets of *L. papulosa* available, the lectotype selected have the label marked "*original*", and "*autoica, c. per.*" handwritten by Stephani. This is also the type designated by Miller (1981) when he replaced its epithet by *papulimarginata*.

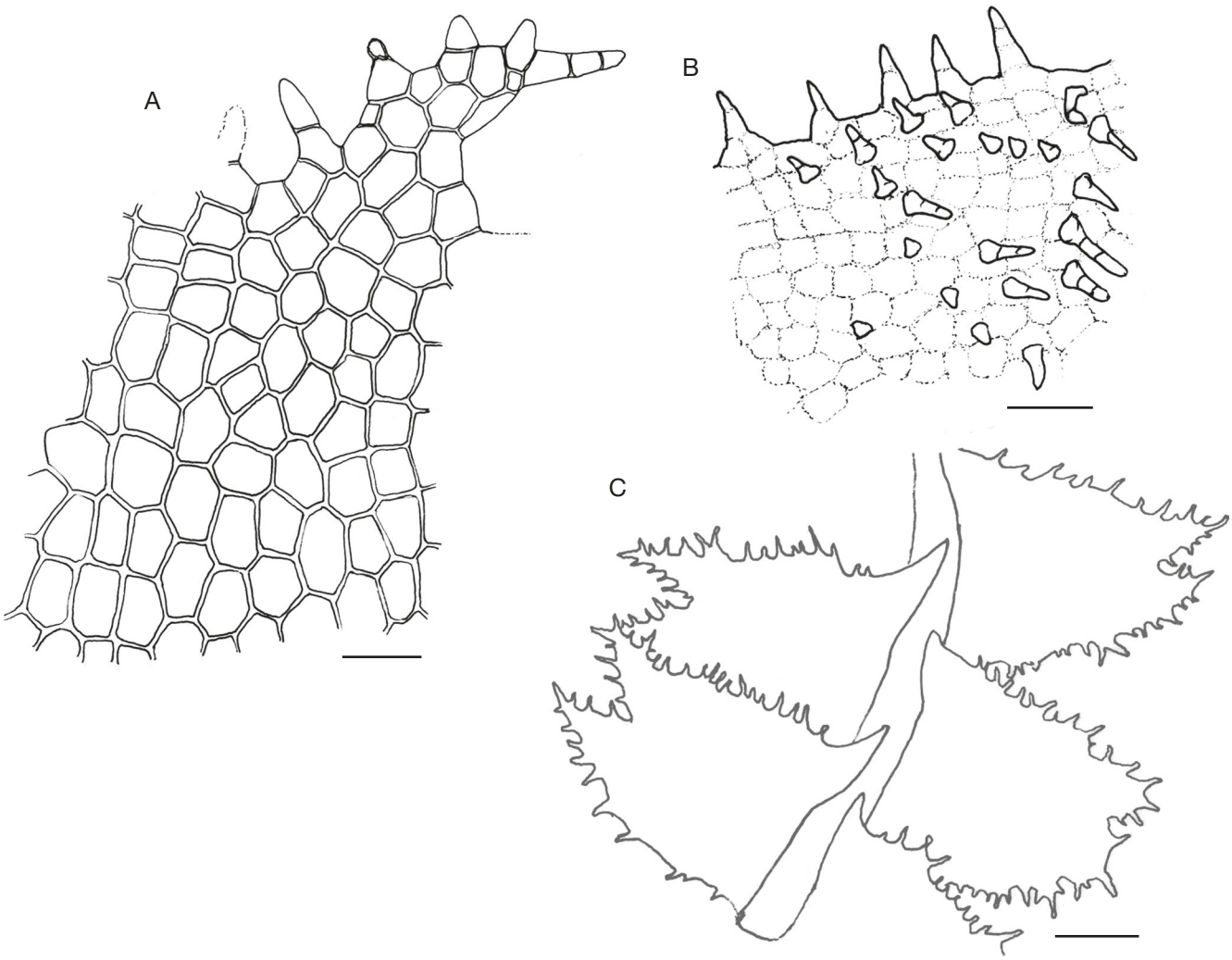

FIG. 27. — *Lophocolea muricata* (Lehm.) Nees: **A**, cells from lobe apex (top) to median portion of leaf; **B**, leaf margin in dorsal view, with focus on the echinae; **C**, shoot portion, dorsal view. All drawn from *Hürlimann 2090* (Z007-1972) (from photos by H. Hofmann). Scale bars: A, B, 20 µm; C, 100 µm.

Lophocolea muricata (Lehm.) Nees
(Fig. 27)

Synopsis Hepaticarum: 169 (Gottsche *et al.* 1845). — *Jungermannia muricata* Lehm., *Linnaea* 4: 363 (Lehmann 1829). — *Chiloscyphus muricatus* (Lehm.) J.J. Engel & R.M.Schust., *Nova Hedwigia* 39: 419 (Engel & Schuster 1984 [1985]). — Type: **South Africa**. In parietibus saxorum in vertice montis Tafelberg, Cape of Good Hope, *Ecklon s.n.*, not seen.

REFERENCE SPECIMEN EXAMINED. — **New Caledonia**. South Province, Mts. Koghis, SE ridge of Mt. Bouo, on bark in meso-hygrophilous forest, 830 m, 12.XI.1950, *Hürlimann 2090* (Z[007-1972]).

DISTRIBUTION IN NEW CALEDONIA. — South Province. Hitherto only known from a single collection by Hürlimann (1998).

TOTAL RANGE. — Pantropical-South temperate.

DESCRIPTION

Further description and illustrations in Fulford (1976) or Engel (2010 as *Chiloscyphus muricatus*).

Autoecious.

Habit

Plants soft, shoots up to 1 mm wide, branches common, stems smooth; leaves alternate or subopposite, usually subhorizontal ± dorsally assurgent in basal portions, imbricate, the base of dorsal margins reaching the midline of the stem but not fused.

Leaves

Ovate-oblong, shortly bifid to 0.15-0.20, the lobes triangular, medium acute; dorsal leaf surface hispid, except near ventral base, armed with 1-3-celled erect, acute echinae, one per cell, half ventral leaf surface armed with scattered 2-4-celled similar echinae; lateral and lobe margins copiously spinose-dentate to ciliate-dentate, the teeth 2-3(4) cells long.

Cells

Leaf cells 14-18 µm wide, 17-20 µm long, walls moderately thickened, trigones small to medium.

Underleaves
1.4-1.6 times the stem width, narrowly connate on one side, mostly cuneate to long rectangular, bifid to 0.74 or more, lobes diverging or subparallel, long linear, margins and lobes ciliate.

Gametangia
Gametangia terminal or intercalary on main shoots or ± long normal leaved branches, androecia in short spikes, bracts much smaller than leaves, strongly ventricose; except the reflexose distal portion, bifid and ornamented as in the leaves; antheridial stalk uniseriate; gynoecia with innermost bracts much larger than leaves, elliptic convex, short bifid, with both surfaces armed as in the leaves, lobes broadly acute, margins copiously spinose-dentate or ciliate-dentate; innermost bracteoles smaller, oblong to narrowly ovate, bifid to ± 0.4-0.5, margins ciliate; perianth long exserted, nearly cylindrical, somewhat dorsally compressed, ± trigonous when young, the surface densely hispid with echinae as in the leaves, perianth mouth 3-lobed, lobes shallowly bifid, the segments acute to subacuminate, lobe margins spinose dentate; calyptra small, included within periant at maturity.

Comments
Lophocolea muricata is easily distinguished from all other New Caledonian species by the acute echinae set on both dorsal and ventral leaf surfaces. Otherwise, it could be confused with *Lophocolea caledonica* with which it shares size, colour, leaf and underleaf shapes, but the latter has both leaf surfaces smooth, the spinose papillae being restricted to the perianth surface, and leaf cells with conspicuous medium trigones vs trigones lacking or very small in the former. The single reference specimen reported from New Caledonia (Hürlimann 1998) could be checked thanks to photos and observations from Heike Hofmann (Z+Zt). According to the original diagnosis (Lehmann 1829) and further descriptions (Fulford 1976; Engel 2010), the organisation and morphology of the gametangia are characteristic of the genus *Lophocolea*.

Lophocolea savesiana Steph.
(Fig. 28)

Species Hepaticarum 3: 122 (Stephani 1906). — *Chiloscyphus savesianus* (Steph.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 422 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. *Savès s.n.* (lecto-, here designated, *fide* Kitagawa 1969 in sched. G[Nouméa, 1887, *Savès s.n.*, G00061342]!).

Distribution in New Caledonia. — Only known from the type ("Nouméa").

Total range. — Endemic.

Description
Dioecious.

Habit
Medium plants with shoots 2.50 mm wide when flattened; leaves imbricate, ⅓ overlapping, horizontally spreading at right angle, slightly convex, alternate but slightly so, seeming subopposite, dorsally free, dorsal insertion separated by four cell rows.

Leaves
Oblong to trapezoid, margins nearly parallel below middle then width progressively decreasing in upper part or ventral margin nearly orthogonal to the stem and dorsal margin oblique, 1.00-1.20 mm long, 0.60-0.90 mm wide near base, 0.35-0.45 below apex, leaf apices truncate, flat to slightly concave with a single tooth at both angles, acute, (1-)3(-4) cells long, leaf margins entire.

Cells
Hexagonal, (25-)30-40 µm, thin-walled, without trigones.

Underleaves
Small, as wide as stems, narrowly connate to both nearest leaves, connation 1-3 cells wide, insertion in an inverted U, apices deeply bifid with lunate sinus, discs arched, narrow, usually two cells high, nine cells wide, lobes linear lanceolate, each lateral margins with a single short to filiform tooth.

