

## **Studies on Lophocoleaceae XXI. *Otoscyphus* J.J. Engel, Bardat *et* Thouvenot, a new liverwort genus from New Caledonia with an unusual morphology**

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**Abstract** – A new genus of liverwort in the family Lophocoleaceae is described and illustrated. The genus *Otoscyphus* presents a suite of original characters for this family. It is placed in the subfamily *Lophocoleoideae*. It has, in particular, a unique feature among leafy liverworts: The leaves have a very broad foliar base forming a longitudinally inserted pocket. The feature involves several characters. This genus is represented by a single species, *Otoscyphus crassicaulis* comb. nov., from New Caledonia. The species is montane and occurs on the dead, rotted wood.

**Marchantiophyta / Jungermanniales / Australasia / bryophytes / liverworts / new genus / *Otoscyphus* / Pacific region**

**Résumé** – Un nouveau genre d'hépatique de la famille des Lophocoleaceae est décrit et illustré. Le genre *Otoscyphus* présente un ensemble de caractères originaux pour cette famille. Il est placé dans la sous-famille des *Lophocoleoideae*. Caractère unique chez les hépatiques à feuilles, ses feuilles présentent une base très large formant une poche insérée longitudinalement. Ce genre est représenté par une seule espèce, *Otoscyphus crassicaulis* comb. nov., uniquement connue actuellement de la Nouvelle-Calédonie. L'espèce est montagnarde et vit sur les bois morts pourrissants.

**Marchantiophyta / Jungermanniales / Australasie / bryophytes / hépatiques / nouveau genre / *Otoscyphus* / région Pacifique**

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## INTRODUCTION

New Caledonia is rich in endemism of genera: 105 of the 711 genera of seed plants recorded from the islands are considered to be endemics of this archipelago (Heads, 2010). Notable among these are three genera of conifers, including the only known species of parasite conifer *Parasitaxus usta* (Vieill.) de Laub.; 15 of the 17 palm genera are endemics; and 32 monotypic genera of dicotyledons, e.g. *Amborella*, *Strasburgeria*, *Captaincookia*. According to Jaffré *et al.* (2001), the genera with more numerous endemic species are in the families Cunoniaceae (30 *Pancheria*, 13 *Codia*), Proteaceae (13 *Bauprea*, 6 *Viotia*), Fabaceae (20 *Arthroclanthus*), and Guttiferae (6 *Montrouziera*). However, the ferns have only one endemic genus *Stromatopteris* (Gleichenaceae) and mosses have three endemic genera, *Cyrtopodendron*, *Franciella* (both monotypic) and *Parisia* (3 species) (Thouvenot & Bardat, 2010; Bell & Hyvönen, 2010). The high degree of supraspecific endemism is not represented in hepatics, with New Caledonia having only one endemic genus, *Meinungeria* Frank Müll. (Müller, 2007). Four subgenera are endemic to New Caledonia, *Chloranthelia* Schust. subg. *Chloranthelia*, with only *C. denticulata* (Steph.) Schust. (Schuster and Engel, 1987), *Frullania* Raddi subg. *Huerlimannia* S. Hatt. with only *F. elephantina* S. Hatt. (Hattori, 1977) and *Mastigophora* subg. *Eomastigophora* R.M. Schust., with only *M. caledonica* Steph. (Schuster, 1987), and *Nardia* subg. *Aponardia* R.M. Schust., with only *N. huerlimannii* Váňa & Grolle (Váňa, 1970).

Study of liverworts from New Caledonia has revealed a new endemic genus, which is described in this paper.

## DESCRIPTION OF THE NEW GENUS

### ***Otoscyphus* J.J. Engel, Bardat *et* Thouvenot, gen. nov.**

*Caulis ex cellulis incrassatis corticalibus medullaribusque comparate paucis compositus. Rami prope omnes ventrali-intercalares; rami frullanioidei rari. Rhizoidea ex cellulis amphigastrii orientia, nunquam ex cellulis caulinis. Foliae area concava distincte saccata praeditae, quaeque area per basem dilatatam marginis dorsalis folii superioris dorsaliter obiecta. Amphigastria lobis longe ciliiformo-setaceis praedita, paene ad angulum 180° divergentis. Discus amphigastrii cuneatus, pauci-cellulatus, amplis cellulis marginatus.*

