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A revision of the genus Odontolejeunea (Spruce) Schiffn. (Leujeuneaceae, Hepaticae)

by

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With 3 maps and 5 plates

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Abstract: A taxonomic revision is presented for the epiphyllous liverwort genus *Odontolejeunea* (Lejeuneaceae subf. Ptychantoideae). Three species are accepted: *O. decemdentata* (Spruce) Steph.; *O. lunulata* (Web.) Schiffn. and *O. rhomalea* (Spruce) Steph. All three species occur in tropical America, and *O. lunulata* occurs also in tropical Africa.

Introduction

Odontolejeunea is one of the most common epiphyllous liverwort genera in tropical South America and tropical Africa. About twenty-four species have been described but most of them are of doubtful status and a critical investigation of the species concept is lacking.

The aim of this paper is to redefine the species of *Odontolejeunea,* based on a revision of the types and further herbarium materials.

Material was seen from the following herbaria: BM, G, JE, L. MANCH, NY, PC-Mont, S, U, UPS, YU. I express my gratitude to the curators of these herbaria for the loan of the specimens.

History of the genus

The name *Odontolejeunea* was introduced by Spruce (1884), as *Lejeunea* subgenus *Odontolejeunea* Spruce. About fourty years earlier, Gotsche, Lindenberg & Nees (1845) had recognised a certain affinity of four species of *Lejeunea* now known as members of *Odontolejeunea: L. lunulata* (Web.) Nees (*Jungermannia lunulata* Web.) — with four varieties including *Phragmicoma calcarata* Mont. —, *L. tortuosa* (Lehm.) Lehm. & Lindenb., *L. sieberiana* Gott. and *L. martinicensis* Lindenb.

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Spruce (1884) accepted ten species in *Lejeunea* subg. *Odontolejeunea,* including the previously described *L. lunulata* and *L. calcarata* and eight new species. He placed the subgenus between *Dicranolejeunea* and *Prionolejeunea* and divided it into two groups. The first group consisted of two subgroups, one of these containing *L. lunulata* (Web.) Nees, *L. calcarata* Mont., *L. rhomalea* Spruce, *L. chaerophylla* Spruce, *L. decemdentata* Spruce, and *L. hapalochroa* Spruce, and the other containing *L. surinamensis* Mont., *L. stachyclada* Spruce and *L. truncatula* Spruce. The second group contained only one species, *L. peruviana* Lehm. & Lindenb. In 1889, Bescherelle & Spruce validated two new species in *Lejeunea* subg. *Odontolejeunea: Lejeunea glaziovii* (= *L. glaziovii* Spruce (1888) (nom. nud.)) and *L. scalpellifolia.*

Schiffner (1893) raised *Odontolejeunea* to generic rank and accepted eighteen species.

Evans (1904) divided the genus into two genera: *Odontolejeunea* and *Cyclolejeunea.* Discriminating characters where this division was based on are a.o. underleaf shape, vegetative reproduction and dentation of the lobe. He placed *Odontolejeunea* between *Anoplolejeunea* and *Cyclolejeunea,* with a close relationship to *Dicranolejeunea* and *Prionolejeunea,* and accepted only two species in *Odontolejeunea: O. lunulata,* which he choose as the lectotype species of the genus (1904: 184), and *O. sieberiana.* Four years later (1908) he added a new species *O. longispica.*

Stephani (1888, 1890, 1896, 1904, 1905, 1912) added nineteen species, one time using the generic rank and another time using the subgeneric rank. In 1912 the number of species increased tremendously when Stephani described ten new species (all of them now synonyms), while excluding a number of species at the same time. Some epithets synonymized several years before, however, were used again. In total twenty-two species were accepted in this work: *O. mauritiana, O. hanningtoni, O. sieberiana, O. tortuosa, O. thomeensis, O. tocoriensis, O. longispica, O. decemdentata, O. rhomalea, O. angustifolia, O. calcarata, O. lunulata, O. martinicensis, O. chaerophylla, O. ecuadoriensis, O. cubensis, O. spiniloba, O. paranensis, O. nigrescens, O. grandiloba, O. levistipula* and *O. contractilis.*

Since Stephani's treatment only two new species were described: *O. armitagei* Pearson (1922) and *O. obversilobula* Herzog (1931).

As to the classification of *Odontolejeunea,* Evans (1904) placed the genus in the tribe Lejeuneae, close to *Cyclolejeunea.* Verdoorn (1934) found an affinity with *Dicranolejeunea,* but also placed it in the Lejeuneoideae. Schuster (1963) placed *Odontolejeunea* together with *Cyclolejeunea* and *Prionolejeunea* in a genus complex between Ptychanteae and Lejeuneae, related to *Dicranolejeunea* and to complexes in *Lejeuneae.* Gradstein (1975, 1979) put *Odontolejeunea* and *Dicranolejeunea* in the *Dicranolejeunea-complex.* The complex was placed in the Archilejeuneae, one of the two tribes of the subfamily Ptychanthoideae (the other tribe being the Ptychantheae). He estimated the real number of species in *Odontolejeunea* three to five. Van Slageren (1985) placed *Odontolejeunea* in the subfamily Ptychanthoideae, tribe Brachiolejeuneae.

Following the latest studies on members of this tribe by Gradstein (1987) and Kruijt (1988), *Odontolejeunea* is considered by the present author to belong to the *Brachiolejeunea*-complex (Ptychanthoideae, tribe Brachiolejeuneae); other genera of this group are *Brachiolejeunea, Blepharolejeunea, Acanthocoleus, Dicranolejeunea* and *Lindigianthus*. The main area of distribution of this complex is tropical America.

In this monograph, the genus *Odontolejeunea* is being reduced to only three species, viz. *O. decemdentata, O. lunulata* and *O. rhomalea*.

Morphology and anatomy

a. Leaves

Gradstein (1975) used three main characters to determine whether a genus belongs to the Archilejeuneae (tribe now ± abolished) or Ptychantheae: trigone shape, cell shape and arrangement, and leaf position in the dry state. "Leaves which do not have cordate trigones (Archilejeuneae) are usually spreading both in the dry and in the wet state. They may be somewhat involuted when dry, though, particularly in *Dicranolejeunea, Odontolejeunea* and *Spruceanthus*. The cells of the lobe as a rule are isodiametric and consequently they are not arranged in diverging rows" (p. 144).

Based on my study, the above observations of *Odontolejeunea* may be modified as follows. In contrast with other Archilejeuneae, two of the three species recognized in *Odontolejeunea,* viz. *O. lunulata* and especially *O. rhomalea,* have cordate trigones as in Ptychantheae (Pl. 3C, 5E). Only in *O. decemdentata* the trigones may be simple triangular (or weakly cordate) (Pl. 1D). However, spreading dried leaves are usually only found in *O. decemdentata*. In *O. lunulata* the leaf appearance in the dry state is very variable and may be spreading to very much crisped and erecto-patent. In *O. rhomalea* the leaves are usually revoluted when dry.

The leaf cell shape and arrangement are not quite so constant throughout the genus as in other members of the Archilejeuneae. *O. lunulata* generally has isodiametrical cells (Pl. 3C), arranged in longitudinal rows at the antical margin, the rows becoming indistinct towards the postical margin. In *O. decemdentata* the cells are irregularly angular to more or less isodiametric (Pl. 1D), and they are arranged irregularly. In *O. rhomalea* the cells are exceptionally broad when compared to the other species (Pl. 5E) and are arranged in latitudinal rows.

These three characters are very useful for species determination.

Spruce (1884) and also Herzog (1931) use the dentation of the postical leaf margin to differentiate between the species. I found that the dentation of the entire leaf margin, including the shape of the teeth, can be used to that purpose, with some care though. As a rule *O. decemdentata* has few teeth (up to 12) which can be obtuse instead of sharp as in the other species and are situated mainly at the apex and the antical side of the leaves, just occasionally at the postical margin. *O. lunulata* and *O. rhomalea* usually possess much more teeth (up to 25), which are very sharp; the postical margin, moreover, often has teeth that are much larger than the other teeth.

Herzog (1931) uses form and dentation of the lobule as differentiating characters. In his 1952 article, however, he considers these characters to be unreliable.

I found that some lobule forms can be characteristic for species. Strongly inflated lobules with one big tooth characterize *O. decemdentata* (Pl. 1F), whereas lobules with 5 or even 6 teeth are found only in *O. rhomalea* (Pl. 5G).

b. Stem anatomy

According to Bischler (1964) characters of the stem anatomy can be used to classify species: "Il est souvent possible de classer une espèce sans équivoque, si on connaît son type d'anatomie de la tige, même si elle peut, selon ses charactères morphologiques, appartenir à deux genres apparantés par leur morphologie (p. ex. *Ptychocoleus* et *Phragmilejeunea, Lopho-* et *Dicranolejeunea, Odonto-* et *Cyclolejeunea*)" (p. 452).

However, she does not use the characters to discriminate the species on species level. I found that the cross section of the stem is more or less similar in all three species as concerns the cortical cells. The diameter of the stem and the number of medullary cells may provide differentiating characters, though. *O. decemdentata* tends to have rather small stems (smaller than 130 μm in diameter) with less than 25 medullary cells (Pl. 1A, B), whereas *O. rhomalea* usually has much larger stems (diameter usually much more than 120 μm, up to 285 μm) with up to 70 medullary cells (Pl. 5A, B). The stem of *O. lunulata* is somewhat intermediate in these respects (Pl. 3A).

c. Underleaves

The shape of the underleaf base of *Odontolejeunea* and especially of *O. rhomalea* (Pl. 5I, J, K), has been subject of repeated discussion. Spruce (1884) considers it a very important character: "My plant I believe perfectly distinct from *L. lunulata,* especially by the sagittate underleaves, produced at each basal angle into a long sharp spur, or spine, and not unlike a swallow's tail, or the tailed wings of a *Papilio,* whence the name I gave it many years ago. *Lejeunea chelidonura*" (p. 147).

Evans (1904) asserts about the acuminate spurs of *O. rhomalea:* "... this peculiarity is not very clearly exhibited ..." and therefore "... the plant is hardly worthy of the specific rank" (p. 191). Herzog (1931), in his description of *O. obversilobula* Herz. (another synonym of *O. rhomalea*) uses the shape of the underleaf base to distinguish this species from *O. chaerophylla* (a synonym of *O. lunulata*).

Evans (1904) gives a very good description of the underleaf base: "The line of insertion is long and sharply arched, and the basal part of the underleaf broadens out so abruptly from this line that it becomes folded upon itself, the fold forming what is apparently the inner edge of a large basal auricle" (p. 185). In fact, the basal margin of the underleaf does not extend beyond the insertion line, so that there are no real auricles (Pl. 3D, 5C); the underleaves of *O. lunulata* may seem to have auricles though.