Gametangia
Male and female gametangia set at apices of main shoots or long branches with normal leaves; gynoecia with two pairs of bracts, bract shapes like the normal leaves but larger, 1.8 mm long, ventral margins with one tooth, bracteoles oblong, margins toothed with 3-4 strong teeth in upper part; perianths oblong, cupulate at base, trigone in upper part, not winged, mouth shallowly 3-lobed, the lobes strongly toothed, acute teeth triangular to lanceolate; androecia with up to eight pairs of bracts.

Comments
The type specimen at G is copiously fertile with both kinds of gametangia and the dioecious condition is likely since no connection between the male and female shoots could be noted. Superficial view could lead to assign this species to the genus *Heteroscyphus* considering the shape and nearly subopposite insertion of the leaves and it may be closer to *Heteroscyphus etesseanus* which has similar leaves, underleaves and cells, but the gametoecia locations and shapes separate them as well as some vegetative characters, *H. etesseanus* having smaller size, with shoots 1.50 mm wide when flattened, and leaves contiguous to distant. *Lophocolea savesiana* has gametangia as in *Lophocolea*, set at the end of long normal-leaved shoots, oblong perianths that are conspicuously trigonous in upper part, and androecial bracts smaller than normal leaves, in series of 8 pairs. The species may be compared with *L. convexula*, but the latter is smaller with ovate leaves that are strongly narrowed to the apex, and with bulging leaf cells making the leaf margins crenulate. The species also resembles *Heteroscyphus parapilistipulus* but the latter species is a larger plant with shoots up to 4.5 mm wide, leaves rather oval and gynoecia and androecia on short leafless lateral branches.

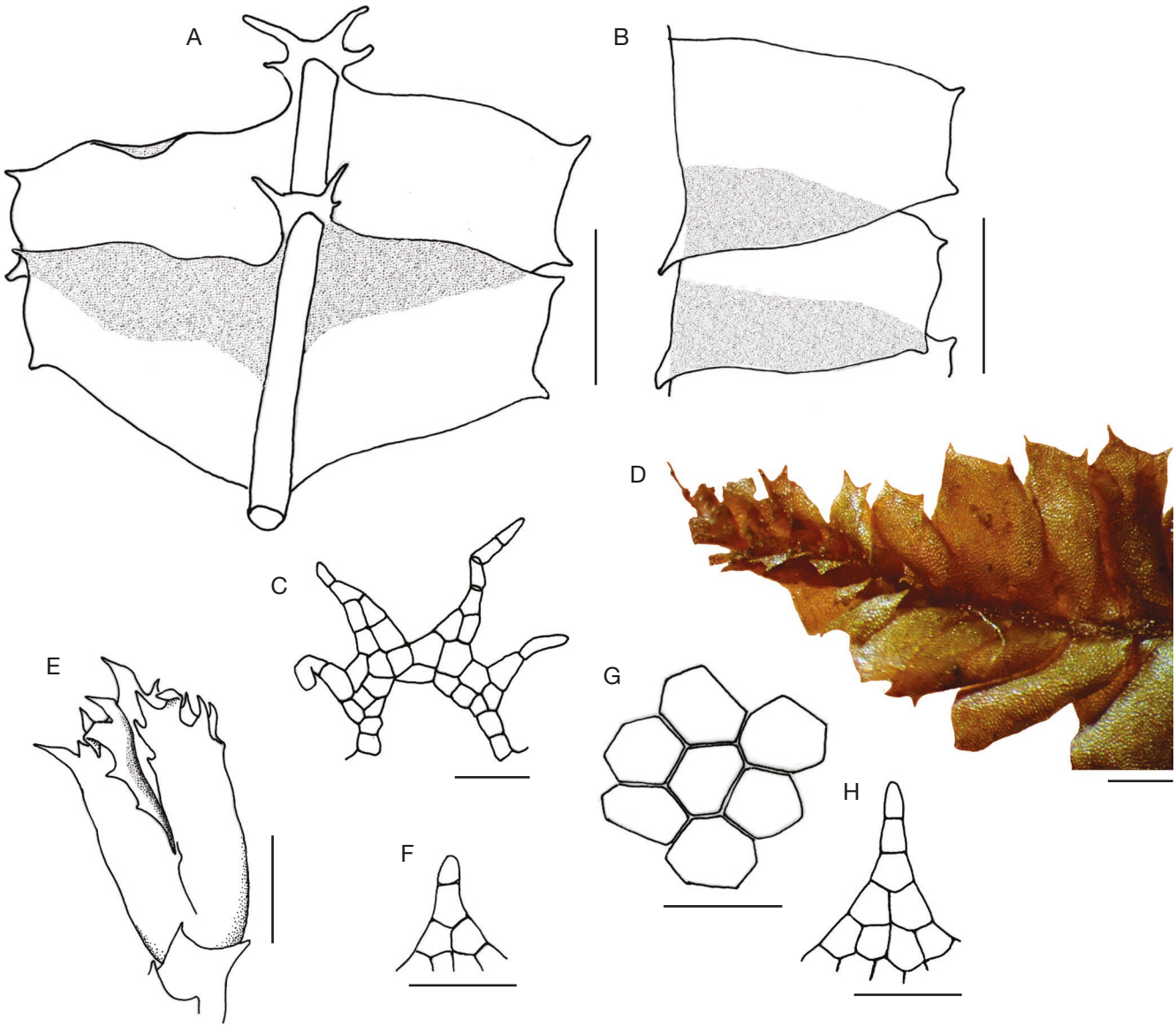

Fig. 28. — *Lophocolea savesiana* Steph.: **A**, shoot portion, ventral view; **B**, adjacent leaves, dorsal view; **C**, underleaves; **D**, top part of a male shoot, dorsal view; **E**, perianth; **F**, **H**, teeth at leaf apex angles; **G**, median cells. All illustrated from the lectotype (G00061342). Scale bars: A, B, D, E, 500 µm; G, 50 µm; C, F, H, 100 µm.

Genus *Otoscyphus* J.J.Engel, Bardat & Thouvenot

Otoscyphus crassicaulis (Steph.) J.J.Engel, Bardat & Thouvenot (Fig. 29)

Cryptogamie, Bryologie 33 (3): 280 (Engel *et al.* 2012). — *Lophocolea crassicaulis* Steph., *Species Hepaticarum* 6: 268 (Stephani 1922). — *Chiloscyphus crassicaulis* (Steph.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 413 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. *Franc s.n.* (lecto-, G[Mt. Mou, 1200 m, 17.VII.1909, *Franc s.n.*, G00017607]!).

Further specimens examined. — **New Caledonia**. South Province, Dumbéa, Montagne des Sources strict nature reserve, on dead wood in mountain wet forest with *Araucaria rulei*, 950 m, 21.IX.2016, *Thouvenot NC1992*; Païta, Mt. Humboldt, on peridotite rocks in mountain scrubland with *Araucaria humboldtensis*, 1400 m, 1.X.2008, *Thouvenot NC1730*; Mt. Ouin, on dead wood in mountain wet forest, 1000-1025 m, 19.IX.2016, *Thouvenot NC2098*; Dzumac massif, on dead wood in mesophilous mountain forest, 915 m, 18.IX.2008, *Thouvenot NC486*; Yaté, base of Pic du Grand Kaori, on peridotite rock, 250 m, 22.X.2012, *Thouvenot NC736*; Wé Toa, on dead wood, in rain forest, 500 m, 8.IX.2019, *Thouvenot NC2872* (PC[PC0779846]); Mont Dore, Mouirange, on dead wood in *Nothofagus* rain forest, 546 m, 16.IX.2019, *Thouvenot NC2883*.

Distribution in New Caledonia. — Fairly frequent on dead hard wood, more rarely on rocks, in various woodland habitats on ultramafic soils, from lowland photo-xerophytic forests to wet mountain forests or scrublands, at all altitudes (collected from 250 to 1400 m).

Total range. — Endemic to the southern ultramafic massif of New Caledonia, South Province.

Description

Further description and illustration in Engel *et al.* (2012).

Dioecious.

Habit
Plants delicate, shoots up to 0.6-1.0 mm wide; branching occasional, exclusively of ventral-intercalary type, *Frullania*-type branches rare; stems zig-zag in growth, markedly narrow for shoot size; leaves alternate, with basal sector vertically dorsally assurgent and defining an adaxial concavity, the leaf then strongly convex-arched, in cross section forming a ± inverted U or, with further curvature of the lobes, even a semicircle; at the base, the vertical sectors of opposing leaves fused.

Leaves
0.37-0.38 (0.40) mm long, bilobed, each leaf with dorsal base abruptly and strongly dilated resulting in a conspicuous flange of tissue extending towards shoot base at least to the level of the median sector of the leaf immediately below; leaves with a pronounced adaxial concavity toward base that is totally covered by the gently convex decurrent flange of tissue, the concavity pocket-like; the exposed, main portion of the leaf convex, narrowly elongate sub-rectangular, the sides from the base to lobe tip gently incurved, the leaves bifid to 0.40-0.45 of leaf length; lobes subparallel to ± divergent, subequal in size, long ciliform-setaceous; leaf disc 15-17 cells wide at base, the median sector 4-6 cells wide, the dorsal margin plane, entire, the ventral margin plane, with a conspicuous tooth near the base, this tooth asymmetrical, curved towards the stem and forming an orbicular mouth-like opening for the pocket-like leaf base.

Cells
Median leaf cells 25-30 µm wide, 35-50 µm long; cells of the exposed main portion of the leaf with massive trigones that are confluent or separated by narrow thin-walled places; cells in basal 4-5 rows of cells and flange with trigones minute to small; marginal cells with exposed wall notably thick; surface of disc finely striate, of lobes finely papillose.