**Type:** *Lophocolea crassicaulis* Steph.

A genus with only one species:

### ***Otoscyphus crassicaulis* (Steph.) J.J. Engel, Bardat *et* Thouvenot, comb. nov.**

*Lophocolea crassicaulis* Steph., *Spec. Hep.* 6: 268. 1922. *Chiloscyphus crassicaulis* (Steph.) J.J. Engel *et* R.M. Schust., *Nova Hedwigia* 39: 413. 1985 (1984). **Type:** New Caledonia, Mt Mou, 1200 m, 17 July 1909, *Franc*, “(Thériot misit)” (G 17607!).

**Plants** delicate, soft yet  $\pm$  rigid and wire-like, creeping, often locally arcuate and then again creeping, light yellowish green when live, very pale whitish green in herb, rather translucent, distinctly nitid and with a glassy appearance

when dry, the shoots small, up to 665-1000  $\mu\text{m}$  wide. **Branching** occasional, the branches nearly exclusively of ventral-intercalary type; *Frullania*-type branches rare, the half leaf long attenuate, the first branch underleaf at branch base bilobed, the 2 lobes markedly divergent, with 1 lobe arching across branch base, the other stiffly diverging and arching toward shoot base; stolons absent. **Stems** zig-zag in growth, markedly narrow for shoot size, comprised of relatively few, firm-walled cells, the cortical cells somewhat larger, 2-4 dorsally and laterally and 2-4 ventrally; medullary cells 3-6. Rhizoids hyaline, long for plant size (mostly 300-400  $\mu\text{m}$  long), in tight fascicles from cells of underleaves. **Leaves** alternate, bilobed, 375-380(400)  $\mu\text{m}$  long, with orientation and insertion strongly succubous, sublongitudinal, the basal sector (exclusive of the dilated dorsal base *ca* 320-330  $\mu\text{m} \times 75$ -80  $\mu\text{m}$ ) initially vertically dorsally assurgent and defining an adaxial concavity, the leaf then strongly convex-arched to form a crest at about the midpoint before becoming moderately to sharply decurved so that the lobes are oriented  $\pm$  vertically and  $\pm$  parallel with the leaf base; leaf in cross section forming a  $\pm$  inverted U or, with further curvature of the lobes, even a semicircle; leaf with dorsal base abruptly and strongly dilated resulting in a conspicuous flange of tissue  $\pm$  equal in basal width to the non-dilated sector and extending towards shoot base at least to the level of the median sector of the leaf immediately below, the free portion of the flange 4-5 cells high for most its width, convex but abruptly becoming vertical at the base, the vertical sectors of opposing leaves fused; leaves widely spreading to squarrose, basally imbricate but appearing distant, on one side each separated from the leaf above and below by about half the width of a leaf disc or a little less; 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 subrectangular, the sides from the base to lobe tip forming a gently incurved, symmetrical arch, the leaves bifid to 0.4-0.45 of leaf length. **Lobes** subparallel to more often moderately to broadly divergent, rather closely proximated, subequal in size, long ciliform-setaceous, comprised of 2 biseriate tiers and a long, whip-like uniseriate sector of 5-6 variously elongated cells [(2)4(6)/1], the cells of uniseriate row with septa variable: not or at most somewhat constricted at the septa, but the leaves at shoot tips with cells of uniseriate row as well as those of the subtending biseriate tiers typically turgid, barrel-shaped and with a distinctly constricted septa, the apex otherwise entire. **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** of the exposed main portion of the leaf with massive, nodular or protuberant, irregularly triangular to rectangular trigones that are confluent or separated by narrow thin-walled places, the cell lumen bounded mostly by the massive trigones, the longitudinal walls often evenly thickened, the middle lamella not evident; median leaf cells 25-30  $\mu\text{m}$  wide, 35-50  $\mu\text{m}$  long; basal 4-5 rows of cells basal 4-5 rows of cells + those of flange with trigones minute to small; marginal cells with exposed wall notably thick; surface of disc finely striate, of lobes finely papillose. **Underleaves** with disc a little wider than stem but with lobes laterally extending at least to level of sinus bases of the adjacent leaves, free, the underleaves moderately spreading, distant, the stem broadly exposed, the underleaves plane, disc cuneate, bifid nearly to base, the line formed by lobes and disc apex maximally lunate to straight; lobes diverging by an angle of *ca.* 180° or nearly so, the shape much like those of the leaves but comprised of 1-3 biseriate tiers and a uniseriate row of 3-6 cells, the cells of uniseriate row similar to those of leaves