The shape of the underleaf base proved to be a valuable differentiating character. Acuminate spurs occur in *O. rhomalea* only, although specimens without such spurs also occur in this species. Specimens with a cuneate instead of a cordate base always belong to *O. decemdentata*. In *O. lunulata* the underleaves have cordate bases and the "auricles" may be angular or rounded.

Evans (1904) uses underleaf dentation as a differentiating character between *O. lunulata* and *O. sieberiana* (the latter species is being synonymized with *O. lunulata* here). In *O. sieberiana* the margins are said to be "entire in the basal portion, and, if they are dentate at all, the teeth increase in size toward the plane apex", while "in *O. lunulata* the basal portions often project outward as sharp teeth, while the revolute apex is very minutely denticulate" (p. 190). Underleaf dentation of *O. lunulata* is very variable, however, and underleaves can be heavily dentated to entire. *O. decemdentata* always has untoothed underleaves, while the underleaves of *O. rhomalea* are sharply, frequently even squarrosely dentated.

The underleaf dentation alone is too variable to be of discriminating value but is diagnostic in combination with the shape of the underleafbase. Thus, *O. decemdentata* is characterized by untoothed underleaves with a cuneate base and *O. rhomalea* by squarrosely toothed underleaves with long basal spurs.

All three species have a relatively long tristratose underleaf attachment, consisting of one layer of superior central cells, one layer of modified cortex cells and one layer of 2 or 3 inferior central cells: 2 in *O. lunulata* (Pl. 3B) and *O. decemdentata* (Pl. 1C), and 3 (rarely 2) in *O. rhomalea* (Pl. 5C, D).

Apart from the occasional exception in *O. rhomalea,* the presence of 1-1-2 or 1-1-3 underleaf attachment is a very good species character.

d. Rhizoids

A striking adaptation to the epiphyllous habitat are the large bundles of rhizoids "like a chimney sweeper's brush" (Pearson 1922, p. 217), which provide for the attachment to the living leaf.

Winkler (1967, 1970) made a thorough study of the development of the primary rhizoid disc from which the bundles of rhizoids arise. The primary rhizoid disc develops from the cells forming the elongated underleaf attachment. The cells of the primary rhizoid disc eventually stretch as a result of a "Berührungsreiz" — contact stimulus —, thus forming the rhizoids. The rhizoids can be branched at their apices and often form a secondary rhizoid disc.

I have found no differences between the rhizoids and rhizoid discs of the three species of *Odontolejeunea*'s.

e. Branching

As was also found by Thiers (1985), all three species have *Lejeunea*-type branching and innovations of the *Radula*-type. In addition, I found an occasional *Frullania*-type branch in *O. decemdentata.*

f. Sexuality

O. decemdentata and. *O. rhomalea* are dioic, *O. lunulata* is polyoic (monoic or dioic). The polyoicy of *O. lunulata* has caused a lot of confusion amongst previous authors. Spruce (1884) asserts about *O. chaerophylla* (synonym of *O. lunulata*) that it is "apparently the only monoicous species among the *Odontolejeunea* (p. 148)". About *O. sieberiana,* another synonym of *O. lunulata,* he writes: "Moreover *L. sieberiana* is said to be sterile, and is therefore probably dioicous (Spruce 1895, p. 336)". Schiffner (1893), however, considered *O. sieberiana* and *O. chaerophylla* to be conspecific.

For Evans (1904) sexuality is an important discriminating character and he therefore treats *O. sieberiana* as different from *O. lunulata:* "It will be seen from the descriptions given above that *O. lunulata* and *O. sieberiana* are very closely related species. The most important difference between them is in the inflorescence, which is monoicous in one and dioicous in the other" (p. 190).

Spruce (1895) and Evans (1908) recorded paroicous specimens of *O. sieberiana* but in all the material of *Odontolejeunea* that I have studied, I have never seen a distinctly paroicous specimen!

Vanden Berghen (1952) was the first author to recognize the polyoicy of *O. lunulata.* He also remarks that the African specimens are usually monoicous. I have found that all the African specimens are monoicous, except for some extremely small collections, which are sterile or female.

In cultivation experiments with *Lophocolea heterophylla* and *L. bidentata.* Vogelpoel (1982) found that "the frequency, abundance and vitality of the male and female gametangia of *L. bidentata* can be manipulated in the cultures by different combinations of day length and light intensity" (p. 120). He also found that female and male gametoecia of *L. bidentata* do not necessarily mature simultaneously, and, above all, he could obtain asexual, female and bisexual plants from one clone. If *Odontolejeunea* behaves similarly as *Lophocolea bidentata,* than *O. lunulate* is not really polyoicous, but "just" monoicous. Since cultivation experiments have not been done with *Odontolejeunea,* I consider *O. lunulata* polyoicous.

g. Gametoecia

The length of the male spike is very variable and varies between 250 μm (1-2 pairs of bracts) and 5700 μm (up to 35 pairs). *O. lunulata* and *O. rhomalea* have closely imbricated bracts, but in *O. decemdentata* the spikes can be very tenuous (Pl. 1K). This tenuity causes the impression as if the spike were very long. Specimens of *O. decemdentata* with very tenuous spikes were previously described as *O. longispica* Evans (1908).

The male lobules of *O. decemdentata* differ from those of the other two species in being rounded instead of ellipsoid and bearing a very big tooth instead of a very inconspicuous one or none at all.

The male bracteoles in *O. decemdentata* are lingulate, in *O. rhomalea* they are very broad and in *O. lunulata* they are lingulate to obovate. The margins of the bracteoles are entire except in *O. lunulata,* where they are usually toothed (occasionally entire). In *O. rhomalea* they can occasionally bear a few teeth.

The gynoecium varies in position even in the same species, being sometimes born on a leading branch and sometimes on a short branch. The gynoecium innovates on one side and frequently the innovation itself is repeatedly floriferous. Occasionally the innovation is lacking, though. The innovations are of the *Pycnolejeuneoid*-type (Thiers 1985).

The perianths are obovate and dorsi-ventrally flattened. They usually bear lateral wings, but these may be lacking partially or even totally. Sometimes a short ventral wing occurs. The wings bear teeth, which are the longest in the apical parts, becoming shorter downwards. In *O. decemdentata* the teeth can be ciliate, consisting of a 2-celled base and a unicellular apex of several cells long. In *O. rhomalea* they are usually short and broad, although ciliate teeth occur also. However, these character states are not very constant within the same species.

Female bracts resemble the vegetative leaves, but the lobules are reduced to a small, short slap at the side of the innovation and to a long narrow fold at the other side.

Female bracteoles are entire in *O. decemdentata,* toothed in *O. rhomalea* and usually toothed (occasionally ± entire) in *O. lunulata.*

The differences between the gynoecia of the species — apart from the dentation of the bracteoles perhaps — are to subtile to be of important discriminating value.

h. Sporophyte

The sporophyte of *Odontolejeunea* is of the nodular type (Van Slageren & Berendsen 1985). Only the sporophyte of *O. lunulata* has been studied (Pl. 2D): no sporophytes were found for the other two species.

i. Vegetative reproduction

A very characteristic feature for the genus *Odontolejeunea* is the presence of branch-like propagules, the cladia. According to Goebel (1915) cladia exist only in a very few, epiphyllous genera. A cladium is a modified branchlet with about 2-5 series of leaves and underleaves, which breaks off very easily. The two or three lower leaves differ from normal leaves in that they have a reduced lobule and numerous (much more than usual) rather small teeth along the margin. The apex of these leaves is rounded in *O. rhomalea* (Pl. 5M), acute in *O. lunulata* (Pl. 3O) or extended to a long and narrow accumen in *O. decemdentata* (Pl. 1M). The two lower leaves are pointed towards the base of the cladium.

The first underleaf of the cladium resembles the first underleaf of a normal *Lejeunea*-type branch and is undivided, smooth and cuneate and has no rhizoid

disc. The second underleaf, however, differs very much from normal underleaves, bearing a very dense, circular disc of unbranched rhizoids, which covers the underleaf completely. Towards the apex of the cladium, leaves and underleaves gradually gain their 'normal' features. The cladia are soon branching (Pl. 3O), sometimes even when they are still attached to the stem.

j. Modifications

O. decemdentata often has reduced lobules, leaf cells irregularly orientated and trigones tending to become simple triangular. Moreover, the underleaves are always distant (often in *O. lunulata* as well). These characters, together with the suppression of *Frullania*-type branching, may be hygrophytic modifications (Müller 1951), but this has never been empirically proven for *Odontolejeunea.*

Genus description

The genus is distributed in Central and South America and Africa, ranging in altitude from sealevel up to 3200 m. The highest records are from Ecuador (3200 m) and Colombia (3000 m). The main centres of diversity are Costa Rica, Ecuador and French Guiana, each with all 3 species.

All species of *Odontolejeunea* are epiphyllous, occasionally ramicolous, however.

Stem with leaves 0.8-3.6 mm wide, appressed to substrate, irregularly to regularly branched; herbarium material greenish to brownish; leaf appearance variable when dry, widely spreading, wrinkled, convoluted or revoluted; when wet, always widely spreading, though sometimes with convoluted postical margin; branching predominantly of the *Lejeunea*-type.

Stem in cross section ca. 75-275 μm; cortex consisting of one layer of convex cells, in 10-12(-25) rows, with slightly thickened and brownish cell walls, especially on the ventral side of the stem, surrounding a medulla consisting of 10-70, usually thin-walled cells, the cortical cells wider, higher and much shorter than medullary cells. Ventral merophyte 2 cells wide outside the underleaf insertion, 2(-4) cells within the underleaf insertion.

Mature leaves ovate to broadly ovate; lobe margin sharply dentate throughout, the teeth consisting of 1 to 30(50) cells and terminating in a rhomboic top cell.

Cells isodiametrical, broadly hexagonal to sometimes irregularly shaped, irregularly orientated or arranged in rows, either lengthwise or broadwise; basal cells largest, smaller towards the apex; cell walls with cordate to $\pm$ simple trigones; intermediate thickenings fusiform to elliptical, 1(-2) per each longer cell wall.

Oilbodies homogeneous, *Massula*-type (Schuster & Hattori 1954, Gradstein 6183, obs. Gradstein, Gradstein & Aguirre 6565, obs. Kruijt, Pócs 8410, obs. Pócs).

Lobule round to broadly ovate, 1/6-1/3 $\times$ the length of the lobe, sometimes reduced to a narrow fold; inflated along the keel (forming a watersac) and flattened to

the free margin, the flattened part appressed to the lobe and varying in width; keel curved or almost straight; lobule free margin curved to almost straight, usually flat, in *O. rhomalea* often incurved, with 1-5 teeth; the first tooth of the lobule bearing an entally displaced hyaline papilla. Sometimes 1 or 2 extra hyaline papillas, situated at the outer ends of the insertionline of the leaflobe.