Underleaves
Free, distant, the stem broadly exposed; disc a little wider than stem but with lobes laterally extending at least to level of sinus bases of the adjacent leaves; disc cunate, bifid nearly to base, small, with a distal row of 2-3 larger cells with the exposed wall distinctly thickened, basal to this row is a feebly dome-like cluster of *c*. 8 smaller, quadrate, rhizoid initials, the summit of disc truncate or (often) broadly rounded, entire, the lateral margins entire or at times with a 1-2-celled tooth, the disc margins decurrent; lobes diverging by an angle of *c*. 180° or nearly so, the line formed by lobes and disc apex maximally lunate to straight, the lobe shape much like those of the leaves but comprised of 1-3 biseriate tiers and a uniseriate row of 3-6 cells, the lobe margins uniformly entire.

Gametangia
Androecia terminal but becoming intercalary in position on main shoot or rather long ventral-intercalary branches, somewhat narrower than sterile sectors; bracts in 2-4 pairs, dorsally assurgent, densely imbricate, strongly ventricose in basal ± 0.5, the bracts deeply bilobed, the lobes similar to those of the leaves except shorter; antheridia solitary, the stalk not seen; gynoecia terminal on main shoot, or on short ventral-intercalary branches lacking normal vegetative leaves; bracts bifid to ± 0.35-0.5, the dorsal lobe smaller or reduced to a small rounded projection; bracteoles of innermost series somewhat smaller than bracts, symetrically bifid to ± 0.25-0.5; perianths long exserted, 1.7-2.2 mm long, subterete toward base, obscurely trigonous above, oblong-elliptic, not or slightly narrowed toward the deeply 3-lobed mouth, the lobes subequal, free for ± 0.30-0.35 the perianth length; lobes deeply bifid with several often long ciliiform processes; keelar wings common, 1-2 per perianth; calyptra extending ± 0.4 the perianth length.

Comments
This small species is easily separated from all other New Caledonian liverworts by the combination of the following characters: 1) leaves rectangular with apices deeply bifid, lobes long linear; 2) dorsal leaf margins widely expanded, forming a pouch together with the underlying ventral margins of the adjacent leaves; 3) underleaves transversely elongate, bifid, with sinus at a flat angle and long linear lobes widely spreading, lateral margins very short, entire; 4) stems thin; and 5) branching nearly exclusively ventral-intercalary. As discussed by Engel *et al*. (2012), this species is close to *Chiloscyphus* but differs from that genus by the above-mentioned set of morphological traits. Notably, the underleaves of *Otoscyphus crassicaulis* are very unusual and resemble those found in *Drepanolejeunea* and *Leptolejeunea* (Lejeuneaceae), while the pouches made of superimposed bases of leaves are unique in liverworts.

Following Engel *et al*. (2012), who described the type at G, the lectotype is formally designed here. The relationships of the genus *Otoscyphus* are unclear and await molecular study (Söderström *et al*. 2013a).

Incertae sedis

Genus *Chiloscyphus* Corda

Chiloscyphus longifissus Steph.
(Fig. 30)

Species Hepaticarum 6: 310 (Stephani 1922). — Type: **New Caledonia**. *Franc s.n.* (lecto-, here designated, G[env. de Tao, 100 m, I.1910, *Franc s.n.*, hb. Thériot 225, G00069456]!; isolecto-, PC[PC0101940]!).

Chiloscyphus longifissus Steph. ex Paris, *Revue bryologique* 37: 129 (Paris 1910), nom. inval. (no description). — Reference specimen: **New Caledonia**. "In jugo Dogny (1050 m)", VII.1909, *L. Le Rat s.n.* (REN[herb. E. G. Paris]!; duplicate, PC[PC0103808]!) **syn. nov.**

Chiloscyphus beesleyanus Pearson, *Journal of the Linnean Society, Botany* 46: 22 (Pearson 1922). — Type: **New Caledonia**. Ignambi, on rocks by creek, 3000 ft., *Compton 1530* (holo-, BM[BM013409500]!) **syn. nov.**

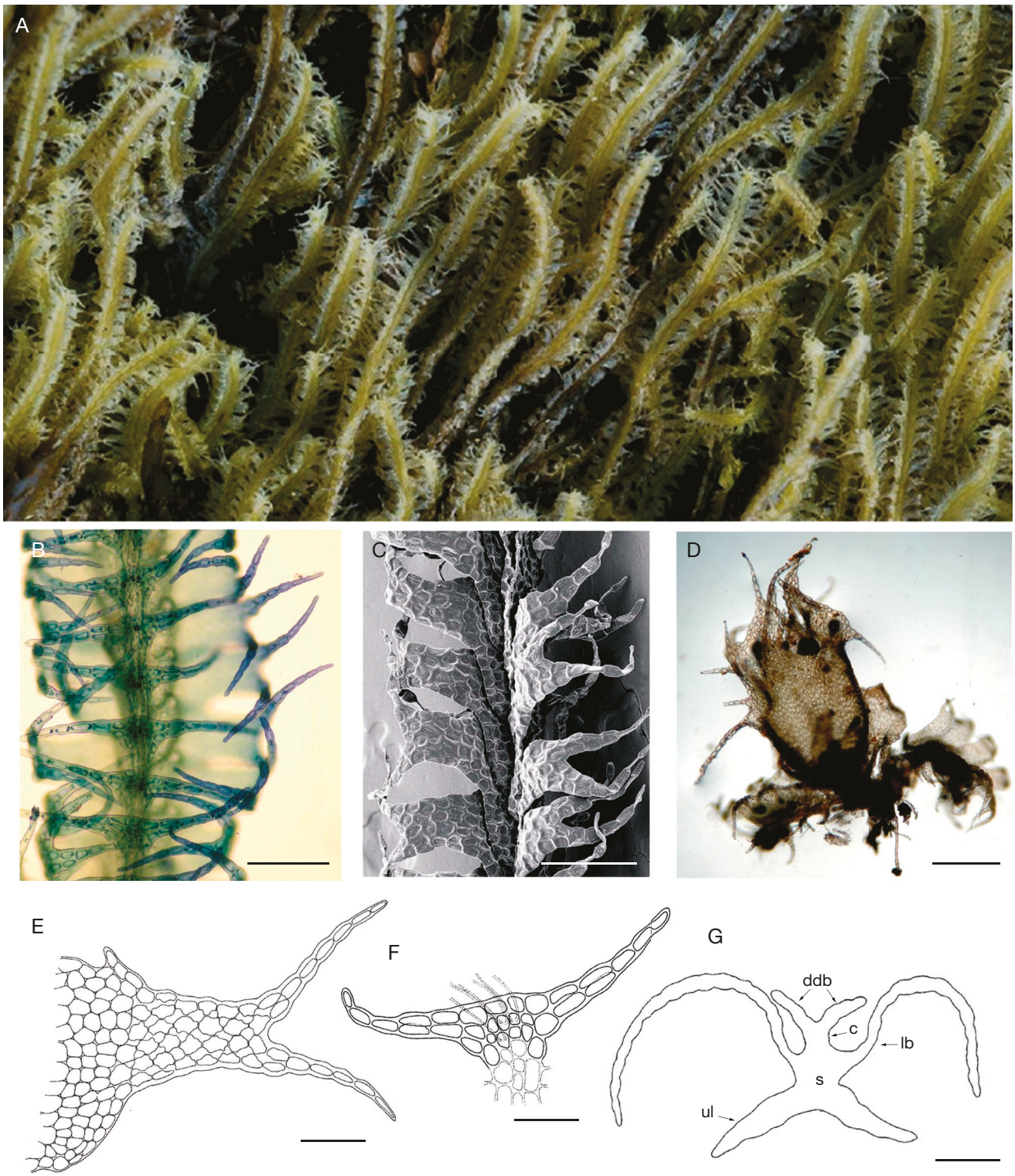

Fig. 29. — *Otoscyphus crassicaulis* (Steph.) J.J.Engel, Bardat & Thouvenot: **A**, habit; **B**, shoot portion, ventral view; **C**, shoot portion, dorsal view showing dilated dorsal leaf bases overlapping the previous leaf ventral bases (SEM); **D**, gynoecium; **E**, leaf; **F**, underleaf; **G**, shoot cross section showing connation (**c**) of dilated dorsal leaf bases (**ddb**), the concave sector of leaf base (**lb**), the stem (**s**) and the underleaf (**ul**). All illustrated from the specimen *Thouvenot NC486* (photos J. Bardat, drawings J.J. Engel). Scale bars: B, C, 200 µm; D, 500 µm; E-G, 100 µm.

Distribution in New Caledonia. — Scattered in North and South Provinces, in wet forest from 100 to 1200 m, rarely collected.

Total range. — Endemic.

Further specimens examined. — **New Caledonia**. North Province, "inter Panié et Hienghène", II.1910, *Le Rat s.n.* (REN); South Province, "in jugo Dogny (1050 m)", VII.1909, *L. Le Rat s.n.* (REN); North Province, Tao, forest, 600-800 m, I.1910, *Franc s.n.* as "*Lophocolea*

latistipula" (PC[PC0102424]); South Province, Pic des Mousses, Mt. Mou, 1200 m, 28.VIII.1950, *Baumann-Bodenheim 5704* (GOET); South Province, "Inter Farino et Table Unio", VII.1909, *Le Rat s.n.* as "*Chiloscyphus Le Rati*" Steph. nom. herb. (REN).

Description

Habit

Plants large, with shoots up to 6.00 mm wide; leaves spreading, subopposite to moderately staggered, dorsally free.