except the tip cell is capped by a slime papilla, the lobe margins uniformly entire; disc 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 ca. 8 smaller, quadrate, rhizoid initials, with a rhizoid potentially emerging from each, the summit of disc truncate or (often) broadly rounded, entire, the lateral margins plane and not reflexed, entire or at times with a 1-2-celled tooth, often with a slime papilla near lobe base, the disc margins decurrent; ventral merophyte 3-4 cells wide; underleaves at shoot tips with lobes similar to those of leaves. Asexual reproduction unknown.

**Plants dioecious.** **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 (the entire ventricose base stiffly so), densely imbricate, strongly ventricose in basal ca 0.5, the saccate portion free from opposing bract, the bracts deeply bilobed, the lobes sharply reflexed and similar to those of the leaves except shorter, with a uniseriate row of 2-4 cells; lobule margin inflexed to involute, dilated, sparingly crenate-denticulate; antheridia solitary, the stalk not observed (only very old antheridia seen). **Gynoeceia** terminal on main shoot, or on short ventral-intercalary branches lacking normal vegetative leaves; bracts and bracteoles in 3 series, those of first (outermost) series much smaller (0.35-0.45 mm long), the bracts of innermost series larger (ca 1 mm long), symmetrically or more often asymmetrically bifid to ca 0.35-0.5, the dorsal lobe smaller or reduced to a small rounded projection, the lobes plane or a little ventrally sulcate, narrowly acuminate to attenuate, entire or with a sharp tooth, the lamina margins each with 1-3 teeth, the teeth small and few-celled to larger and spine-like, the dorsal base at times with an attenuate process, the lamina cells with massive trigones in distal portion, the basal ca 0.4 with slightly firm-walled cells with trigones totally lacking; bracteoles of innermost series somewhat smaller than bracts, to 1 mm long, free or narrowly connate on 1 side, symmetrically bifid to ca 0.25-0.5, the lobes ventrally sulcate, with a few small teeth, the lamina margins entire or with a few small teeth near the base. **Perianths** long exerted, 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 ca 0.3-0.35 the perianth length; lobes conspicuously and gradually narrowing toward apex, deeply bifid, the segments usually caudate, occasionally narrowly acuminate, terminating in a uniseriate row of 5-6 cells, the main segments usually 3-5 cells wide at base, with margins entire or with a ciliiform process toward base, the lobes otherwise with several often long ciliiform processes below level of segments; keelar wings common, 1-2 per perianth, incomplete, of a few cells high, entire or with a tooth-like process. **Calyptra** extending ca 0.4 the perianth length, the unfertilized archegonia remaining at base of calyptra, a shoot calyptra lacking.

**Seta** elevating **capsule** well beyond the perianth mouth, with ca 9 rows of outer cells with thickened walls surrounding an inner core of ca 6 much smaller cells. Capsule walls 19-20  $\mu$  thick, bistratose, the outer layer of cells 1.7-1.8 times thicker than inner layer; outer layer of cells quadrate to short rectangular, with nodule-like to short spur-like thickenings on longitudinal walls, the transverse walls with fewer and often weaker thickenings or altogether devoid of thickenings; inner layer of cells short to long sub-rectangular, the radial walls with nodule-like to spine-like thickenings, also with a few, sporadic, weak, non-pigmented, complete semi-annular bands. **Spores** and **elaters** not seen.



## DISCUSSION

The liverwort described here has a number of novel features which together merit generic rank.