Underleaves entire, orbicular, reniform to ovate, the margins entire to toothed, sometimes even squarrose, the apex rounded to truncate, plane or recurved, the central part of the underleaf flat, but convex in *O. rhomalea;* underleaf base cuneate, in optical view cuneate to cordate, with rounded or angular "auricles" or even with long spurs, the insertion line strongly arched, forming wings along the underleaf attachment, the wings being attached to the stem; cells irregularly shaped with much less pronounced trigones and intermediate thickenings than in leaf lobe cells; a primary rhizoid disc present at the base of most underleaves, usually bearing a stellate bundle of unicellular rhizoids (forming together a secondary rhizoid disc), the rhizoids often more or less irregularly branched at their apices; underleaf attachment to the stem very long, 90-200 μm, in longitudinal section made up of 1 curved superior central cell, 1 cylindrical modified cortex cell and 2-3 inferior central cells, the upper most being curved.

Cladautoicous or dioicous.

Androecia bearing 2-25 pairs of male bracts and bracteoles throughout the spike, but occasionally with sterile lobules at the base or at the apex, the bracts with (1-) 2 antheridia each, the spikes branching occasionally; bracts distant to imbricate, the lobes 1/5-2/3 × the length of a vegetative leaf, the margins entire to toothed; lobules inflated, 1/3-2/3 × the length of the lobe, epistatic, bearing 0-1 tooth; antheridium globular, diameter 70-150 μm, the jacket 3-12 μm thick, the stalk uniseriate, 8-18 μm thick; bracteoles 1/3-1 × the length of underleaves; usually entire, sometimes toothed.

Gynoecium terminating stem, branch or innovation, with 1(-2) *Pycnolejeuneoid* innovations, appearing as if placed laterally, consisting of 1 archegonium surrounded by a beaked perianth and 1 series of 2 bracts and 1 bracteole; female bracts resembling vegetative leaves but the lobules reduced to narrow folds, bearing 0-2 rudimentary teeth (reduced to mere protruding cells); female bracteole 1.5-3.5 times larger than the underleaves, entire, ovate, the central part often very convex, the margins entire to toothed, the teeth usually consisting of 1 sharp, protruding cell.

Perianth obovate, dorsiventrally flattened, with 3 keels: 2 lateral and 1 ventral, the lateral keels almost always sharply winged for up to 2/3 downwards the length of the perianth, the wings bearing teeth or ciliae, the ventral keel very obtuse, usually unwinged, sometimes winged at the upper half of the perianth; beak 2-6 cells long, not or slightly recessed, longer beaks may be toothed.

Sporophyte seen in *O. lunulata* only; seta articulate; capsule valves of the nodular type (Van Slageren & Berendsen 1985), 350-550 × 200-300 μm, opening for 3/4 of their length, bearing 5-6 spiralled elaters of 200-400 μm length.

Spores elongated, irregularly shaped, their surface covered with numerous verrucae and several rosettes (Van Slageren & Berendsen 1985).

Vegetative reproduction by means of cladia (modified branches).

Key to the species

1a Cladia present 2
1b Cladia lacking 3

2a Apex of first 2-3 leaves of cladia rounded ..... *O. rhomalea*
2b Apex of first 2-3 leaves of cladia acute ..... *O. lunulata*
2c Apex of first 2-3 leaves of cladia acuminate ..... *O. decemdentata*

3a Androecia present 4
3b Androecia lacking 5

4a Male bracts distant; male lobules rounded, with a conspicuous, 2 cells long tooth; leaf cells orientated irregularly; underleaf bases cuneate, the margins entire ..... *O. decemdentata*
4b Male bracts imbricated; male lobules ellipsoid, with 0-2 small teeth consisting of one protruding cell only 5

5a Leaves strongly revoluted when dry; leaf cells orientated in transverse rows (extending from antical to postical leaf-margin); underleaf attachment (section) normally 1-1-3, exceptionally 1-1-2 ..... *O. rhomalea*
5b Leaves not or but weakly revoluted when dry; leaf cells orientated irregularly or in length rows (from leafbase to leafapex); underleaf attachment 1-1-2 6

6a Leaf cells orientated irregularly; lobule with 0-1(-2) tooth or reduced; underleaf bases cuneate, the margins entire ..... *O. decemdentata*
6b Leaf cells orientated in lengthrows; lobule with 2-4 teeth; underleaf bases cordate, the margins toothed or, occasionally, entire ..... *O. lunulata*

Species descriptions

Odontolejeunea decemdentata (Spruce) Steph. Plate 1, map 1

Odontolejeunea decemdentata (Spruce) Steph., Spec. Hep. V: 171 (1912); Herzog (1955: 176).
Lejeunea decemdentata Spruce, Trans. Proc. Bot. Soc. Edinburgh **15:** 148 (1884).
Type: "Peru. Bombonasa, in palma foliis", Spruce L215 (MANCH holo, G).

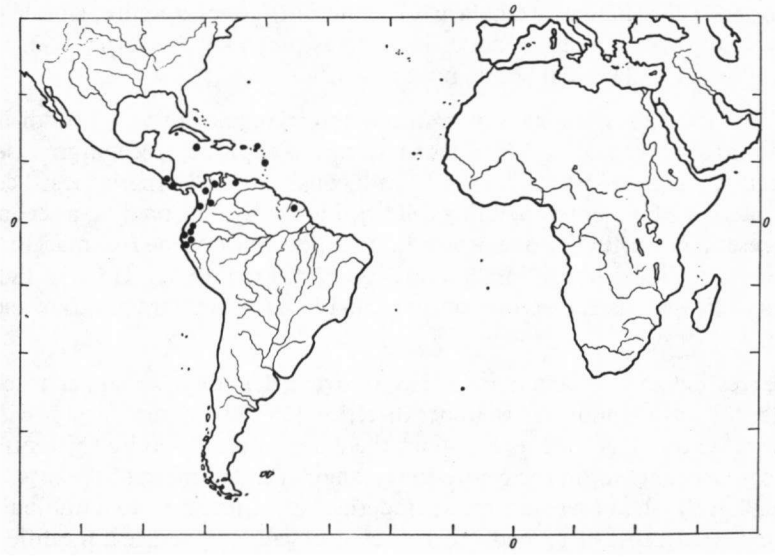
Heterotypic synonyms:

Odontolejeunea longispica Evans, Bull. Torrey Bot. Club **35:** 380 (1908); Stephani (1912: 171) syn. nov.
Type: "Jamaica, Lapland near Catadupa in damp forest, alt. 580 m", Harris 11119 p.p. (YU holo, NY).

Odontolejeunea tocoriensis Steph., Hedwigia **35:** 117 (1896); Stephani (1912: 171).
Type: "Costa Rica, Zuebrada de Tocori (Quebranada)", Tonduz 3077b (G holo, BM).

Nomenclatural notes:

1: Names in Stephani's "Icones Inedits" are considered as not effectively published (art. 29 ICBN).
2: In these cases Stephani did not designate a specimen as the type of a species, the material used for the "Icones Inedits" is considered to be holotypes.



Map. 1: Distribution of *Odontolejeunea decemdentata* (Spruce) Steph.

DISTRIBUTION AND ECOLOGY: Colombia, Costa Rica, Ecuador, French Guiana, Jamaica, Martinique, Saba, Venezuela (map 1); 0-1800 m. In moist, primary forest. On living leaves, occasionally on twigs. *O. decemdentata* is the rarest species of the genus.

Stem with leaves 0.8-1.9 mm wide, appressed to substrate, irregularly branched; herbarium material greenish to brownish; leaves spreading when dry, widely spreading when wet; branches predominantly of the *Lejeunea*-type, occasionally of the *Frullania*-type (Pl. 1J, K).

Stem in cross-section 80-130 μm; cortex in cross section composed of (9-)10-11(-13) cell rows, the cortex cells smooth to slightly convex, the cell walls not or slightly thickened; dorsal cortical cells (10-)15-32 μm high, (10-)15-35 μm wide and 30-70 (-80) μm long, ventral cortical cells slightly darkened, larger than the dorsal cortical cells, 15-50 μm high, 20-45 μm wide and (30-)45-85 μm long; medulla in cross-section composed of 10-23 cells, the cell walls usually not or slightly thickened, the cells (5-)15-25 μm in diameter, up to 5 times narrower than the dorsal cortical cells, (50-)100-150 μm in length (Pl. 1A, B).

Leaf lobe ovate, 0.5-1 × 0.3-0.7 mm, distant to slightly imbricate, inserted along 1/2-2/3 of the length of the merophyte, the apex obtuse, the margin toothed with 5-12 teeth consisting of 1-6(-13) cells, the postical margin usually straight and sometimes untoothed; cells midleaf more or less isodiametrical, 20-45 μm, basal cells

larger, apical cells smaller, irregularly orientated; trigones obscure, simple triangular to weakly cordate; intermediate thickenings narrowly fusiform, 1(-2) per each longer cell wall (Pl. 1D). Oil bodies not known.

Leaf lobule 100-250 × 50-300 μm, reduced and triangular or very roundish, about 3-5(-6) times as short and 2-4(-6) times as narrow as the lobe; free margin inserted on the stem at an angle of 50-150°, with 1 tooth consisting of 2 superimposed cells on a 2-celled base or of a mere protruding cell bearing the hyaline papilla, a second tooth rarely present, consisting of one protruding cell; the apex of the free margin 2-3 cells long from keel to first tooth; lobule sinus 100-175°, lobule apex (115-)130-180(-205)°, keel sinus 125-180°, keel insertion on stem 50-150°, the keel straight to rounded (Pl. 1F, G, H).

Underleaves distant, orbicular to widely obovate, length from upper insertion to apex 115-285 μm, from lower to upper insertion (25-)50-135 μm, largest width 150-295 μm, 1.5-3 times as wide as the stem, the margins plane, entire to crenulate, the cells irregularly angular in the centre to rectangular at the margin, the insertion line arched (Pl. 1E), the bases decurrent; underleaf attachment in longitudinal section 65-115 μm, tristratose, 1 arched superior central cell, 1 cylindrical modified cortex cell, 2 interior central cells (Pl. 1C); primary rhizoid disc present on older underleaves, often absent on younger branches, usually giving rise to secondary rhizoid disc, bearing numerous rhizoids.

Plants dioicous.

Androecia (0.5-)2.5-5.7 mm long; male bracts in 3-15 pairs, distant to serried, 400-570(-700) × 225-400(-435) μm, (1-)1.5-3(-5) times as small as vegetative leaves, the apex obtuse (Pl. 1I), the margin toothed with 3-8 teeth, the teeth mainly situated at the apex, consisting of (1-)3-6 cells; bract lobule very roundish to broadly ellipsoid, (85-)125-250 × (100-)125-250 μm, 2-3 times as small and 1.5-2.5 times as narrow as the lobe, with 1 tooth consisting of 2 superimposed cells on 2-celled base; hyaline papilla usually present, entally displaced, keel very rounded; bracteoles distant, 160-270 × 135-195 μm, the margins plane, entire; mature antheridia 90-115(-130) μm in diameter, the jacket 5-10(-12.5) μm thick, the stalk 10-15 μm in diameter.