Leaves

Oval-oblong to trapezoid, sizes uneven in successive segments of a same shoot, 1.50-3.00 mm long, 1.00-1.50 mm wide near the base; leaf apex *c.* ½ the base width, truncate to widely concave, with a single tooth at both angles, teeth short and acute, margins otherwise entire.

Cells

Hexagonal, 40-80 µm with strong trigones bulging to truncate.

Underleaves

Asymmetrically connate to the adjacent leaves, one side narrowly connate, the opposite side connate or narrowly decurrent onto the respective leaf, underleaves widest than long, deeply bifid, ½-¾ the whole length at stem insertion, sinus lunate to acute, lobes triangular acuminate, spreading at right to obtuse angle from each other, discs transversely elongate, lateral margins with 1-2 sharp teeth.

Gametangia

Androecia in sets of up to nine pairs of bracts, terminal or intercalary on main shoots or on long leafy branches; gynoecia not seen.

Comments

Gametangia are lacking in the type specimen at G which seems sterile even though Stephani underlines the presence of androecia ("*androecia parva cauligena*…"). The isolectotype in PC, however, contains several male shoots with series of bracts terminal or intercalary. Therefore, the genus *Chiloscyphus* might be appropriate if the shape of the bracts would not be so different from the leaves, as in the genus *Lophocolea*, and the subopposite leaves ventrally connate to the underleaves which are conspicuously wider than the stem, reminiscent of *Heteroscyphus*. The combination of these features is more consistent with *Cryptolophocolea*, as defined in Söderström *et al.* (2013a) but the lack of gynoecium and the impossibility of checking the thickness of antheridia stalks prevent allocation to a genus and it is necessary to keep the current name pending the availability of fertile female material.

On the other hand, original specimens collected by Le Rat are kept in the herbarium of E. G. Paris (REN) and can be reference vouchers for *Chiloscyphus longifissus* Steph. ex Paris. The duplicate seen at PC was previously misidentified as *Heteroscyphus grandiflorus* so that *Chiloscyphus longifissus* Steph. ex Paris was said a synonym of the latter in the checklist (Thouvenot *et al.* 2011). Both REN specimens and their duplicate at PC were checked again and confirmed to be identical to *Chiloscyphus longifissus* Steph. During the examination of the samples present in the three herbariums, the author found some more misidentifications. Some specimens of *C. longifissus*, collected by Franc in Tao in January 1910, likely part of the type material, were labelled *Lophocolea latistipula* Steph., and one of them kept in G as a type of the latter (G00112472), with a duplicate in PC (PC0102424) (see comments under *Heteroscyphus coalitus*).

The checked type of *Chiloscyphus beesleyana* is not different from the type of *C. longifissus*.

Species transferred to other families

Family Acrobolbaceae E.A.Hodgs.

Genus *Conoscyphus* Mitt.

Conoscyphus trapezioides

(Sande Lac.) Mitt. ex Schiffn.

Conspectus Hepaticarum Archipelagi Indici 125 (Schiffner 1898). — *Chiloscyphus trapezoides* Sande-Lac., *Nederlandsch Kruidkundig Archief. Verslangen en Mededelingen der Nederlandsche Botanische Vereeniging* 3: 417 (Sande Lacoste 1855). — Type: **Java**. s. dat., *Junghuhn s.n.*, not seen.

Specimen examined. — **New Caledonia**. South Province, near Sunshine Mine, on trunk in rain forest, 700 m, 15.III.1951, *Hürlimann 2426* (G).

Distribution in New Caledonia. — Known from a few collections in South Province where it grows on barks in rain forests (collected from 700 to 950 m).

Total range. — Paleotropical: Africa, Indomalaya, Melanesia, South Pacific.

Description and illustrations

See Piippo (1985).

Genus *Goebelobryum* Grolle

Goebelobryum unguiculatum

(Hook.f. & Taylor) Grolle

Journal of the Hattori Botanical Laboratory 25: 137 (Grolle 1962). — *Jungermannia unguiculata* Hook.f. & Taylor, *London Journal of Botany* 5: 279 (Taylor 1846). — Type: **New Zealand**. *Hooker 258* (FH), not seen.

Lophocolea purpurea Steph., *Species Hepaticarum* 6: 289 (Stephani 1922). — *Chiloscyphus novae-caledoniae* J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 419 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. "*Lerat*" *s.n.* (lecto-, here designated, G["In jugo Dogny (1040 m)", *L. Le Rat 211 bis*, "General Paris misit", G00112486]!; isolecto-, PC[PC0102405]!; REN[herb. E. G. Paris]!) **syn. nov.**

Further specimen examined. — **New Caledonia**. South Province, Mt. Mou, on shady bare soil in trail side across shrubland in ultramafic massif, 750-850 m, 17.IX.2016, *Thouvenot NC2105*; "in jugo Dogny (1050 m), Catene centralis", VII.1909, *L. Le Rat s.n.* as "*Lophocolea defectistipula*" (REN[herb. E. G. Paris]).

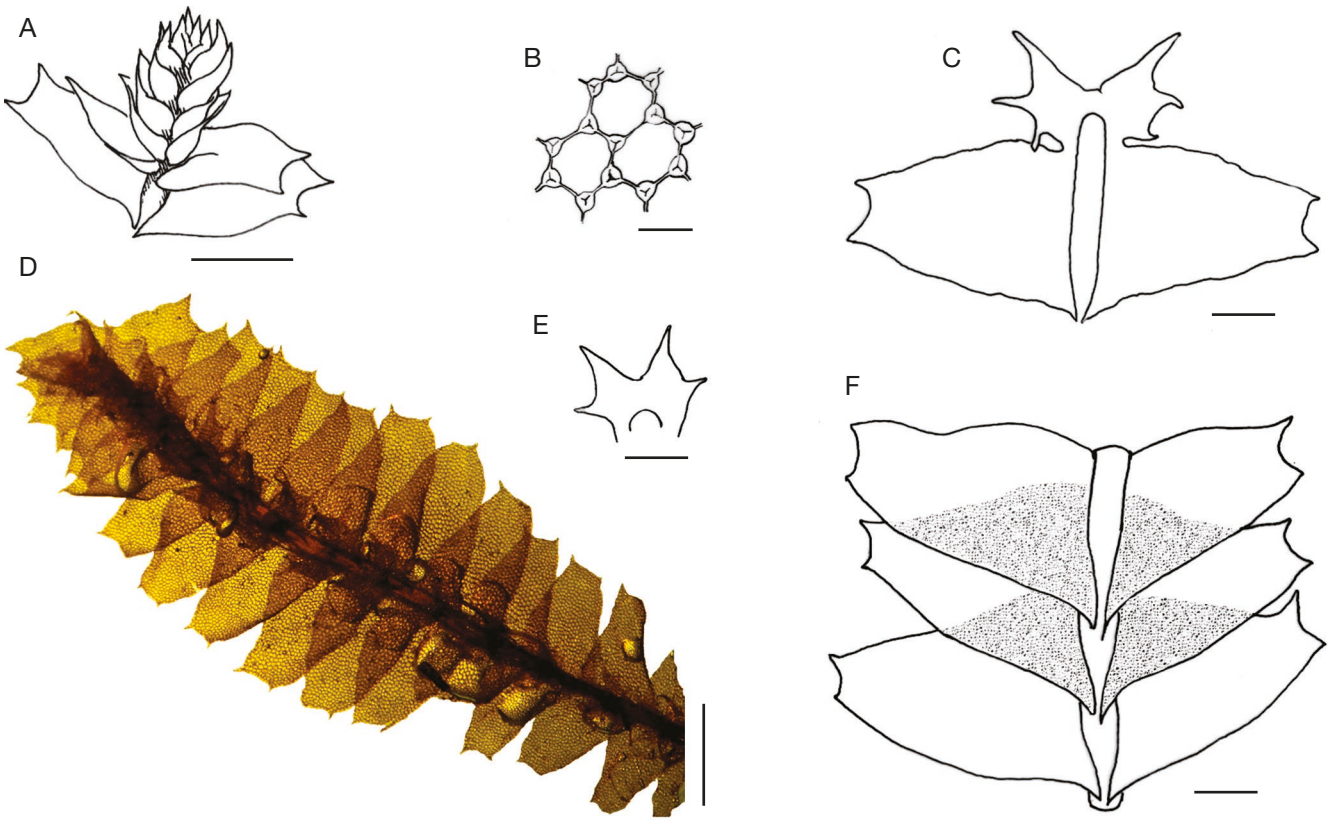

Fig. 30. — *Chiloscyphus longifissus* Steph.: **A**, male shoot end with androecium, dorsal view; **B**, leaf cells; **C**, **D**, shoot portions, ventral view; **E**, underleaf; **F**, shoot portion, dorsal view. **A**, **D**, **F**, from the isotype (PC0101940); **B**, **C**, **E**, from the lectotype (G00069456). Scale bars: A, D, 1 mm; B, 50 µm; C, E, F, 0.5 mm.

Distribution in New Caledonia. — *Goebelobryum unguiculatum* is known from a few collections in both provinces where it grows on bare soils in mountain shrublands and forests (collection data from 700 to 1000 m).

Total range. — Australasia.

Description

Based on the type material of *Lophocolea purpurea*. Further descriptions and illustrations in Grolle (1962), Engel & Glenny (2012).

Habit

Plant medium sized, light green and purple tinged to wine-red coloured, blackish in older parts, shoots 3.00 mm wide, stem relatively thick, 0.30 mm wide; leaves alternate, dorsally assurgent-convex, spreading at right angle when flattened, dorsally free; rhizoids thin, hyaline, dense, obscuring the ventral face of the stems and the underleaves, inserted on bulging rhizoidal plates at the bases of the underleaves and leaf ventral margins.