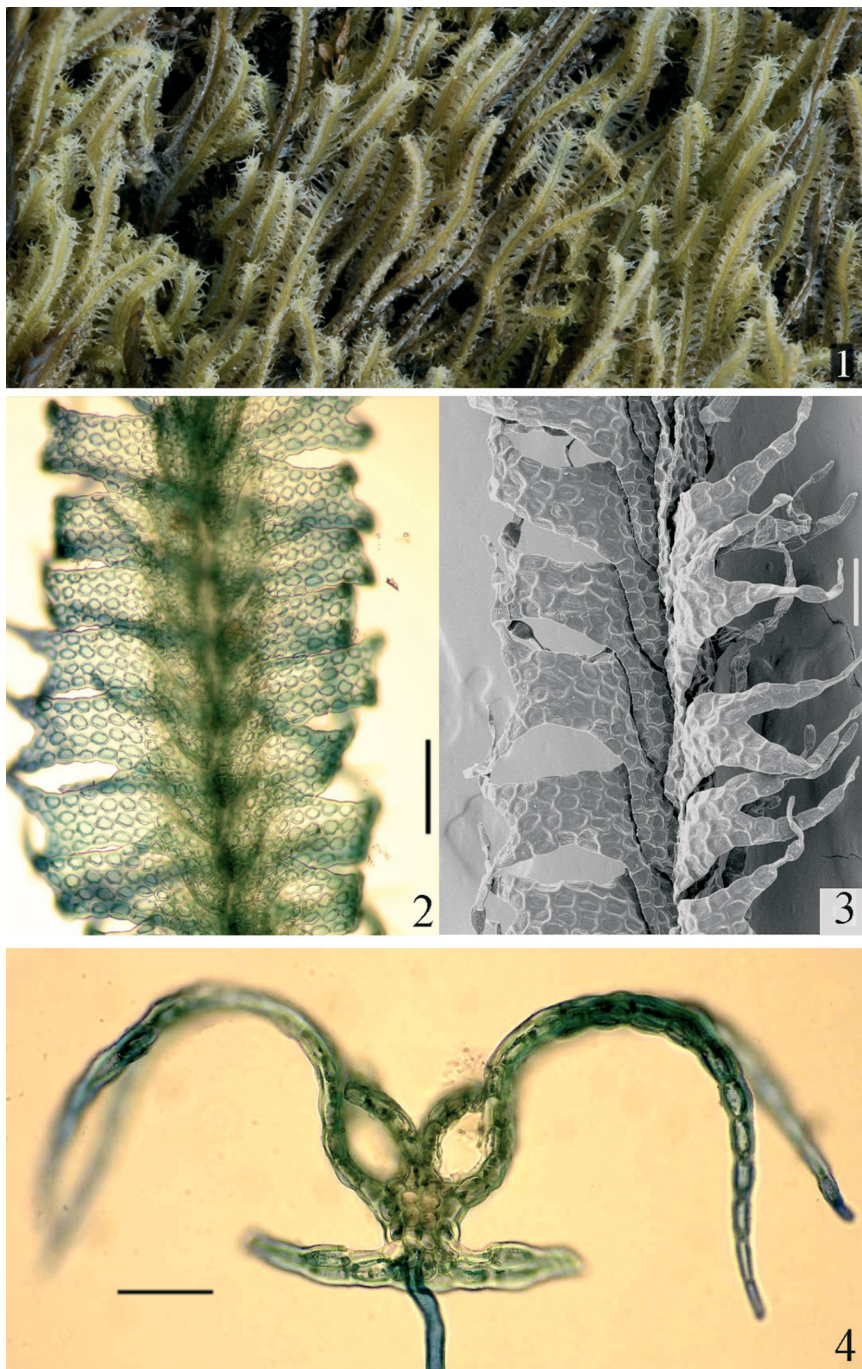
At first glance the shoots, in both dorsal and ventral view, appear to have a stem that is oversized for the magnitude of the shoot. This feature, together with a leaf disc that is, at least distally, in part four cells wide, suggests *Zoopsis*, with similarities in particular to *Z. ceratophylla* (Spruce) Hamlin (Schuster, 2000) (Fig. 2). On close examination, however, the illusion of a broad, robust stem is due to the presence of closely spaced, symmetrically elliptic, inflated, bulging pockets. The illusion is enhanced by the translucent quality of the shoots, with the tight vertical alignment of the pockets lending the central or middle sector of the shoot slightly opaque. The pockets are derived from the leaves which each have a pronounced adaxial concavity in the basal portion (Fig. 2). The pocket-like concavities, however, are not evident in a dorsal view of the plant, since each is totally covered dorsally by a gently convex decurrent flange of tissue of the leaf above (Figs 3, 4). The flange of tissue is the conspicuously dilated dorsal base of the leaf and is 4-5(6) cells high for most its width, (Figs 3, 4, 21). The flange becomes sharply vertical at the base and the vertical sectors of opposing leaves are fused (Figs 3, 4, 19, 20). The pocket-like concavities and the flap-like flanges are tightly aligned vertically, lending the illusion of a broad, *Zoopsis*-like stem. The formation of inflated pockets in this manner is unique among liverworts.