Female bracts (475-)600-800(-850) μm, the margins toothed, with (1-)4-12 teeth, the teeth 1-4 cells long and 2-3 cells wide at the base; bract lobules usually reduced to a narrow fold, 100-150(-190) × 40-115 μm with 1(-2) teeth, reduced to protruding cells; bracteoles 375-475(-525) × 250-400(-500) μm, the margins plane, entire to crenulate, the apex obtuse (Pl. 1L).

Perianth emergent for 1/2-2/3 of its length, 675-1250 × 550-650 μm, the lateral wings 1-3 cell rows wide, extending downwards for 1/3-1/2 of the length of the perianth, with 5-9 teeth, mainly at the apex, the teeth 1-4 cells long and 1-2 cells wide at the base; ventral keel bluntly rounded, unwinged; apex with a non-recessed beak of 2-3 cells long.

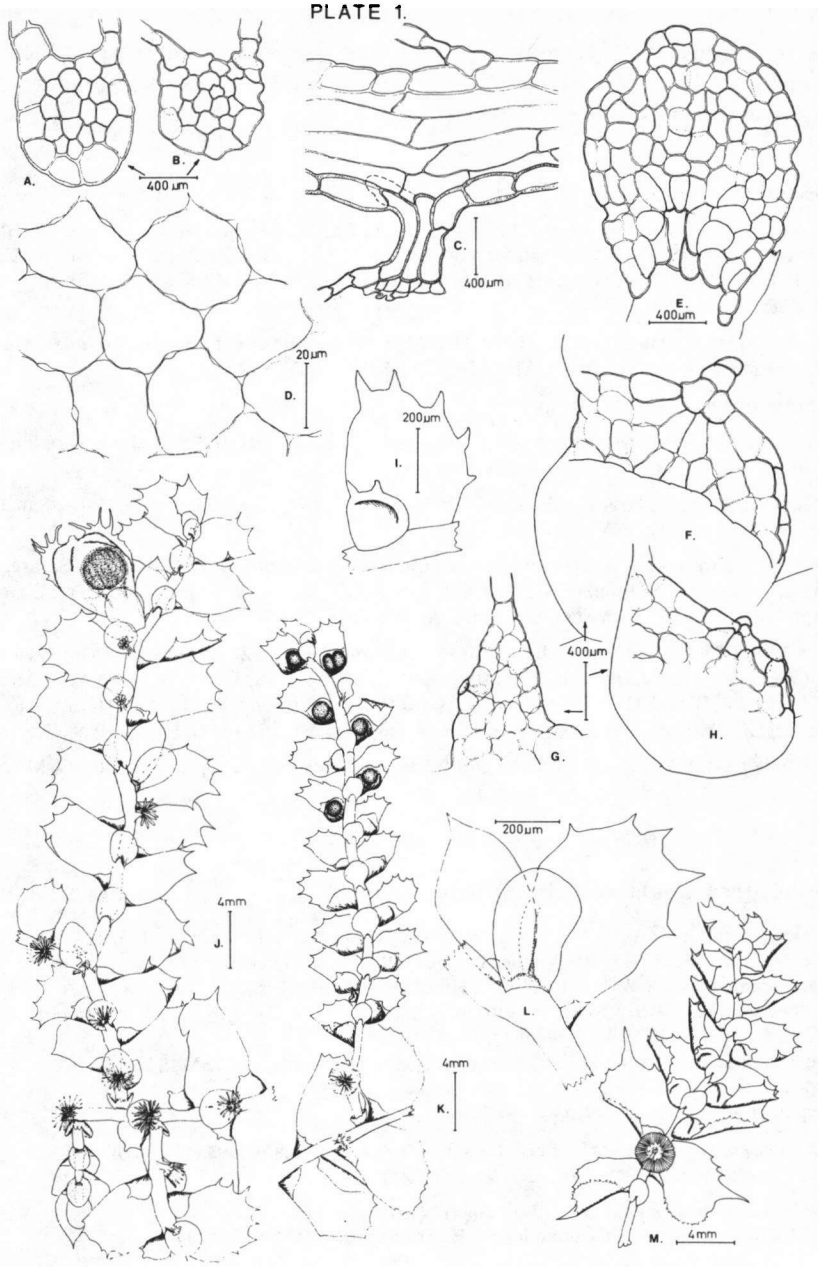


Plate 1. *Odontolejeunea decemdentata* (Spruce) Steph.: A, B. Stems in cross section. C. Underleaf attachment in longitudinal section. D. Leaf cells. E. Underleaf. F. Full grown leaf lobule. G, H. Reduced leaf lobules. I. Male bract. J. Type, habitus ventral of female plant. K. Habitus ventral of male plant. L. Female bracts and bracteole. M. Cladium. — A, I from Apollinaire s.n., 1907. B, C, D, K from Harris 11119 pp, Jamaica (type of *O. longispica* Evans). E, F, G, H, M from Tonduz 3077b, Costa Rica (type of *O. tocoriensis* Steph.). J, L from Spruce L215, Peru (type of *O. decemdentata* (Spruce) Steph.).

Sporophyte not seen.

Cladia numerous, the margins of the lower 3-4 leaves densely toothed with numerous small teeth of 1(-4) cell(-s); apex of the lower 3-4 leaves acuminate, about 7 cells long and 5 cells wide at the base (Pl. 1M).

Specimens seen

COSTA RICA: Zuebrada, Tonduz 3077b, 1893, type of *Odontolejeunea tocoriensis* Steph. (BM, G); Naranjo, Tonduz 15573, 1887 (NY); San Marcos, Tonduz 15576, 1893 (G); Cordillera Central, Alajuela, Eggers CR 1,36, 1985 (U); Guanacaste, El Arenal, Standley & Valerio 45161a, 1926 (JE, S); Pittier & Durand 8528, 1894 (JE).

JAMAICA: Lapland, near Catadupa, Harris 11, 119 pp, 1906, type of *Odontolejeunea longispica* Evans (NY, YU); Seamen's Valley, Portland, Maxon & Killip 8, 1920 (NY, S).

SABA: Suringar s.n., 1885 (L).

FRENCH GUIANA: Saül, Mt Galbao, alt. 670 m, Bekker 2322, 1986 (U); Saül, Mt Galbao, alt. 650 m, ORSTOM 3951, 1976 (U).

VENEZUELA: Aragua, Maracay, Onraedt 78 V 5645a, 1978 (JE); Sierra de Perija, Zulia, San José de los Altos, Griffin 188, 1975 (NY, U).

COLOMBIA: Between Cali and Buenaventure, alt. 1200 m, Bischler 489, 1958 (U); Sarare, Santa Librada, alt. 1300-1600 m, Bischler 2009, 1959 (U); Andes of Bogota, Weis s.n., 1906 (NY); Bogota, La Vega, Apollinaire s.n. (G); La Vega pres Bogota, Apollinaire s.n., 1907 (NY).

ECUADOR: Los Rios, Elementina, alt. 300 m, Harling 296, 519, 520, 2145, 2137 and 5538, 1947 (JE, S); Santiago-Zamora, Méndez, alt. 700 m, Harling 969 or., 1947 (JE, S, UPS); Napo-Pastaza, Mera, alt. 1160 m, Harling 3170 and 3183, 1958 (S, UPS); Napo-Pastaza, El Topo, alt. 1250 m, Harling 3409, 1958 (S); Chimborazo, Spruce s.n. (MANCH); Azuay, Gualaquiza, Allioni 6484 and 6591, 1909 (G, S).

PERU: Bombonasa, Spruce L215, type of *Odontolejeunea decemdentata* (Spruce) Steph. (G, MANCH).

Odontolejeunea lunulata (Web.) Schiffn. Plate 2-3, map 2

Odontolejeunea lunulata (Web.) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. I, 3: 128 (1893); Evans (1904: 186); Herzog (1931: 340); Vanden Berghen (1952: 166); Herzog (1957: 52).
Jungermannia lunulata Web., Hist. Musc. Hepat. Prodr.: 33 (1815).
Lejeunea lunulata (Web.) Nees, in Gottsche, Lindenberg & Nees, Syn. Hep. 326 (1845); Gottsche (1863: 288); Spruce (1884: 145); Stephani (1890: 19).
Type "E regionibus tropicis in foliis Musae cuiusdam", Sprengler s.n. (BM, S).

Heterotypic synonyms:

Odontolejeunea angustifolia Steph., Spec. Hep. V: 176 (1912); Pearson (1922: 220) syn. nov.
Type: "Insula Dominica", Elliott 1200 p.p. (G holo).

Odontolejeunea armetagei Pearson, J. Bot. **60**: 217 (1922) syn. nov.
Type: "Dominica, W. I., Mountain lake", E. Armitage s.n. (MANCH holo).

Odontolejeunea calcarata (Mont.) Steph., Spec. Hep. V: 171 (1912); Spruce (1884: 146); Herzog (1931: 340); Herzog (1952: 88); Herzog (1955: 199); Herzog (1957: 52).
Phragmicoma calcarata Mont., Ann. Sci. Nat. (Paris) **19**: 259 (1843); Gottsche (1845: 326); non Mitten (1873: 413).
Lejeunea lunulata fo. *calcarata* (Mont.) Gott. Lindenb. & Nees, Syn. Hep: 326 (1845).
Type: "Ad folia repens in sylvis Surinamensibus", Splitgerber 1206 (PC-Montagne holo, BM, G, L).

Note: Most authors (e.g. Spruce 1884, Stephani 1912) misapplied the name *O. calcarata* for *O. rhomalea* as presently understood.

Odontolejeunea chaerophylla (Spruce) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. I, 3(1): 127 (1893); Stephani (1895: 239); Schiffner (1897: 588); Stephani (1912: 172); Herzog (1931: 340) syn. nov.
Lejeunea chaerophylla Spruce, Trans. Proc. Bot. Soc. Edinburgh **15:** 147 (1884); Spruce (1895: 336).
Type: "Andes Peruvianensis et Quitensis, Tarapoto, alt. 600 m, in foliis vivis", Spruce s.n. (MANCH holo, BM).

Odontolejeunea chaerophylla fo. *brachycolea* Herz., in Feddes Repert. **57:**(1/2): 199 (1955), syn. nov.
Type: "Peru, Dep. Junin, Pichis Trail, Yapas, 1350-1600 m, dense forest, on leaves, Killip 25559 pp." (JE, holo).

Odontolejeunea chaerophylla var. *multiserrata* Herz., in Feddes Repert. **57**(1/2): 199 (1955), syn. nov.
Type: "Peru, Dep. Junin, Pichis Trail, Yapas, 1350-1600 m, dense forest, on leaves, Killip 25559 pp." (JE, holo).

Odontolejeunea chaerophylla var. *paroica* Spruce, J. Linn. Soc., Bot. **30:** 336 (1895), nom. nud.