Leaves

1.40-2.00 mm long, 1.50-2.50 mm wide, rounded to reniform, apices somewhat angular or emarginate, margins long ciliate, more distantly on the lower parts, with up to 10 rigid whitish cilia, made of 4-5 elongate, uniseriate, thick-walled cells.

Cells

Leaf cells large, 40-80 µm wide, cell walls thin, red tinged as well as the medium globose trigones, external wall of marginal cells thicker.

Underleaves

Very small to vestigial, associated with a large bulging rhizoidal plate, underleaves not connected to the leaves, at most 80-160 µm long, 80-120 µm wide, narrower than the stem, sometimes inconspicuous, reduced to a few cells, when developed bifid, with two short lobes erect linear, up to three cells long, separated by a "v" shaped sinus; the lamina null or, at most, small rectangular, 3-4 cells long or wide, lateral margins with a single small unicellular tooth if any.

Marsupium

Developed at the arched end of some shoots, long cylindrical, hidden in the substrate; gynoecia and androecia not seen.

Comments

The type specimen of *Lophocolea purpurea* seen by Stephani was sterile so that he missed the marsupium-bearing condition of this species and, although the specimen exhibits vegetative characters unusual in the family Lophocoleaceae, namely the small or vestigial underleaves, Stephani described it as *Lophocolea purpurea*. Later, when Engel & Schuster (1984) downgraded *Lophocolea* to a subgenus of *Chiloscyphus*, they

replaced this name by *Chiloscyphus novae-caledoniae* (the blocking name *Chiloscyphus purpureus* Steph. is from South America), likely without reviewing the type. There is a part of the original type material sent to Stephani in the herbarium of E. G. Paris (REN). This specimen has some shoots with marsupia so that it belongs to *Goebelobryum*. *Goebelobryum unguiculatum* was already known from New Caledonia (Thouvenot *et al*. 2011).

The checklist of the liverworts of New Caledonia (Thouvenot *et al*. 2011) mentions a doubtful record of *Plagiochila blepharophora* (Nees) Lindenb., according to a specimen reported by Paris (1910) under the name *Lophocolea defectistipula* Steph. The relevant specimen at REN has been checked and has proven to be a poorly coloured *Lophocolea purpurea*. Therefore, *Plagiochila blepharophora* must be removed from the New Caledonian bryophyte flora.

Family Brevianthaceae J.J.Engel & R.M.Schust.
Genus *Tetracymbaliella* Grolle

Tetracymbaliella comptonii (Pearson) Grolle

Revue bryologique et lichénologique 32: 164 (Grolle 1963). — *Chiloscyphus comptonii* Pearson, *Journal of the Linnean Society, Botany* 46: 23 (Pearson 1922). — *Heteroscyphus comptonii* (Pearson) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 402 (Engel & Schuster 1984 [1985]). — Type: **New Caledonia**. *Pearson 740*, not seen.

Tetracymbaliella ratiana Grolle, *Nova Hedwigia* 3: 51-52 (Grolle 1961). — *Chiloscyphus grossitextus* Steph. ex Paris, nom. inval. — Type: **New Caledonia**. Pic des Sources, *Le Rat s.n.* (holo-, M[*fide* Grolle 1961]; iso-, REN["*Chiloscyphus grossitextus*, Nov. Caledon. Pic des Sources", VII.1909, *Le Rat s.n.*, herb. E. G. Paris]!).

Further specimens examined. — **New Caledonia**. South Province, Yaté, Wé Toa, on dead wood in wet forest in ultramafic massif, 500 m, 8.IX.2019, *Thouvenot NC2857*; Mt. Mou, VII.1909, *Le Rat s.n.* as "*Chiloscyphus cymbaliferus*" (REN); Mt. Dzumac, "ad arbores in silvat., 1000 m alt", VII.1905, *Le Rat s.n.* (REN).

Distribution in New Caledonia. — Scattered in South Province where it grows on dead wood in rain forest at medium elevations (collected from 500 to 1000 m).

Total range. — Endemic.

Description and illustration
Grolle (1961) as *Tetracymbaliella ratiana*.

Comments
This species is very distinctive by the conspicuous pouches on leaf and underleaf margins. This character is shared with *Tetracymbaliella cymbalifera* (New Zealand) that might introduce some misidentification (see below). *T. ratiana* is distinguished from the latter by: 1) larger trigones almost as wide as the cell lumina; 2) pouches longer than wide; 3) dorsal leaf margins not connivent; and 4) leaf cells strongly mammillose.

Tetracymbaliella decipiens (Gottsche) Grolle

Nova Hedwigia 3: 49-50 (Grolle 1961). — *Chiloscyphus decipiens* Gottsche, *Synopsis Hepaticarum*: 176 (Gottsche *et al*. 1845). — *Heteroscyphus decipiens* J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 402 (Engel & Schuster 1984 [1985]). — Type: **New Zealand**. Menzies, not seen.

Comments
The only New Caledonian report of this species, otherwise known as endemic to New Zealand, was by Furuki & Higuchi (1996). It was impossible to check the sample the record was based on and its presence in New Caledonia needs confirmation.

Taxa excluded from the New Caledonian bryophyte flora

Genus *Cryptolophocolea* L.Söderstr.

Cryptolophocolea levieri (Schiffn.) L.Söderstr.

Phytotaxa 112: 21 (Söderström 2013b). — *Lophocolea levieri* Schiffn., *Die Hepaticae der Flora von Buitenzorg* 182 (Schiffner 1900). — *Chiloscyphus paroicus* J.J.Engel & R.M.Schust., Nova Hedwigia 39: 420 (Engel & Schuster 1984 [1985]). — Type: **Indonesia**. *Schiffner 1207-1210* (isosyn-, PC[PC0102563]!).

Further specimens examined. — **Java**. Preanger province, Tjiburrum near Tjibodas, in primary cloud forest, 1575 m, 28.IV.1894, *Schiffner 1207* as *Lophocolea levieri* (PC[PC0102563]).
New Caledonia. Mts. Koghis, 21.IV.1914, *Compton 801* as *Lophocolea levieri* (BM[BM013409501, BM013409504]); Mt. Mou, on stone and mud in stream, 8.III.1914, *Compton 444* as *Lophocolea levieri* (BM[BM013409502]).

Comments
This species was reported from New Caledonia by Pearson (1922) as *Lophocolea levieri* and included as *Chiloscyphus paroicus* in the checklist (Thouvenot *et al*. 2011). The description given by Pearson does not match the original diagnosis of *L. levieri* (Schiffner 1900) in the following features: 1) entire leaf margins; and 2) deeply bilobed underleaves, free or narrowly connate on a single side, with a single tooth on each lateral margin. Furthermore, Pearson stated that his specimen was close to *Lophocolea heterophylla* (Schrad.) Dumort. The three checked parts of the Compton collection named by Pearson as *L. levieri* (BM) turned to be *Lophocolea convexula*, which fits Pearson's remarks on the likeness to *L. heterophylla*. Therefore, *Cryptolophocolea levieri* (as *Chiloscyphus paroicus*) must be removed from the bryophyte flora of New Caledonia.

Genus *Heteroscyphus* Schiffn.

Heteroscyphus hebridensis (Steph.) Schiffn.

Oesterreichische Botanische Zeitschrift 60: 172 (Schiffner 1910). — *Chiloscyphus hebridensis* Steph., *Hedwigia* 32: 323 (Stephani 1893). — Type: **Vanuatu**. "Novae Hebridae", comm. K.Müller, Hal. (G[G00283079, G00283073, G00069477]!).

Further specimens examined. — **New Caledonia**. South Province, Mts. Koghis, 1.XI.1909, *Franc s.n.* (G[G005125], PC[PC0167675]).

Comments

Unpublished specimens labelled "*Chiloscyphus hebridensis*, from Mts. Koghis, *Franc s.n.*, 1/11/1909, determinavit Stephani", have been found at PC and G, and turned to be *Heteroscyphus asellifomis*. The features distinctive from *H. hebridensis* are: 1) leaves rounded with margins dorsally confluent vs widely triangular-ovate and dorsally free; 2) underleaf margins toothed vs deeply laciniate; and 3) leaf cells with large trigones vs minute trigones. The presence of this species in New Caledonia remains unconfirmed.

Heteroscyphus jackii (Steph.) Schiffn.

Oesterreichische Botanische Zeitschrift 60: 172 (Schiffner 1910). — *Chiloscyphus jackii* Steph., *Botanisches Centralblatt.* 60: 102 (Jack & Stephani 1894). — Type: **Samoa**. *Graeffe 1636* (G[G00069467]!).

Further specimens examined. — **New Caledonia**. North Province, Mt. Dzumac, IV.1907, *Le Rat s.n.* (REN); "sine schedule", 1907, *Le Rat s.n.* (G).

Comments

Hürlimann (1998) mentions New Caledonia as part of the range of this species, likely following Paris (1908) who reports a specimen of *Chiloscyphus jackii* Steph. collected by Le Rat, also reported by Miller *et al.* (1983). In G, only one specimen collected in New Caledonia by Le Rat is labelled *Chiloscyphus jackii* by Stephani. This specimen turned to be *Heteroscyphus argutus*. In the herbarium of E. G. Paris (REN), a duplicate of the original sent to Stephani has the same misidentification. All the Hürlimann's specimens in G are from Tonga. As the only voucher from New Caledonia is not this species, *Heteroscyphus jackii* must be removed from the New Caledonian flora.

Genus *Leptoscyphus* Mitt.