The ventral margin of the leaf has a tooth toward the base (Fig. 19). The tooth is sometimes hidden in a ventral view of the shoot in transmitted light since the base of the ventral margin of the leaf is masked or hidden by the stem or the leaf tissue of the pocket-like base. However, the tooth usually appears as a bump along the side of the stem and, when varying the plane of focus, the margin of the tooth appears to delimit a circular orifice at the free margin of the corresponding pocket (Figs 5, 6). The exact role of this tooth remains unclear, but may function in the role of plant water relations, perhaps a water retentive device.

In actuality the stem is distinctly narrow for the shoot size, and, in transmitted light, is only a little darker than the laterally adjacent pockets and not conspicuously apparent (Fig. 2). The stem has a zig-zag arrangement, seeming laterally “displaced” by each leaf (Fig. 2).

*Otoscyphus* is also distinctive in the leaf and underleaf lobes, which are nearly identical in being long filiform-setaceous (Figs 6, 7, 23). The lobes are whiplike and comprised of 1-3 biseriate tiers and a uniseriate row of moderately elongated cells often somewhat to distinctly constricted at the septa (Figs 5, 23). The leaf lobes are strongly deflexed and, as seen in a cross section of the shoot, form an inverted “U” or continue an even curvature to delimit a semicircle (Figs 4, 19, 20). The underleaf lobes diverge from a cuneate disc by an angle of 180° or nearly so, with the divergent angle so strong that a sinus is not defined. Rather, the line formed by the lobes and the underleaf apex is slightly incurved to straight, *i.e.*, the underleaf summit is then truncate (Figs 6, 7, 23). The tip cell of each underleaf lobe usually terminates in a small slime papilla.

The underleaf disc is also distinctive. The disc has a distal row of 2-3 cells that are more or less isodiametric, slightly shorter than those of the paired cells at the lobe bases, but are consistently larger than the field of cells immediately below (Fig. 23). The distal cells never give rise to rhizoids, *i.e.*, they do not subdivide to form rhizoid initials. The upper wall of the distal cells is distinctly



Figs 1-4. *Otoscyphus crassicaulis*. **1.** Habit, *in situ*. **2.** Sector of main shoot, dorsal view (scale 200  $\mu$ ). **3.** SEM dorsal view of shoot (scale 100  $\mu$ ). **4.** Cross section of stem, leaves and underleaf (scale 100  $\mu$ ).