Odontolejeunea cubensis Steph., Spec. Hep. V: 179 (1913) syn. nov.
Type: "Cuba", Wright s.n. (G holo).

Odontolejeunea ecuadoriensis Steph., Spec. Hep. V: 179 (1913) syn. nov.
Type: "Ecuador, Azuay. Gualaquiza, jucta via, inter Derrumbo et Rosario", Allioni 6553 (G holo).

Cyclolejeunea elliottii Steph., Spec. Hep. V: 185 (1913), syn. nov.
Type: "Dominica, Elliott 1769 e.p. (G holo).

Dicranolejeunea grossiloba Steph., Spec. Hep. V: 166 (1912), syn. nov.; Kruijt (1988: 113).
Type: "Ecuador", (G holo).

Dicranolejeunea herzogiana Steph., Biblioth. Bot. **87:** 253 (1916), syn. nov.; Kruijt (1988: 113).
Lectotype: "Bolivia, Tablas, 1800 m, Herzog 4603"; designated by Kruijt 1988 (G lecto).

Odontolejeunea levistipula Steph., Spec. Hep. V: 181 (1913) syn. nov.
Type: "Brasilia", Dusén 8395 (G holo).

Lejeunea lunulata fo. *pallida* Gott., Lindenb. & Nees, Syn. Hep.: 326 (1845), syn. nov.
Type: "In regionibus tropicis ad Musae folia etiam in alio ex Hispaniola insula ad lato." (S).

Lejeunea lunulata fo. *fusca* Gott., Lindenb. & Nees, Syn. Hep.: 326 (1845), syn. nov.
Type: "In regionibus tropicis ad Musae folis (etiam) in frondibus filicum ex Insul. Guadalupa." (S).

Lejeunea lunulata fo. *lobulata* Gott., Kongel. Danske Vidensk-Selsk. Skr. **6:** 288 (1863).
Type: Not seen.
Judging from the original description, this species is placed in the synonymy of *O. lunulata.*

Lejeunea lunulata fo. *pinnata* Gott., Lindenb. & Nees, Syn. Hep.: 327 (1845).
Type: "In follis Dareae silvarum prope Sta. Anna Brasiliae, leg. Beyrich." (BM, G, S).

Odontolejeunea lunulata var. *calcarata* (Mont.) Herz. (1957), nom. inval., art. 43.1 ICBN.

Lejeunea lunulata var. *major* Gott., Lindenb. & Nees, Syn. Hep.: 752 (1847).
Type: "Mirador Mexicanorum, ubi etiam forma originalis in folio Amomi a cel. Liebman lecta est." (Not seen).
Judging from the original description, this species is placed in the synonymy of *O. lunulata.*

Odontolejeunea lunulata var. *paucidentata* Pearson, J. Bot. **60:** 220 (1922), syn. nov.
Type: "Brasilia, opp. Caldas, Oct. 1854, G.A. Lindberg S.O.L.". (BM holo, L, MANCH, S).

Odontolejeunea martinicensis (Lindenb.) Steph., Spec. Hep. V: 171 (1912).
Lejeunea martinicensis Lindenb., in Gottsche, Lindenberg & Nees, Syn. Hep.: 328 (1845); Stephani (1890: 20); Evans (1904: 186).
Type: "Martinique, in folio Cordiae laevigatae", Sieber s.n. (S holo, G).

Odontolejeunea mauritiana Steph., Spec. Hep. V: 172 (1912), syn. nov.
Type: "Insula Mauritius", (not seen).
Judging from the original description, this species is placed in the synonymy of *O. lunulata*.

Odontolejeunea nigrescens Steph., Spec. Hep. V: 181 (1913), syn. nov.
Type: "Ecuador, Cerier", Allioni 6557 (G holo).

Phragmicoma palisotii Tayl. ex Mitt., J. Linn. Soc., Bot., **22**: 324 (1886); Vanden Berghen (1952: 166), nom. inval.
Material: "Oware, P. de Beauvois s.n." (NY).

Odontolejeunea paranensis Steph., Spec. Hep. V: 180 (1913), syn. nov.
Type: "Brasilia, Parana, Etarunandes, Peirheiso", Dusén 4378 (G holo).

Jungermannia phyllogenides Brid.; Gottsche, Lindenberg & Nees (1845: 327); Evans (1904: 186); syn. fide Lehm. & Lindenb. (Gottsche, Lindenberg & Nees 1845: 327).
Type: Not seen.

Odontolejeunea sieberiana (Gott.) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. I, 3: 127 (1893); Schiffner (1897: 588); Evans (1904: 188); Evans (1908: 382); Vanden Berghen (1952: 166); Herzog (1957: 55); Schiffner & Arnell (1964: 112).
Odontolejeunea sieberiana (Gott.) Steph., Spec. Hep. V: 171 (1912); Bischler (1964: 425).
Lejeunea sieberiana Gott., in Gottsche, Lindenberg & Nees, Syn. Hep.: 328 (1845); Spruce (1884: 143); Stephani (1892: 171); Stephani (1895: 238).
Type: "Mauritius, Memecylo cordato", Sieber s.n. (S).

Odontolejeunea sieberiana var. *africana* Steph. (1892), nom. inval.

Odontolejeunea sieberiana var. *spinosa* Arnell, österr. Akad. Wiss. Math.-Naturw. Kl. Denkschr. III. Band: 112 (1964), syn. nov.
Type: "Schiffner 156, Hb. W." (FH holo) (not seen).
Paratypes: Schiffner 199, 988, s.n. (UPS).

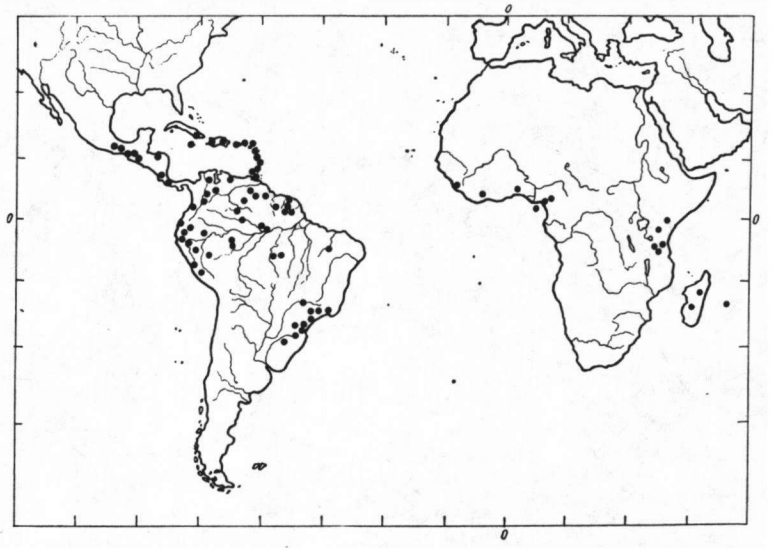
Odontolejeunea spiniloba Steph., Spec. Hep. V: 180 (1913), syn. nov.
Type: "Ecuador, Azuay, Gualaquiza, in silva jupta domum Kayapa", Allioni 6588 (G holo).

Odontolejeunea thomeensis Steph., Spec. Hep. V: 174 (1912); Vanden Berghen (1952: 168): Herzog 1957: 58).
Type: "Africana occidentalis, Insula St. Thomé", Moller inter 7 (G holo).

Odontolejeunea tortuosa (Lehm. & Lindenb.) Steph., Spec. Hep. V: 171 (1912); Vanden Berghen (1952: 166); Vanden Berghen (1962: 52); Bischler (1964: 425); Jones & Harrington (1983: 269).
Lejeunea tortuosa Lehm. & Lindenb., Syn. Hep.: 327 (1845); Mitten (1886: 324).
Jungermannia tortuosa Lehm. & Lindenb., in Lehmann, Novarum et minus cognitarum stirpium Pugillus 4: 50 (1832).
Type: "Africa, Oware", (S holo, G, MANCH, W vide Stephani 1890: 20, not seen).

Lejeunea tortuosa var. *viridis* Gott., Lindenb. & Nees, Syn. Hep.: 327 (1845).
Type: "Porto Rico, Balbisio, in folio Citri Aurantii", (G, S).

DISTRIBUTION AND ECOLOGY: Bolivia, Brasil, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, Ecuador, French Guiana, Grenada, Guadeloupe, Guatemala, Guyana, Haiti, Honduras, Jamaica, Martinique, Mexico, Mont Serat, Peru, Puerto Rico, Saba, St. Eustatius, St. Thomas, Suriname, Trinidad, Venezuela; Camerun, Ivory Coast, Kenya, Macabé, Madagascar, Mauritius, Mozambique, Nigeria, San Thomé, Sierra Leone, Tanzania (map 2); 0-3000 m. Very common in moist, primary or secondary forest. On living leaves, occasionally on twigs or on bark, very rarely on humid soil. *O. lunulata* is the most common species of the genus in South America and the only one occurring in Africa. In South America the



Map. 2: Distribution of *Odontolejeunea lunulata* (Web.) Schiffn.

species may be dioicous or monoicous, whereas in Africa it is normally monoicous — except for some extremely small collections, which are sterile or female —.

Stem with leaves 1-3 mm wide, appressed to substrate, regularly pinnate to irregularly branched; herbarium material greenish to brownish; leaves very variable when dry, spreading, convoluted postically or both postically and antically, crisped, widely spreading when wet, but postical margin may be convoluted; vegetative branches of the *Lejeunea*-type (Pl. 2A, B, C).

Stem in cross-section 70-155 μm; cortex in cross section composed of 10-12 cell rows, the cortex cells smooth to slightly convex, the cell walls not or slightly thickened; dorsal cortical cells 15-32 μm high, 12-30(-50) μm wide and 25-70 μm long, ventral cortical cells about the same size as or slightly larger than the dorsal cortical cells, 10-35 μm high, 20-55 μm high wide and 25-80 μm long; medulla in cross-section composed of 10-55 cells, the cell walls slightly thickened, the cells up to 5 times narrower than the dorsal cortical cells, 4-35 μm in diameter and 60-200 μm in length (Pl. 3A, B).