Leptoscyphus physanthus (Hook.f. & Taylor) J.J.Engel

Nova Hedwigia 99: 168 (Engel 2014). — *Jungermannia physantha* Hook.f. & Taylor, *London Journal of Botany* 3: 561 (1844). — *Heteroscyphus physanthus* (Hook.f. & Taylor) R.M.Schust., *The Hepaticae and Anthocerotae of North America* 4: 248 (1980). — Type: **New Zealand**. Not seen.

Specimen examined. — **New Caledonia**. South Province, Rivière Bleue valley, on dead wood in forest, 160 m, 15.V.1970, *Schmid 148* as "*Chiloscyphus physanthus*" (PC[PC0146342]).

Comments

Heteroscyphus physanthus (Hook.f. & Taylor) R.M.Schust. is reported as doubtful record in Thouvenot *et al.* (2011). The only report in New Caledonia of this species, regarded as endemic to New Zealand, was from Tixier (1972) as *Chiloscyphus physanthus* Taylor. The relevant voucher in the Muséum national d'Histoire naturelle of Paris (PC[PC0146342]) turned out to be *Heteroscyphus deplanchei* (as *H. heteromorphis*). Therefore, this species must be removed from the New Caledonian flora.

Genus *Lophocolea* (Dumort.) Dumort.

Lophocolea autoica Steph.

Species Hepaticarum 6: 262 (Stephani 1922). — *Chiloscyphus autoicus* (Steph.) J.J.Engel & R.M.Schust., *Nova Hedwigia* 39: 411 (Engel & Schuster 1984 [1985]). — Type: **Haïti**. *Faurie s.n.*!

Further specimen examined. — **New Caledonia**. *Lerat s.n.* (G[G00128109]).

Comments

Stephani (1922) published *Lophocolea autoica* based on two syntypes, from Hawaï (Faurie) and New Caledonia (Lerat). The type specimen from Haïti in G matches the protologue well. The New Caledonian specimen, however, is *Lophocolea convexula*. Since this is the only mention of this species in New Caledonia, it must be removed from the bryophyte flora of the territory.

Genus *Plagiochila* (Dumort.) Dumort.

Plagiochila blepharophora (Nees) Lindenb.

Species Hepaticarum 2-4: 102 (Lindenberg 1840). — Type: **Java**. (G[G00115176]), not seen.

Lophocolea defectistipula Steph., *Species Hepaticarum* 3: 130 (Stephani 1906). — Type: **Caroline Islands**. *Parkinson s.n.* (G[G00061183]), not seen.

Specimen examined. — **New Caledonia**. South Province, "in jugo Dogny (1050 m), Catene centralis", VII.1909, *L. Le Rat s.n.* as "*Lophocolea defectistipula*" (REN[herb. E. G. Paris]).

Comments

Treated as doubtful record in Thouvenot *et al.* (2011), this species must be removed from the New Caledonian flora since the reference specimen turned to be *Goebelobryum unguiculatum* (see above).

Genus *Tetracymbaliella* Grolle

Tetracymbaliella cymbalifera (Hook.f. & Taylor) Grolle

Nova Hedwigia 3: 50 (Grolle 1961). — *Jungermannia cymbalifera* Hook.f. & Taylor, *Flora Antarctica* 1: 151 (Hooker 1845). — *Chiloscyphus cymbaliferus* (Hook.f. & Taylor) Gottsche, Lindenberg & Nees, *Synopsis Hepaticarum* 5: 711 (Gottsche *et al.* 1847). — Type: **New Zealand**. Auckland Islands, not seen.

Specimen examined. — **New Caledonia**. South Province, Mt. Mou, VII.1909, *Le Rat s.n.* as "*Chiloscyphus cymbaliferus*" (REN); Mt. Dzumac, "ad arbores in silvat., 1000 m alt", VII.1905, *Le Rat s.n.* as "*Chiloscyphus cymbaliferus*" (REN).

Comments

The only report of this species in New Caledonia is from E. G. Paris (1906, 1910) as *Chiloscyphus cymbaliferus*. The two specimens in his herbarium kept at Rennes University (REN) are not different from *Tetracymbaliella comptonii*. Therefore, *T. cymbalifera* must be removed from the New Caledonian flora.

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REFERENCES

Ah-Peng C. & Bardat J. 2005. — Checklist of the bryophytes of Reunion Island (France). *Tropical Bryology* 26 (1): 89-118. https://doi.org/10.11646/bde.26.1.14

Bonner C. E. B. 1963. — *Index Hepaticarum Pars IV.* Ceratolejeunea *to* Cystolejeunea. Weinheim, J. Cramer: 321-636.

Bonner C. E. B. 1966. — *Index Hepaticarum Pars VI.* Goebeliella *to* Jubula. Vaduz, J. Cramer: 481-793.

Chuah-Petiot M. S. 2011. — A checklist of Hepaticae and Anthocerotae of Malaysia. *Polish Botanical Journal* 56: 1-44.

Crandall-Stotler B., Stotler R. E. & Long D. G. 2009. — Phylogeny and classification of the Marchantiophyta. *Edimburg Journal of Botany* 66 (1): 155-198. https://doi.org/10.1017/S0960428609005393

Dimon R. J., Váňa J., Schäfer-Verwimp A., Heinrichs J. & Renner M. A. M. 2018. — *Conoscyphus* belongs to Acrobolbaceae (Jungermanniineae) not Lophocoleaceae (Lophocoleineae). *Australian Systematic Botany* 31 (3) 209-218. https://doi.org/10.1071/SB17041

Dumortier B. C. 1835. — *Recueil d'Observations sur les Jungermanniacées* 1. J.-A. Blanquart, Tournay, 27 p.

Engel J. J. 2010. — Austral Hepaticae 45. A monograph of the genus *Chiloscyphus* Corda (Lophocoleaceae) for Australasia. *Fieldiana: Botany* 48: 1-209. https://doi.org/10.3158/0015-0746-48.1.1

Engel J. J. 2013. — Studies on Lophocoleaceae XXII. New taxa and combinations in New Zealand *Heteroscyphus* Schiffn. *Polish Botanical Journal* 58 (1): 95-106. https://doi.org/10.2478/pbj-2013-0011

Engel J. J. 2014. — Studies on Lophocoleaceae XXIII. Novelties in *Heteroscyphus* Schiffn. together with refinements in *Cryptolophocolea* L.Söderstr., Crand.-Stotl., Stotler & Váňa and *Leptoscyphus* Mitt. *Nova Hedwigia* 99 (1-2): 157-170.

Engel J. J. 2015. — Studies on Lophocoleaceae. XXV. A conspectus of *Heteroscyphus* Schiffn. in temperate Australia together with nomenclatural changes in *Chiloscyphus* Corda and *Leptoscyphus* Mitt., refinements and a range extension of Clasmatocolea Spruce, and a range extension in Stolonivector J.J.Engel. *Nova Hedwigia* 100 (3-4): 553-582. https://doi.org/10.1127/nova_hedwigia/2015/0260

Engel J. J. & Glenny D. 2012. — Austral Hepaticae 48. *Goebelobryum* Grolle (Acrobobaceae). *Nova Hedwigia* 95 (3-4): 319-336. https://doi.org/10.1127/0029-5035/2012/0066

Engel J. J. & Glenny D. 2019. — A Flora of the liverworts and hornworts of New Zealand. Vol. 2. *Monographs in Systematic botany from the Missouri Botanical Garden* 134: 1-750.

Engel J. J. & He X. 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. *The Bryologist* 113 (1): 149-163. https://doi.org/10.1639/0007-2745-113.1.149

Engel J. J. & Schuster R. M. 1984 [1985]. — An overview and evaluation of the genera of *Geocalycaceae* subfamily Lophocoleoideae (Hepaticae). *Nova Hedwigia* 39: 385-463.

Engel J. J., Bardat J. & Thouvenot L. 2012. — Studies on Lophocoleaceae XXI. *Otoscyphus* J.J.Engel, Bardat & Thouvenot, a new liverwort genus from New Caledonia with an unusual morphology. *Cryptogamie, Bryologie* 33 (3): 279-289. https://doi.org/10.7872/cryb.v33.iss3.2012.279

Engel J. J., Thouvenot L. & Müller F. 2021. — Studies on Lophocoleaceae XXVIII. Two new and interesting species of *Heteroscyphus* Schiffn. (Marchantiophyta, Lophocoleaceae) from New Caledonia. *Nova Hedwigia* 113 (1-2): 61-73. https://doi.org/10.1127/nova_hedwigia/2021/0634

Fulford M. H. 1976. — Manual of the leafy hepaticae of Latin America, part IV. *Memoirs of the New York Botanical Garden* 11 (4): 395-535.

Furuki T. & Higuchi M. 1996. — Studies of oil bodies and oil droplets of some hepatics (Jungermanniales) from New Caledonia. *Bulletin of the National Science Museum, Tokyo, Series B, Botany* 22: 59-75.

Gbif. 2021. — Available from https://www.gbif.org/occurrence/search?q=Heteroscyphus%20succulentus.

Glenny D. 1998. — A revised checklist of New Zealand liverworts and hornworts. *Tuhinga* 10: 119-149.

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 (2): 93-105. https://doi.org/10.1179/174328209X427524

Gottsche C. M. 1853. — Muscorum hepaticorum species novae Javanenses. *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 4: 573-576.

Gottsche C. M., Lindenberg J. B. W. & Nees C. G. 1845. — *Synopsis Hepaticarum* 2. Meissner, Hamburg: 145-304.

Gottsche C. M., Lindenberg J. B. W. & Nees C. G. 1847. — *Synopsis Hepaticarum* 5. Meissner, Hamburg: 625-834.