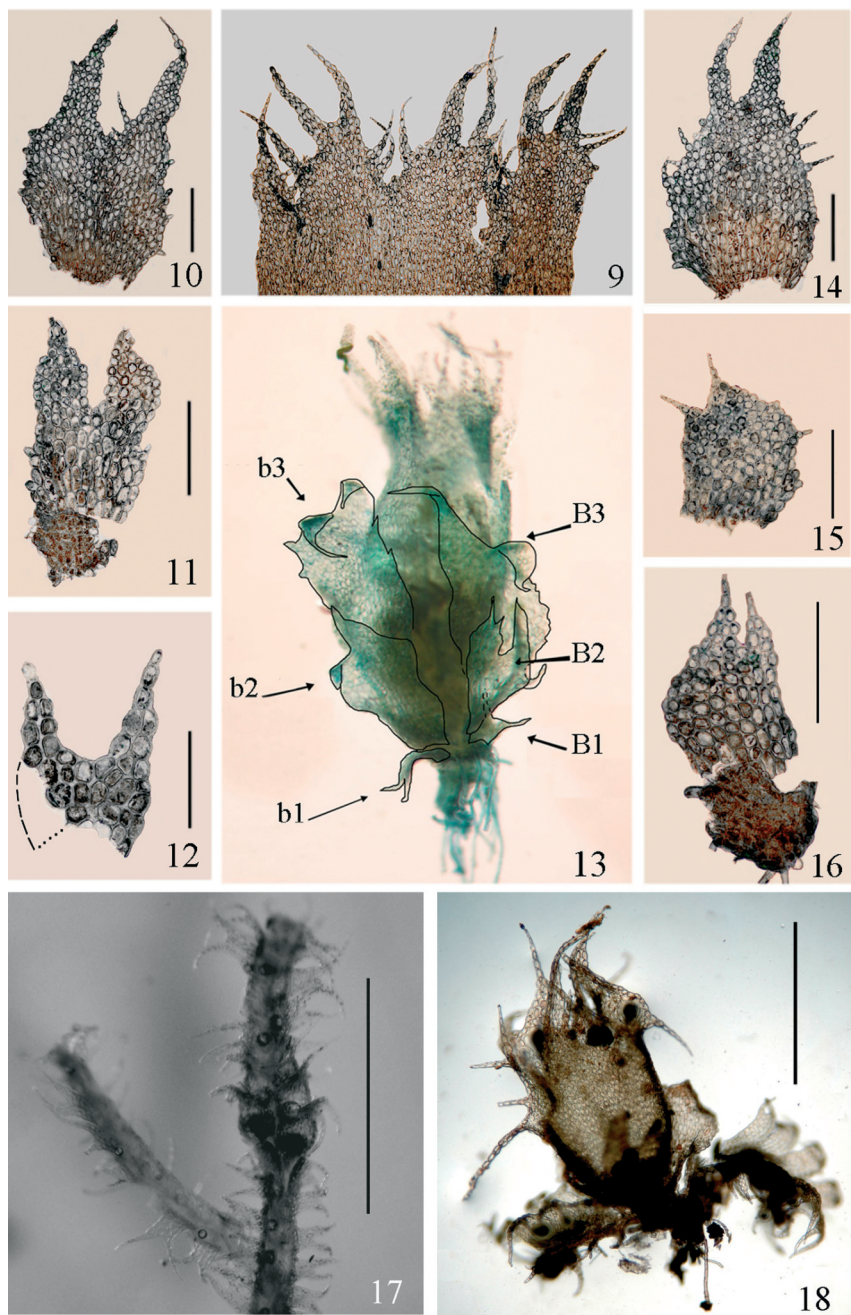




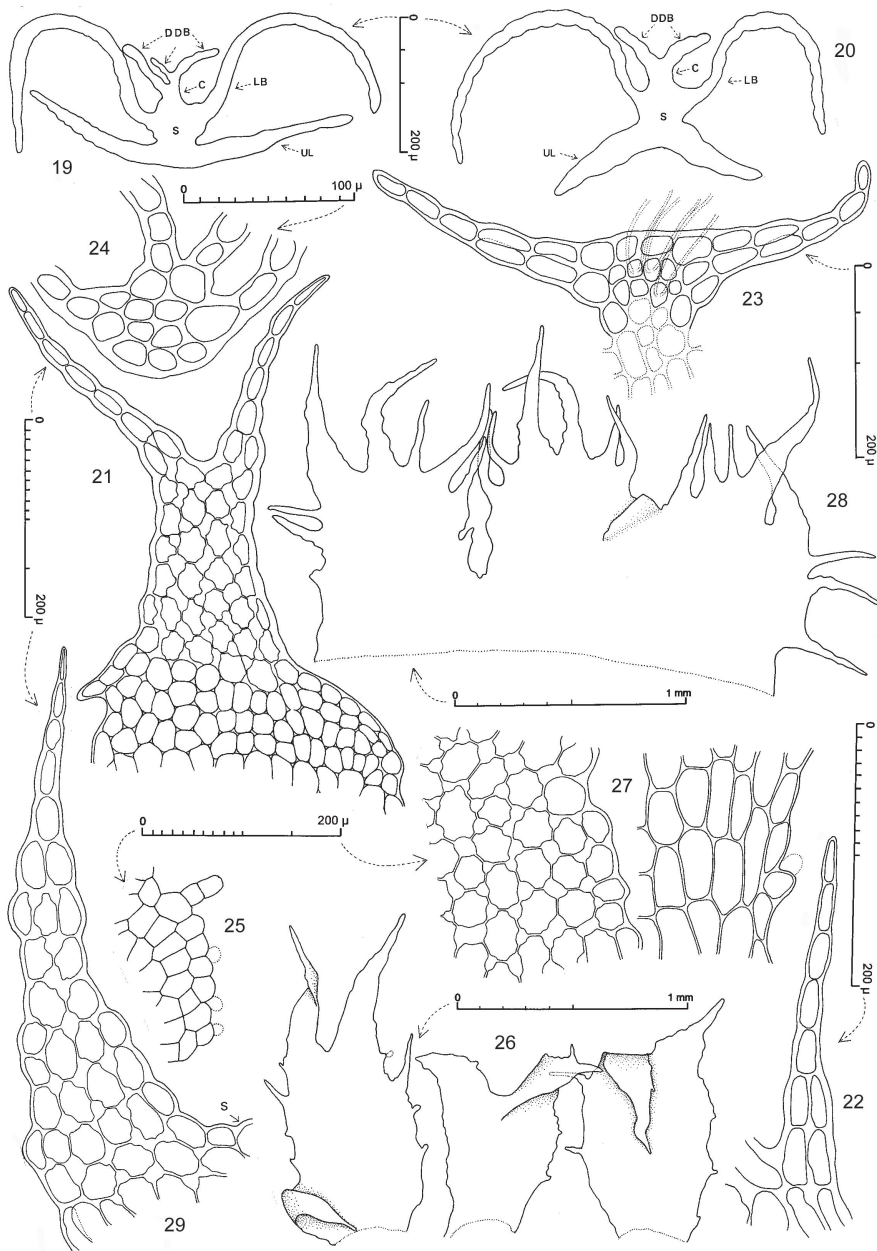
Figs 5-8. *Otoscyphus crassicaulis*. **5.** Sector of shoot showing basal tooth of leaf forming a circular hole (arrow), ventral view (scale 100  $\mu$ ). **6.** *Ibidem* (SEM) (scale 100  $\mu$ ). **7.** Sector of main shoot, ventral view (scale 250  $\mu$ ). **8.** sector of main shoot showing apparent wide stem in transmitted light, dorsal view (scale 200  $\mu$ ).

thickened (Fig. 23). Immediately basal to the distal row of cells are 2 tiers of smaller, quadrate to subquadrate cells, with each tier potentially formed of 2-4 cells depending upon cell subdivision (Fig. 23). The two tiers together form a weak dome. This composition of underleaf disc, i.e., with a distal row of 2-3 large cells + 2 rows of smaller cells may be seen even on underleaves very near the shoot apex. Each of these smaller cells may act as a rhizoid initial, with a rhizoid potentially emerging from each (Fig. 23).

Branching is nearly all ventral intercalary, with terminal, *Frullania*-type branches only rarely produced, a feature unusual in the family. If ventral-intercalary branches are present in taxa of Lophocoleaceae, they are accompanied



Figs 9-18. *Otoscyphus crassicaulis*. **9.** Distal portion of perianth. **10.** Bracteole of innermost series (b3). **11.** Bracteole of 2<sup>nd</sup> series (b2). **12.** Bracteole of 1<sup>st</sup> series (b1) (all scales 250  $\mu$ ). **13.** Gynoecium showing position of bracts and bracteoles. **14.** Bract of innermost series (B3). **15.** Bract of 2<sup>nd</sup> series (B2) (both scales 250  $\mu$ ). **16.** Bract of 1<sup>st</sup> series (B1) (scale 100  $\mu$ ). **17.** Androecium (scale 1 mm). **18.** Gynoecium (scale 1 mm).