Leaf lobe narrowly to broadly ovate, 0.5-2 × 0.3-1.3 mm, serried to slightly imbricate, inserted along 1/3-1/2(-2/3) of the length of the merophyte, the apex obtuse, the margin toothed with (3-)7-24 teeth, each tooth consisting of 1 up to 10 cells, the postical tooth being much bigger, up to 30 cells; leaf cells isodiametrical, (15-)20-35

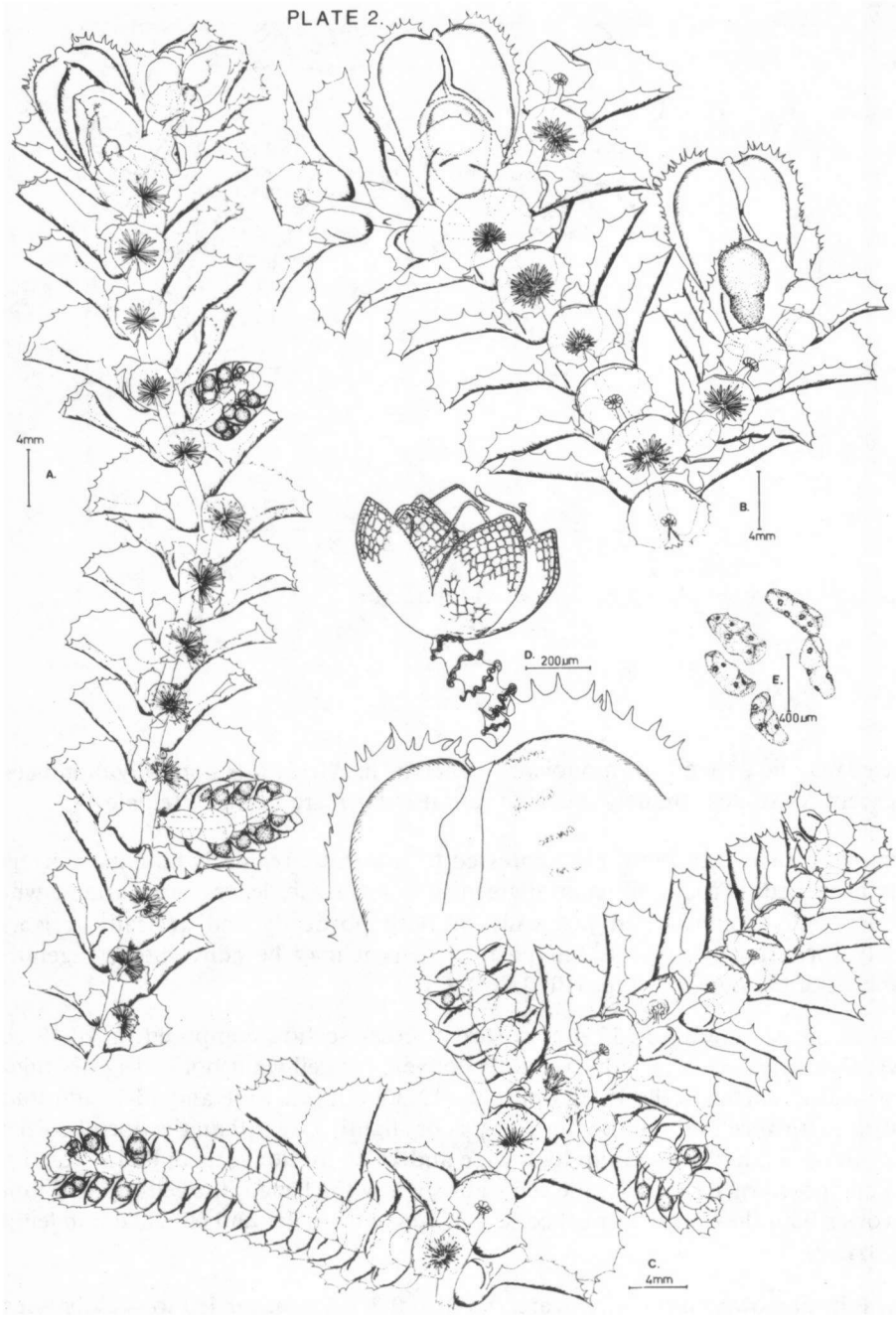


Plate 2. *Odontolejeunea lunulata* (Web.) Schiffn.: A. Habitus ventral of autoicous plant. B. Habitus ventral of female plant. C. Habitus ventral of male plant. D. Sporophyte. E. Spores. — Notice the difference between the male spikes of A and C. — A from Spruce s.n., Peru (type of *O. chaerophylla* (Spruce) Schiffn.). B, C, D, E from Allioni 6588, Ecuador (type of *O. spiniloba* Steph.).

(-45) μm, orientated in lengthrows mainly; trigones cordate; intermediate thickenings ellipsoid to fusiform, 1(-2) per each longer cell wall (Pl. 3C); oil bodies of the *Massula*-type, 6-25 per cell (Schuster & Hattori 1954; del. Pócs 8410, E. Africa, Usambava Mts, February 1984, obs. Pócs; del Gradstein & Aguirre 6565, Colombia, Merenberg, obs. Kruijt; del. Bekker 1709, Surinam, Kabalebo Dam, obs. Gradstein; del. Hegewald 7888 & 8294, Peru, Huanco, Prov. Leoncio Prado, Tingo Maria, obs. Gradstein).

Leaf lobule 160-545 × 125-620 μm, about 2-4 times as small and 1.5-4.5 times as narrow as the lobe; free margin inserted on the stem at an angle of 100-165 °, with 2-4 teeth, the teeth straight or incurved, consisting of 2-3 superimposed cells on a 2-celled base or of mere protruding cells (Pl. 3H, I); the apex of the free margin 2-4 (-6) cells long from keel to first tooth; lobule sinus 35-170°, lobule apex (80-)130-180 (-210)°, keel sinus (70-)110-180°, keel insertion on stem 20-140°, the keel rounded.

Underleaves reniform to orbicular, entire, length from upper insertion to apex 170-630 μm, from lower to upper insertion 50-300(-500) μm, largest width 220-850 (-1200) μm, (2-)2.5-5.5(-7) times as wide as the stem, the margins occasionally entire, usually scarsely to rather heavily toothed, 2-25 teeth, the teeth consisting of protruding cells of 5-12 μm long, the cells in the centre irregularly angular to rectangular or square at the margin, the insertion line arched, the bases decurrent (Pl. 3D, E, F, G); underleaf attachment in longitudinal section 85-210 μm long, 1 arched superior central cell, 1 cylindrical modified cortex cell, 2 inferior central cells; primary rhizoid disc present, usually giving rise to a second rhizoid disc bearing numerous rhizoids (Pl. 3B).

Plants monoicous or dioicous (Pl. 2A, B, C).

Androecia 0.2-2.2 mm long; male bracts in 1-17 pairs, imbricate, (135-)225-550 μm, 2-6 times as small and 1.5-5.5 times as narrow as vegetative leaves, the apex obtuse or acute, the margin usually entire or with 1-10 teeth; bract lobule (115-)175-400 × 115-345 μm, 1-1.5(-2) times as small and 1-2(-2.5) times as narrow as the lobe, without teeth or with 1 very small tooth reduced to a mere protruding cell; keel slightly rounded (Pl. 3J, K, L, M); bracteoles imbricate, 125-300 × (95-)140-310(-420) μm, the margin usually entire, sometimes with up to 12 teeth consisting of protruding cells; mature antheridia 75-125 μm in diameter, the jacket 4-12 μm thick, the stalk 8-17 μm in diameter.

Female bracts ellipsoid to ovate, 500-1350(-2000) × 350-1000(-1215) μm, the margin toothed, 10-26 teeth; bract lobules reduced to a narrow fold, at the side of the innovation reduced to a small slap, 65-335 × 45-185 μm, without teeth or with 1(-2) teeth usually reduced to protruding cells; bracteole ellipsoid to obovate, 500-925(-1135) × (360-)450-850(-1050) μm, the margin usually toothed with (0-)5-15(-25) teeth, plane or slightly incurved, the apex obtuse (Pl. 3N).

Perianth emergent for 1/3-1/2 of its length, 840-1365 × 500-1275 μm, the lateral wings 2-6 cellrows wide, extending downwards for 1/3-2/3 of the length of the perianth, with 3-21 teeth, situated at the apex mainly, the teeth 1-4 cells long and 1-2 (-3) cells wide at the base; ventral keel bluntly rounded, wing usually absent or if

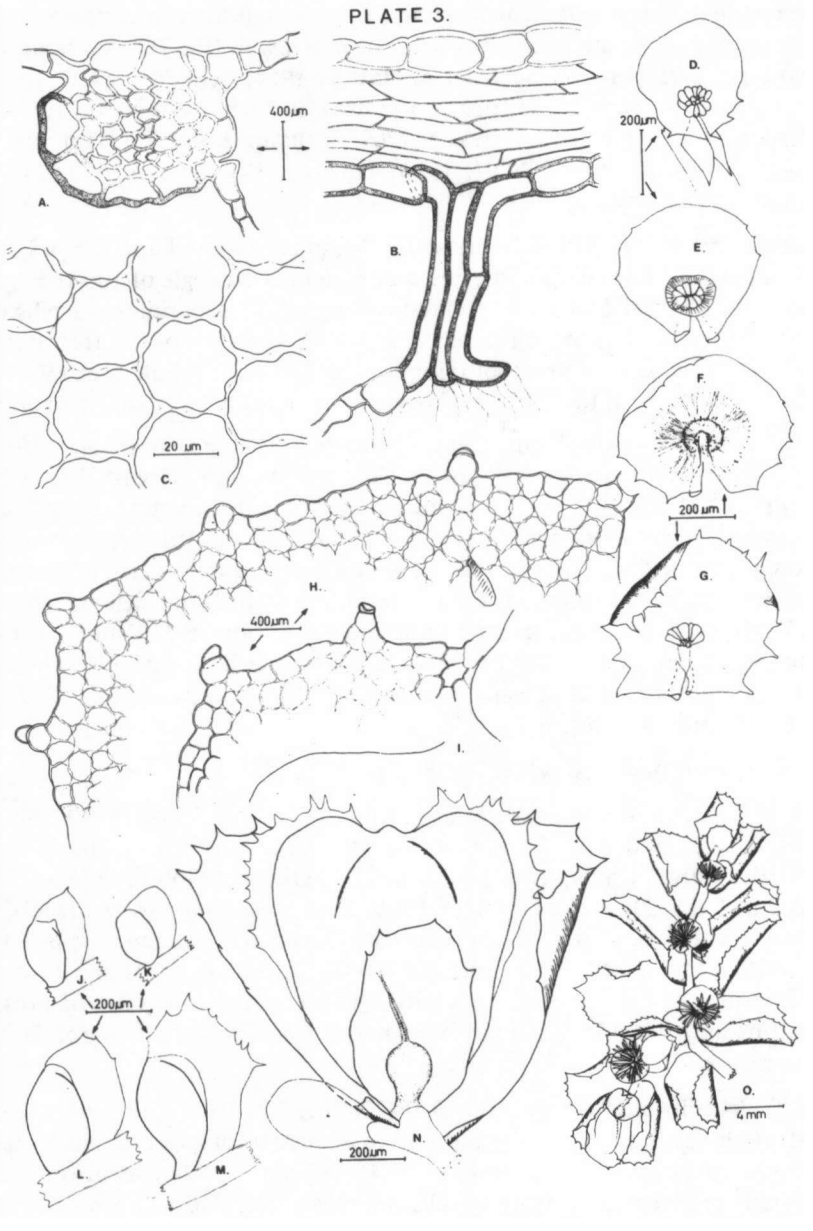


Plate 3. *Odontolejeunea lunulata* (Web.) Schiffn.: A. Stem in cross section. B. Underleaf attachment in longitudinal section. C. Leaf cells. D, E, F, G. Underleaves. H, I. Leaf lobule margins. J, K, L, M. Male bracts. N. Female bracts and bracteole and perianth. O. Cladium. — A, B, H from Allioni 6557, Ecuador (type of *O. nigrescens* Steph.). C, F, I, L, M from Allioni 6588, Ecuador (type of *O. spiniloba* Steph.). D, J, K from Armitage s.n., Dominica (type of *O. armitagei* Pearson). E, N from Dusén 452, Kamerun. G from Sprengler s.n. (type of *O. lunulata* (Web.) Schiffn.). O from Sieber s.n., Mauritius (type of *O. sieberiana* (Gott.) Schiffn.).

present extending downwards for 1/4-2/3 of the length of the perianth, 0-7 teeth; apex with a slightly or non-recessed beak of (2-)3-5(-6) cells long, the beak usually untoothed, occasionally with up to 6 teeth (Pl. 2D, 3N).