Gradstein S. R. 2011. — *Guide to the Liverworts and Hornworts of Java*. Southeast Asian Regional Centre for Tropical Biology (SEAMEO BIOTROP), Bogor, 146 p.

Gradstein S. R. & Pinheiro da Costa D. 2003. — The Hepaticae and Anthocerotae of Brazil. *Memoirs of the New York Botanical Garden* 87: 1-316.

GROLLE R. 1961. — *Tetracymbaliella*, eine neue Lebermoosgattung. *Nova Hedwigia* 3: 47-53, tab. 33-35.
GROLLE R. 1962. — *Goebelobryum*, eine neue marsupiale Lebermoosgattung. *Journal of the Hattori Botanical Laboratory* 25: 135-144.
GROLLE R. 1963. — Notulae hepaticologicae VII-IX. *Revue bryologique et lichénologique* 32: 157-165.
GROLLE R. 1995. — The Hepaticae and Anthocerotae of the East African Islands. An annotated catalogue. *Bryophytorum Bibliotheca* 48: 1-178.
GROLLE R. & PIIPPO S. 1984. — Annotated catalogue of western Melanesian bryophytes. I. Hepaticae and Antocerotae. *Acta Botanica Fennica* 125: 1-86.
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 (5): 317-329.
HENTSCHEL J., WILSON R., BURGHARDT M., ZÜNDORF H.-J., SCHNEIDER H. & HEINRICHS J. 2006a. — Reinstatement of Lophocoleaceae (Jungermanniopsida) based on chloroplast gene *rbc*L data: exploring the importance of female involucres for the systematics of Jungermanniales. *Plant Systematics and Evolution* 258: 211-226. https://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* 262: 125-137. http://doi.org/10.1007/s00606-006-0463-4
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 (4): 1136-1142. https://doi.org/10.2307/25065908
HERZOG T. VON 1953. — Lebermoose aus Neukaledonien gesammelt von Dr. O.H. Selling. *Arkiv för Botanik* 3 (3): 43-61.
HOOKER W. J. 1820. — *Musci Exotici* 2. Longman et al., London, pl. 97-176 + 31 p.
HOOKER J. D. 1845. — *Flora Antarctica* 1. Reeve, London: [1]-208, pl. 1-80.
HÜRLIMANN H. 1998. — Hepaticae aus den Gebieten des südlichen Pazifik XIV. *Bauhinia* 12: 109-119.
JACK J. B. & STEPHANI F. 1894. — Hepaticae in insulis Vitiensibus et Samoanis a Dre Ed. Graeffe anno 1864 lectae. *Botanisches Centralblatt.* 43: 97-109.
JONES E. W. 1953. — African hepatics. V. Lophocolea, with notes on *Chiloscyphus* and *Leptoscyphus*. *Transactions of the British Bryological Society* 2: 172-202, figs 1-10. https://doi.org/10.1179/006813853804878038
KITAGAWA N. 1973. — Micellaneous notes on little-known species of hepaticae, 26-50. *Journal of the Hattori Botanical Laboratory* 37: 263-273.
LAI M.-J., ZHU R.-L. & CHANTANAORRAPINT S. 2008. — Liverworts and hornworts of Thailand: an updated checklist and bryofloristic accounts. *Annales Botanici Fennici* 45 (5): 321-341. https://doi.org/10.5735/085.045.0501
LEHMANN J. G. C. 1829. — Hepaticarum capensium a C.F. Ecklon collectarum. *Linnaea* 4: 357-371.
LEHMANN J. G. C. 1832. — *Novarum et Minus Cognitarum Stirpium Pugillus* 4. Meissneri, Hamburg, 64 p.
LINDENBERG J. B. W. 1840. — *Species Hepaticarum* 2-4. Henry & Cohen, Bonn: 37-120.
LINNAEUS C. VON. 1753. — *Species Plantarum* 2. Laurent Salvi, Stockholm: 561-1200.
LOISEAU P.-A., MAEDER A. & PRICE M. J. (TRAD.) 2019. — *Code international de nomenclature pour les Algues, les Champignons et les Plantes. (Code de Shenzhen) adopté par le dix-neuvième congrès international de botanique, Shenzhen, Chine, 2017*. Publication hors-série 19. Conservatoire et Jardin botaniques de la ville de Genève, 228 p. https://doi.org/10.5281/zenodo.2558315
MCCARTY P. M. 2006. — *Checklist of Australian liverworts and hornworts*. Australian Biological Ressources Study, Camberra. Available from http://www.anbg.gov.au/abrs/liverwortlist/liverworts_intro.html.
MILLER H. A. 1981. — Notulae Hepaticarum Polynesiae. *Phytologia* 47: 319-324. https://doi.org/10.5962/bhl.part.4461
MILLER H. A., WHITTIER H. O. & WHITTIER B. A. 1983. — Prodromus florae hepaticarum Polynesiae. Catalogue of hepaticae and anthocerotae. *Bryophytorum Bibliotheca* 25: 1-423.
MITTEN W. 1871. — Jungermanniae and Marchantiae, *in* SEEMANN B. (ed.), *Flora Vitiensis*. Lovell Reeve & Co, London: 404-419.
MORAT P. 2010. — Les botanistes récolteurs en Nouvelle-Calédonie de 1774 à 2005. *Adansonia* 32 (2): 159-216. https://doi.org/10.5252/a2010n2a1
NEES C. G. 1836. — *Naturgeschichte der europäischen Lebermoose*. Vol. 2. A. Rücker, Berlin, 499 p.
PARIS E. G. 1906. — Hépatiques de Nouvelle-Calédonie (1er article). *Revue bryologique* 33: 27-29.
PARIS E. G. 1908. — Hépatiques de la Nouvelle-Calédonie (2e article). *Revue bryologique* 35: 62.
PARIS E. G. 1910. — Hépatiques de la Nouvelle-Calédonie (3e article). *Revue bryologique* 37: 128-132.
PATON J. A. 1999. — *The liverwort flora of the British Isles*. Harley Books, Colchester, 626 p.
PATZAK S. D. F., RENNER M. A. M., SCHÄFER-VERWIMP A., FELDBERG K., HESLEWOOD M. M., PERALTA D. F., DE SOUZA A. M., SCHNEIDER H. & HEINRICHS J. 2016. — A phylogeny of Lophocoleaceae-Plagiochilaceae-Brevianthaceae and a revised classification of Plagiochilaceae. *Organisms, Diversity and Evolution* 16: 481-495. https://doi.org/10.1007/s13127-015-0258-y
PEARSON W. H. 1922. — A systematic account of the plants collected in New Caledonia and Isle of Pins by Mr R. H. Compton, M. A., in 1914. Part III. Cryptogams. *Journal of the Linnean Society, Botany* 46 (305): 13-96. https://doi.org/10.1111/j.1095-8339.1922.tb00474.x
PIIPPO S. 1985. — Bryophyte flora of the Huon Peninsula, Papua New Guinea. XII. Geocalycaceae (Hepaticae). *Acta Botanica Fennica* 131: 126-167.
PIIPPO S. 1992. — Bryophyte flora of the Huon Peninsula, Papua New Guinea. LI. Additions and corrections to the Geocalycaceae (Hepaticae). *Annales Botanici Fennici* 29: 243-248.
PIIPPO S. 1993. — On the taxonomy and nomenclature of SW Asiatic Geocalycaceae (Hepaticae). *Annales Botanici Fennici* 30: 195-203.
REINWARDT C. G. C., VON BLUME C. L. & NEES VON ESENBECK C. G. D. 1824. — Hepaticae Iavanicae. *Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum Exhibentia Ephemerides sive Observationes Historias et Experimenta* 12 (1): 181-238.
SANDE LACOSTE C. M. 1855. — Novae species hepaticaum ex insula Java detexit Dr. F. Junghuhn. *Nederlandsch Kruidkundig Archief. Verslangen en Mededelingen der Nederlandsche Botanische Vereeniging* 3 (4): 415-424.
SANDE LACOSTE C. M. 1864. — Hepaticae. Jungermanniae archipelagi indici. *Annales Musei Botanici Lugduno-Batavi* 1: 287-314.
SCHIFFNER V. F. 1898. — *Conspectus hepaticarum archipelagi indici*. Staatsdruckerei, Batavia, 382 p.
SCHIFFNER V. F. 1900. — *Die Hepaticae der Flora von Buitenzorg*. I. Band. E. J. Brill, Leiden, 220 p.
SCHIFFNER V. F. 1910. — Über die Gattungen *Chiloscyphus* und *Heteroscyphus* n. gen. *Oesterreichische Botanische Zeitschrift* 60 (5): 169-173.
SCHUSTER R. M. 1980. — *The Hepaticae and Anthocerotae of North America, east of the hundredth meridian*. Columbia University Press, New York, xviii + 1334 p.
SÖDERSTRÖM L., GRADSTEIN S. R. & HAGBORG A. 2010. — Checklist of the hornworts and liverworts of Java. *Phytotaxa* 9: 53-149.