Figs. 19-29. *Otoscyphus crassicaulis*. **19, 20.** Shoot cross sections showing connation (= c) of dilated dorsal leaf bases (= ddb), the concave sector of leaf base (= lb), the stem (= s), and the underleaf (= ul). **21.** Leaf. **22.** Leaf lobe. **23.** Underleaf; note rhizoids (stippled outline) and rhizoid initial cells (stem cells indicated by stippled outline). **24.** Stem, cross section. **25.** Portion of lobule of ♂ bract. **26.** Innermost ♀ bracts and in middle, bracteole. **27.** Distal (left) and basal cells of lamina of same innermost ♀ bract. **28.** Perianth mouth, ventral lobe in middle. **29.** Segment of perianth lobe (s = sinus base). (All from Thouvenot, New Caledonia, Dzumac Massif).



either by lateral-intercalary branches (e.g., *Hepatostolonophora* J.J. Engel *et* R.M. Schust., *Stolonivector* J.J. Engel, *Chiloscyphus* subg. *Septati* J.J. Engel) or by lateral-intercalary as well as *Frullania*-type branches (e.g., *Chiloscyphus* subg. *Notholophocoleus* (Schust.) J.J. Engel *et* R.M. Schust. *Chiloscyphus muricatus* (Lehm.) J.J. Engel *et* R.M. Schust. has both ventral-intercalary and *Frullania*-type branches, but in that species the two types of branches are of about equal frequency (Engel, 2010).

The presence of a distinct perianth with three subequal sides (Figs 9, 28), the relatively large bracteole, only somewhat smaller than the bracts (Fig. 26), the lack of gemmae, and the lack of secondary pigments are characters that would place *Otoscyphus* in subfamily *Lophocoleoideae* (Engel & Gradstein, 2003). The species appears most similar to *Chiloscyphus*, but differs from that genus in several respects, as discussed below.

We know of no other member of *Chiloscyphus* or, for that matter, *Lophocoleaceae*, with underleaves of this form. Stephani (1922, p. 269), in the protologue of *Lophocolea crassicaulis*, referred to the underleaves as “curiosissima.” Oddly, the underleaf form has marked similarities to *Drepanolejeunea* subg. *Rhaphidolejeunea* (Herz.) Grolle *et* R.L. Zhu of the totally unrelated *Lejeuneaceae*; compare Fig. 7 and 23 with fig. 5a, b, i, j in Grolle & Zhu (2000). Also, interestingly, the underleaf lamina is bounded by a  $\pm$  consistent number of much larger cells just as in *Leptolejeunea*, another genus of *Lejeuneaceae* (see Gradstein *et al.*, 2001, fig. 46k).

The rhizoids originate from underleaf cells and never from stem cells (Fig. 23) vs. strictly from stem cells, typically at the immediate base of the underleaves, in *Chiloscyphus*. Within the family *Lophocoleaceae*, the only other instance of rhizoids originating from underleaf cells is in *Leptophyllopsis* Schust. (Engel, 2007).

As discussed above the presence of distinct pockets, each covered dorsally, is unique in liverworts.

The highly reduced stem, comprised of relatively few, firm-walled cortical and medullary cells (Fig. 24), is not found in *Chiloscyphus*.

**Note:** The label of the type bears the notation, in lead pencil, “*Lophocolea crassicaulis* St n sp. - *Aneura leratii* St - *Drepanolej. microphylla* St” with blue pencil numbers, respectively, of 140 - 141 - 142. These numbers are also on micropackets within the larger one, each enclosing a small sample of those species.

## DISTRIBUTION AND ECOLOGY

The genus is endemic to New Caledonia and restricted to peridotitic massifs of Southern Province. The specimen described here (New Caledonia, Province Sud, Païta, Dzumac Massif, 915 m a.s.l., on bits of dead wood in forest, ultramafic massif, L. Thouvenot, 18/08/2008 [F, PC, hb. Thouvenot]) occurred on deadwood with little competition from other bryophytes apart from *Radula amentulosa* Mitt., which is associated. It also was previously reported as *Lophocolea crassicaulis* by Hürlimann (1998) from nine specimens, nearly all collected on dead wood, rarely on roots or other bryophytes on wet ultramafic

rock, in peridotitic mountains, mainly between 500 and 1100 m (one at 240 m), in various hydrometric conditions from montane cloud forests to relatively drier rain forests on the western slide, with rainfall between 1000-2000 mm.

The type specimen was collected on dead wood at ca. 1200 m on Mont Mou and is associated with *Riccardia graeffei* (Steph.) Hewson (= *Aneura leratii* Steph.) very abundant, *Drepanolejeunea microphylla* Steph. *ex* Bonner *nom. inval.*, *Heteroscyphus* sp. and *Trichosteleum* sp.

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