Sporophyte valves 410-550 × 200-285 μm, the elaters 210-400 μm long; seta articulate (Pl. 2D); spores 45-80 × 15-35 μm (Pl. 2E).

Cladia may be present; apex of basal leaves acute, the margins densely toothed with numerous small teeth (Pl. 3O).

Note: The Dominican specimens of *O. lunulata* look a bit different from the ones from other localities (e.g. narrow leaves and lobules, rather small underleaves), yet fall within the range of variability of this species. Stephani (1912) described the Dominican plants as *Odontolejeunea angustifolia* Steph. and Pearson (1922) described them as *Odontolejeunea armitagei* Pearson.

Selected specimens seen

MEXICO: Chaipas, between Pueblo Nuevo Solistahuancan and Simojovel, Sharp s.n., 1962 (NY); Chiapas, Tapachula, Benito Juarez, alt. 1300-1500 m, Eggers & Frahm MX 34,3, 1979 (U); Chiapas, Lagunas de Montebello, alt. 1500 m, Eggers & Frahm MX 34,04, 1979 (U); Chiapas, Agua azul, alt. 250 m, Eggers & Frahm MX 25,1 1979 (U); Oaxaca, alt. 2100 m, Vitt 17736a, 1976 (JE).

GUATEMALA: Alta Verapaz, Cubilquitz, alt. 350m, Türckheim 5067, 1906 (G, NY); Alta Verapaz, between Senahu and Actalá, Maxon & Hay 3322a, 1905 (YU); Alta Verapaz, near Tactic, alt. 1500-1650 m, Standley 69994, 1939 (NY).

HONDURAS: Atlántida, near Tela, alt. 20-600 m, Standley 55586, 1928 (S).

COSTA RICA: Cartago, Tapanti, alt. 1000-1500 m, Griffin & Eakin 321-B, 1973 (U); Santiago, alt. 1050 m, Maxon 99, 1906 (NY, YU); Puntarenas, Cordillera de Tilaran, alt. 1600 m, Eggers CR 5,47, 1985 (U); Buenos Aires, Cobayra, Tonduz 15567, 1892 (G); Esmeralda, alt. 2000 m, Tonduz s.n., 1890 (G); Talamanca, Shirores, alt. 100 m, Tonduz 15502, 1895 (G); Limon, near Cairo, alt. 55 m, Standley & Valerio 48676, 1926 (JE); Herdia, Yerba Buena, alt. 200 m, Standley & Valerio 49802, 1926 (JE); forêts Raucho Flores, Pittier 6041, 1890 (G); Boruca, Tonduz 15507, 1891 (G); Rio Naranjo, Tonduz 15573, 1897 (G).

CUBA: s. loc., Wright s.n., type of *Odontolejeunea cubensis* Steph. (G); Monte Verde, Wright s.n. (YU); Sierra Maestra, Gran Piedra, alt. 1100 m, Pocs & Reyes 9058/S, 1978 (HAC); Sierra de Nipe, Rio Piloto, Ekman 10090, 1919 (UPS); Guatanamo, near Campamento Gupeyal, Schubert s.n., 1968 (JE); Guatanamo, Baracoa, alt. 450-540 m, Pócs & Reyes 9064/BZ, 1978 (HAC).

JAMAICA: Cinchiona, John Crow Peak, Britton 221, 1906 (NY, YU); Mount Diabolo, alt. 610 m, Underwood 1806 pp, 1903 (YU); Cooks Bottom, St. Elisabeth, alt. 400-450 m, Maxon & Killip 1467, 1920 (NY, YU); Clyde Valley, Evans 266, 1903 (YU); Portland, near Hardwar Gap, alt. 1220 m, Griffin 021753, 1968 (U); Morcés Gap, Evans 55, 1903 (BM, NY, YU); St. Catherine's Peak, Evans 426, 1906 (NY, YU); Sulphur River Bath, Evans 319, 1903 (BM, NY, YU); Bog Walk, Evans 619, 1906 (NY, YU); "Belvidere" Montpellier, Britton 606a, 1908 (NY, YU).

HAITI: s. loc., Lindberg s.n., 1830, type of *Lejeunea lunulata* fo. *pallida* Gott., Lindenb. & Nees (S); s. loc., Sprengel s.n. (BM); Massif de la Selle, Riviere Blanche, alt. 1650-1800 m, Judd 4591/b, 1984 (JE); Azua, Santo Domingo, Cordillera Central, alt. 1300-1400 m, Ehrman H6334a, 1926 (JE).

PUERTO RICO: Mount Morales, near Utuado, Howe 1094, 1906 (NY, YU); Indiera Fria, Maricao, alt. 430-800 m, Britton, Cowell, Stewardson & Brown 4391, 1915 (NY, YU); Sierra de Yabucoa, alt. 250-550 m, Britton, Britton & Earle 6317, 1922 (NY, YU); Alto de la Bandera, near Adjuntas, Britton & Marble 2161, 1913 (NY, YU); Luquillo Moutains, El Verde, Blomquist 12568, 1942 (NY); Luquillo Mountains, El Yunque, Evans 182, 1902 (NY, YU).

MONT SERRAT: Chances Pond, Shafer 926b, 1907 (NY, YU).

GUADELOUPE: Basse-Terre, sentier du Morne Léger, alt. 600 m, leg. ? 23598, 1976 (JE); without information, type of *Lejeunea lunulata* fo. *fusca* Gott., Lindenb. & Nees (S); Morne Pavillox, Trou aux

Trois Diable, alt. 560-630 m, Duss 56, 1898 (G, NY); La Désirée, alt. 540 m, Duss 303, 1898 (G, NY); Morne Graine-Verte, Duss 449, 1901 (NY); Bois des Banis-Jannes, Duss 1017, 1903 (G, NY).

DOMINICA: s. loc., Elliott 1200 pp, type of *Odontolejeunea angustifolia* Steph. (G); s. loc., Elliott 1769 ep, type of *Cyclolejeunea elliottii* Steph. (G); Mountain Lake, Armitage s.n., 1896, type of *Odontolejeunea armitagei* Pearson (MANCH); Morne Trois Pitons, Elliott 760, 1892 (BM); Mount Couronne, Spruce E233 (MANCH); Laudat, Lloyd 324a pp, 1903 (NY, YU); Soufriere, Lloyd 547, 1903 (NY, YU).

MARTINIQUE: s. loc., Sieber s.n., type of *Odontolejeunea martinicensis* (Lindenb.) Steph. (G, S); s. loc., Sieber 35 (BM); Bois de la Médaille, Duss 1189, 1903 (NY); Pitons de Fort de France, alt. 700-900 m, Duss 379, 1900 (NY); Deux-Choux, Duss 401, 1901 (NY, YU).

ST VINCENT: Richmond Peak, Elliott 356, 1892 (BM).

GRENADA: Grand Etang, Thaxter s.n., 1913 (YU); s. loc., Broadway s.n., 1895 (BM).

TRINIDAD: Ortinola Estate, Coker & Rowland 1544, 1920 (NY, YU); Mount Tocuche, Britton, Coker & Rowland, 1476, 1920 (YU); Valencia, Britton, Coker & Rowland 1849, 1920 (NY, YU); Morne Bleu, Britton 2303, 1921 (NY, YU); Spring Hill, Fleming s.n., 1960 (NY); Port of Spain, Thaxter s.n., 1913 (YU).

GUYANA: Upper Mazaruni district, Jawalla, alt. 500 m, Gradstein 4850, 1985 (U); Upper Mazaruni district, Mt Latipu, alt. 600 m, Gradstein 5657, 1985 (U); Junction of Mazaruni and Cuyuni Rivers, Graham 293a, 1924 (YU); Kanuku Mts., Cool-wind Mt, alt. 500-800 m, Jansen-Jacobs et al. 389B (U); Bartica, Essequibo River, Richards 492, 1929 (BM, YU).

SURINAME: s. loc., Splitgerber s.n., type of *Phragmicoma calcarata* Mont. (G, L, PC-MONT); Nassau, Lanjouw & Lindeman 2207f, 1949 (U); Lely Mts, alt. 550-710 m, Lindeman et al. 556D, 1975 (U); Brownsberg, alt. 450 m, Gradstein 4686, 1985 (U); Mapane Creek area, Schulz 7726af, 1956 (U).

FRENCH GUIANA: Montagne de Cacao, alt. 150 m, Aptroot 15588a, 1985 (U); Saül, piedmont of Mt Galbao, ORSTOM 3940/a, 1976 (U); Ht Tampoc, Saut Pier Kourou, ORSTROM 4635, 1977 (JE, U); Godebert, Wackenheim 272 (U).