https://doi.org/10.11646/phytotaxa.9.1.7
Söderström L., Hagborg A., Pócs T., Sass-Gyarmati A., Brown E., von Konrat M. & Renner M. 2011. — Checklist of hornworts and liverworts of Fiji. *Telopea* 13 (3): 405-454. https://doi.org/10.7751/telopea20116030
Söderström L., Crandall-Stotler B., Stotler R. E., Váňa J., Hagborg A. & von Konrat M. 2013a. — Notes on Early Land Plants Today. 36. Generic treatment of Lophocoleaceae (Marchantiophyta). *Phytotaxa* 97 (2): 36-43. https://doi.org/10.11646/phytotaxa.97.2.3
Söderström L., Váň J., Crandall-Stotler B. J., Stotler R. E., Hagborg A. & von Konrat M. 2013b. — Notes on Early Land Plants Today. 43. New combinations in Lophocoleaceae (Marchantiophyta). *Phytotaxa* 112 (1): 18-32. https://doi.org/10.11646/phytotaxa.112.1.4
Söderström L., Váňa J., Crandall-Stotler B., Renner M. A. M., Hagborg A. & von Konrat M. 2015. — Notes on Early Land Plants Today. 68. Miscellaneous notes on Marchantiophyta. *Phytotaxa* 202 (1): 69-72. https://doi.org/10.11646/phytotaxa.202.1.10
Söderström L., Hagborg A., von Konratt M., Bartolomew-Began S., Bell D., Briscoe L., Brown E., Cargil D. C., Costa D. P., Crandall-Stotler B. J., Cooper E. D., Dauphin G., Engel J. J., Feldberg C., Glenny D., Gradstein S. R., He X., Heinrichs J., Hentschel J., Ilkiu-Borges A. L., Katagiri T., Kostantinova N. A., Larraín J., Long D., Nebel M., Pócs T., Puche F., Reiner-Drehwald E., Renner M. A. M., Sass-Gyarmati S., Schäfer-Verwimp A., Segarra Moragues J. G., Stotler R. E., Sukkharak P., Thiers B. M., Uribe J., Váňa J., Villarreal J. C., Wigginton M., Zhang L. & Zhu R.-L. 2016. — World checklist of hornworts and liverworts. *PhytoKeys* 59: 1-828. https://doi.org/10.3897/phytokeys.59.6261
Stephani F. 1893. — Hepaticarum species novae IV. *Hedwigia* 32: 315-327.
Stephani F. 1906. — *Species hepaticarum* 3. *Bulletin de l'Herbier Boissier*, série 2, 6 (11): 935-966.
Stephani F. 1907. — *Species hepaticarum* 3. *Bulletin de l'Herbier Boissier*, série 2, 7 (8): 683-698.
Stephani F. 1911. — Botanische Ergebnisse der schweidischen Expedition nach Patagonien und dem Feuerlande 1907-1909. II. Die Lebermoose. *Kongliga Svenska Vetenskaps Academiens Handlingar*, Ny Följd 46 (9): 1-92.
Stephani F. 1922. — *Species Hepaticarum* 6. Genève & Bale, George & Cie, 763 p.
Taylor T. 1846. — New Hepaticae. *London Journal of Botany* 5: 258-284.
Thouvenot L. & Engel J. J. 2021. — Studies on Lophocoleaceae XXVII. A new species of *Heteroscyphus* Schiffn. (Marchantiophyta, Lophocoleaceae) from New Caledonia. *Nova Hedwigia* 112 (1-2): 165-171. https://doi.org/10.1127/nova_hedwigia/2021/0613
Thouvenot L. & Müller F. 2021. — Contribution to the bryophyte flora of New Caledonia IV. Species new to the country, new localities together with taxonomic notes. *Cryptogamie, Bryologie* 42 (13): 181-196. https://doi.org/10.5252/cryptogamie-bryologie2021v42a13
Thouvenot L. & Price M. J. 2020. — *Chiloscyphus parapilistipulus* (Lophocoleaceae), a new species of liverwort from New Caledonia, with the typification of *Lophocolea pilistipula*. *Candollea* 75 (2): 285-289. https://doi.org/10.15553/c2020v752a10
Thouvenot L., Gradstein S. R., Hagborg A., Söderström L. & Bardat J. 2011. — Checklist of the liverworts and hornworts of New Caledonia. *Cryptogamie, Bryologie* 32 (4): 287-390. https://doi.org/10.7872/cryb.v32.iss4.2011.287
Thouvenot L., Müller F. & Gradstein S. R. 2018. — Contribution to the bryophyte flora of New Caledonia III. New and interesting records, new combinations and new synonyms. *Cryptogamie, Bryologie* 39 (3): 361-376. https://doi.org/10.7872/cryb/v39.iss3.2018.361
Tixier P. 1972. — Mousses exotiques. *Bulletin du Muséum national d'Histoire naturelle, Botanique*, série 3, 4 (48): 89-98.
Tropicos. 2021. — Available from http://legacy.tropicos.org/Name/100435046?tab=subordinatetaxa (accessed on 21st December 2021).
Turland N. J., Wiersema J. H., Barrie F. R., Greuter W., Hawksworth D. L., Herendeen P. S., Knapp S., Kusber W. H., Li D. Z., Marhold K., May T. W., Mcneill J., Monro A. M., Prado J., Price M. J. & Smith G. F. 2018. — *International Code of nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Regnum Vegetabile 159. Glashütten, Koeltz Botanical Books. https://doi.org/10.12705/Code.2018
Yamada K. & Iwatsuki Z. 2006. — Catalog of the hepatics of Japan. *Journal of the Hattori Botanical Laboratory* 99: 1-106.

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APPENDIX

APPENDIX 1. — Index of names. The names of taxa included in Lophocoleaceae Vanden Berghen according to the checklist of the New Caledonian liverworts (Thouvenot *et al*. 2011) are listed below with their currently accepted name in **bold**. The new species, unknown in New Caledonia at the time of the checklist publication, are marked with an asterisk.

Chiloscyphus acutus Steph. = ***Heteroscyphus argutus***
C. autoicus (Steph.) J.J.Engel & R.M.Schust. (excluded name)
C. beesleyanus Pearson = ***C. longifissus***
C. confertifolius Steph. = ***Heteroscyphus coalitus***
C. confertus Steph. = ***Heteroscyphus confertus***
C. convexulus (Mitt.) J.J.Engel & R.M.Schust. = ***Lophocolea convexula***
C. cornutistipulus Steph. = ***Heteroscyphus cornutistipulus***
C. crassicaulis Steph. = ***Otoscyphus crassicaulis***
C. etesseanus Steph. = ***Heteroscyphus etesseanus***
C. explanatus (Mitt.) J.J.Engel & R.M.Schust. = ***Cryptolophocolea explanata***
C. fragillimus (Steph.) J.J.Engel & R.M.Schust. = ***Lophocolea convexula***
C. francanus Steph. = ***Heteroscyphus coalitus***
C. heteromorphus (Steph.) J.J.Engel & R.M.Schust. = ***Heteroscyphus deplanchei***
C. kurzii (Sande Lac.) J.J.Engel & R.M.Schust. = ***Lophocolea convexula***
C. latistipulus (Steph.) J.J.Engel & R.M.Schust. = ***Heteroscyphus coalitus***
C. latistipus Steph. = ***Heteroscyphus coalitus***
C. leratii J.J.Engel & R.M.Schust. = ***Lophocolea caledonica***
C. longifissus Steph. (*incertae sedis*)
C. muricatus (Lehm.) J.J.Engel & R.M.Schust. = ***Lophocolea muricata***
C. novae-caledoniae J.J.Engel & R.M.Schust. = ***Goebelobryum unguiculatum*** (Acrobolbaceae)
C. papulimarginatus (H.A.Mill.) J.J.Engel & R.M.Schust. = ***Lophocolea convexula***
C. parapilistipulus* Thouvenot = ***Heteroscyphus parapilistipulus*
C. paroicus J.J.Engel & R.M.Schust. = *Cryptolophocolea levieri* (excluded name)
C. parvus (Steph.) J.J.Engel & R.M.Schust. = ***Lophocolea convexula***
C. pilistipulus (Steph.) J.J.Engel & R.M.Schust. = ***Lophocolea convexula***
C. quadricilius Steph. = ***Heteroscyphus grandiflorus***
C. rotundiphyllus H.A.Mill. = ***Heteroscyphus confertus***
C. savesianus (Steph.) J.J.Engel & R.M.Schust. = ***Lophocolea savesiana***
C. similis Steph. (1908) non *C. similis* Steph. (1911) = ***Heteroscyphus coalitus***
C. subacuminatus Herzog = ***Heteroscyphus subacuminatus***
C. subcostatus (Steph.) J.J.Engel& R.M.Schust. = ***Cryptolophocolea subcostata***
C. subsimilis Steph. = ***Heteroscyphus coalitus***
C. trigonifolius Steph.
Conoscyphus trapezioides (Sande Lac.) Mitt. ex Schiffn. (moved to Acrobolbaceae)
Heteroscyphus argutus (Reinw., Blume & Nees) Schiffn.
H. aselliformis (Reinw., Blume & Nees) Schiffn.
****H. assurgentissimus*** J.J.Engel, Thouvenot & Frank Müll.
H. caledonicus (Steph.) Schiffn.
H. coalitus (Hook.) Schiffn.
H. comptonii (Pearson) J.J.Engel & R.M.Schust. = ***Tetracymbaliella comptonii*** (moved to Brevianthaceae)
H. cymbalifer (Hook.f. & Taylor) J.J.Engel & R.M.Schust. = *Tetracymbaliella cymbalifera* (excluded name)
H. decipiens (Gottsche) J.J.Engel & R.M.Schust. = ***Tetracymbaliella decipiens*** (Brevianthaceae) (presence in New Caledonia needs confirmation)
H. deplanchei (Steph.) Schiffn.
****H. diestianus*** (Sande Lac.) Piippo
H. giganteus (Steph.) Hürl.
H. grandiflorus (Steph.) Hürl.
H. jackii (Steph.) Schiffn. (excluded name)
****H. kanakensis*** Thouvenot & J.J.Engel
H. splendens (Lehm. & Lindenb.) Grolle
****H. succulentus*** (Gott.) Schimp.

****H. supinopsis*** J.J.Engel, Thouvenot & Frank Müll.
****Lophocolea bidentata*** (L.) Dumort.