BRAZIL: s. loc., Dusén 8395, 1910, type of *Odontolejeunea levistipula* Steph. (G); s. loc., Beyrich s.n., type of *Lejeunea lunulata* fo. *pinnata* Gott., Lindenb. & Nees (BM, G, S); Jutica, Varadours, Lützelburg 23753 (JE); Santos Sorororaba, Motén 105, 1875 (S); Oyapock, Lützelburg 20170, 1927 (JE); Amazonas, Edo do Acre, Rio Moa, Prance et al. 12539, 1971 (NY); Amazonas, Rio Cunhua, Deni Indian Village, Prance et al. 16508, 1971 (NY); Amazonas, between Manaus and Caracarai, alt. 50 m, Griffin, Vital & Yano 561, 1974 (U); Amazonas, Manaus, Nelson 19, 1974 (NY); Amazonas, San Gabriel da Cachoeira, Spruce s.n. (NY); Amazonas, San Carlos, Spruce s.n. (BM, G, MANCH, YU); Roraima, Apiahy, Puiggari 846 (G); Roraima, Auaris, alt. 800 m, Prance et al. 21516, 1974 (NY); Pará, Tanaú, Spruce s.n. (MANCH); Pará, Serro do Cachimbo, alt. 400 m, Reese 16060, 1983 (NY); Minas Geraes, Caldas in Serra, Mosén Ff, 1873 (G, S, UPS); Caldas, Lindberg s.n., 1854 type of *Odontolejeunea lunulata* var. *paucidentata* Pearson (BM); São Paulo, Reserva Florestal de Sete Barras, Vital 7120, 1977 (JE); São Paulo, Fazenda Sanharao, Barra de Turvo, Vital 2791c, 1973 (U); São Paulo, near Cerqueira-Cesar, alt. 500 m, Wettstein et al. 2382, 1901 (UPS); São Paulo, near Rio Grande, alt. 800 m, Wettstein et al. 691, 1901 (UPS); São Paulo, near Barra Mansa, alt. 1000 m, Schiffner 1839, 1901 (UPS); São Paulo, Alto da Serra, Hoehne 533, 1922 (JE); Rio de Janeiro, Glaziou 18019, 1889 (G); Paraná, Etarunandes, Peirheiso, Dusén 4378, 1904, type of *Odontolejeunea paranensis* Steph. (G); Paraná, Serra do Mac, Dusén s.n., 1915 (S); Paraná, Roca nova, Dusén 14, 1909 (YU7; Rio Grande do Sul, Excolonia Sante Angelo, Lindeman s.n., 1893 (S, UPS).

VENEZUELA: Amazonas, San Carlos de Rio Alegro, Delascio, Christenia, Broome 3999, 1981 (U); St. Bolivas, near Deborah, alt. 600-1500 m, Steyermark 89218a, 1961 (U); Atabapo, between Los Cerros Duida and Huachamacari, alt. 200-400 m, Guariglia et al. 1442, 1982 (NY); Meride, near Santa Barbara, alt. 100-200 m, Liesmer & González 9235a, 1980 (U); Caracas, Goebel s.n. (BM); Tovar, Movitz s.n. (JE).

COLOMBIA: Bogota, La Vega, Apollinaire s.n., 1906 (L); Santander Las Vegas, alt. 2600-3000 m, Killip & Smith 16042, 1926 (NY, S); Santander, Loso, alt. 2200-2400 m, Killip & Smith 20401, 1927 (NY); Santander, Culagá Valley, Killip & Smith 20341, 1927 (NY); Santander, near Charta, alt. 2300-2500 m,

Killip & Smith 19151, 1927 (JE); Boyacá, Sierra Nevada de Cocky, near Bocota, alt. 2100 m, Grubb & Guymer B348, 1957 (BM); Cundinamarca, between Bogota and Villavicencio, alt. 2000 m, Bischler 33, 1956 (U); Cundinamarca, Laguna Pedro-Palo, alt. 2000 m, Bischler 3026, 1959 (U); El Valle, Cisneros, alt. 300-500 m, Killip 11478a, 1922 (JE); El Valle, La Cumbre, alt. 2100-2400 m, Killip 11387, 1922 (YU); Sarare, Gibraltar, alt. 700-900 m, Bischler 2097, 1959 (U); El Caura, La Gallera, alt. 1400-1500 m, Killip 7750 ep, 1922 (JE).

ECUADOR: Azuay, Gualaquiza, Allioni 6588, 1909, type of *Odontolejeunea spiniloba* Steph. (G); Azuay, Gualaquiza, Allioni 6553, 1909, type of *Odontolejeunea ecuadoriensis* Steph. (G); Cerier, Allioni 6557, type of *Odontolejeunea nigrescens* Steph. (G); Los Rios, Samama, alt. 500 m, Harling 187, 1947 (S); Santiago-Zamora, Méndez, alt. 700 m, Harling 2211, 1947 (S); Zamora-Chinchipe, Zamora, alt. 1000 m, Harling 5924, 1959 (S, UPS); Gualaquiza, Allioni 6471 (G); Napo-Pastaza, Santa Bárbara de Sucumbios, alt. 2400 m, Harling 4181, 1959 (S, UPS); Napo-Pastaza, Inchiyacu, Harling 3611, 1958 (S); Napo-Pastaza, Mfera, alt. 1160 m, Harling 3234, 1958 (S); Chimborazo, Spruce s.n. (MANCH).

PERU: Tarapoto, Tunguaugua, Spruce s.n., type of *Odontolejeunea chaerophylla* (Spruce) Schiffn. (BM, G, MANCH, NY, YU); Tarapoto, Rio Huallaga, Ule 611, 1902 (G, L); Huanuco, Leoncio Prado, Tingo Maria, alt. 700 m, Hegewald 8294, 1977 (U); Huanuco, near Cerros del Sira, Dudley 13338Aa, 1969 (U); San Martin, Rioja, Chachapayas-Moyobamba, alt. 1900 m, Frahm et al. 655, 1982 (U); Loreto, Maynas, alt. 105 m, Timme 4694, 1984 (NY); Jurriu, Pichis Trail, S. Nicolas, alt. 1100 m, Killip 26027, 1929 (JE); Junín, Oichis Trail, alt. 1350-1600 m, Killip & Smith 25559, 1929, type of *Odontolejeunea chaerophylla* fo. *brachycolea* Herz. (JE); Cerro de Escaler, Ule 603, 1903 (BM).

BOLIVIA: s. loc., Stohnes s.n. (NY); s. loc., Mahinka 79/a, 1966 (G); Espiritu Santo, alt. 1400 m, Herzog 2792/c, 1911 (JE).

SIERRA LEONE: Loma Mountains, near Bintimane, alt. 1650 m, Jones 1488, 1971 (BM, G).

IVORY COAST: Mt Tonkovi, Aké Assi 129139 pp, 1975 (G).

NIGERIA: Idanre, Orosun, alt. 855-915 m, Richards 5119, 1958 (BM).

FERNANDO PO: s. loc., Maun s.n., 1868 (NY).

ST THOMÉ: s. loc., Moller inter 7, type of *Odontolejeunea thomeensis* Steph. (G).

CAMEROON: Mt near Etoma, alt. 360 m, Dusén 360, 1892 (BM); Bomana, Dusén 453, 1892 (G); Mts near Bibundi, alt. 300 m, Dusén 452, 1892 (G, UPS); Bibundi, alt. 300 m, Dusén 456, 1892 (BM, G).

ETHIOPIA: Bonga, Friis et al. B146, 1973 (U).

KENYA: Moungu Hills, alt. 900-1050 m, Faden, Smeenk & Kichoi 71/961/A, 1971 (JE, U).

TANZANIA: W. Usambara Mts, Mazumbai, near Kambo, alt. 1620 m, Pócs, Tanner & Jones 6374/RS, 1971 (G); Mt Mindu, near Morogoro, alt. 1200-1240 m, Pócs & Crosby 6842)a, 1972 (G, U); Uluguru Mts, Bondwa, alt. 1600 m, Pócs & Harris 6181/U, 1970 (G).

MOZAMBIQUE: Garuco Mt, Schweickerdt s.n., 1952 (S).

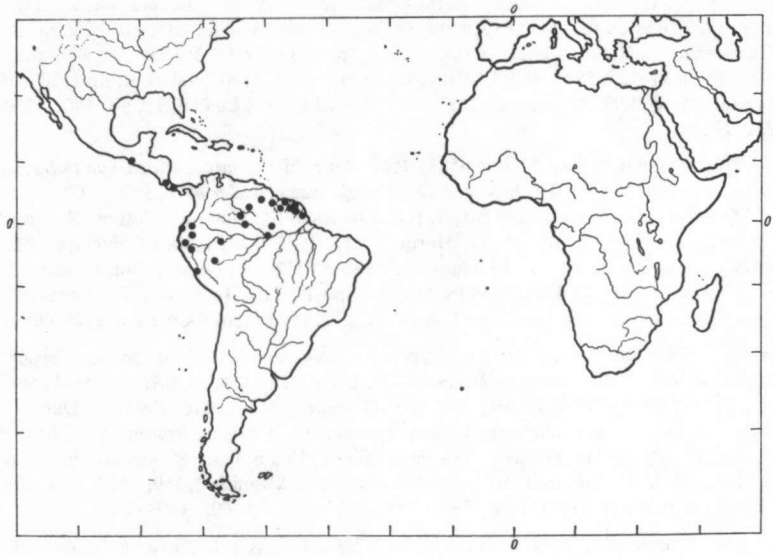
MADAGASCAR: Tamatave, Andasibe, alt. 950 m, Aptroot & Hensen 13473, 1984 (U); Tamatave, Beforona, Cremers 3181, 1974 (JE); Massif de l'Anjanahribe, Hte Andramonta, alt. 700 m, Humbert, Capuron & Cours s.n. (G); Tananarive, Mandrahu, alt. 1200 m, Onraedt 74M2345, 1974 (JE).

MARITIUS: Macabé, alt. 700 m, Onraedt 71Ma134, 1971 (JE); s. loc., Sieber s.n., type of *Odontolejeunea sieberiana* (Gott.) Schiffn. (S).

OWARE: s. loc., Müller s.n., type of *Odontolejeunea tortuosa* (Lehm. & Lindenb.) Steph. (G, MANCH, S).

Odontolejeunea rhomalea (Spruce) Steph. Plate 4-5, map 3

Odontolejeunea rhomalea (Spruce) Steph., Spec. Hep. V: 171 (1912).
Lejeunea rhomalea Spruce, Trans. Proc. Bot. Soc. Edinburgh **15**: 143 (1884).
Type: "Andes Quitensis, Rio Verde, fl. Pastasa affluens, alt 4500 p, Spruce XL78 (MANCH, holo).



Map 3: Distribution of *Odontolejeunea rhomalea* (Spruce) Steph.

Heterotypic synonyms:

Odontolejeunea calcarata auct., non (Mont.) Steph. All previous authors except Herzog (1957) used the name *O. calcarata* for *O. rhomalea* as presently understood.

Odontolejeunea calcarata fo. *longispica* Herz. (1931), nom. inval., art. 43,1 ICBN.
Material: "Rio Uaupés, Juticá, Varadouro, auf Dicotylenblatt." (Lützelburg, n. 22718). (Not seen).

Odontolejeunea grandiloba Steph., Spec. Hep. V: 181 (1913), syn. nov.
Type: "Ecuador, Azuay", Allioni 6466 (G holo).

Odontolejeunea obversilobula Herz., Hedwigia 71: 339 (1931); Herzog (1957: 57).
Type: "Venezuela, Rio Cassiquiare", Von Lützelburg 22263 (JE lecto, S).
(This lectotype has been chosen from the syntypes cited in the original publication.)

Odontolejeunea sagittistipula Steph. (1890), nom. inval., art. 43,1 ICBN.

DISTRIBUTION AND ECOLOGY: Brasil, Colombia, Costa Rica, Ecuador, French Guiana, Guatemala, Guyana, Peru, Suriname, Venezuela (map 3); 0-3200 m. In moist, primary forest. On living leaves, occasionally on twigs, very rarely on humid soil.

Stem with leaves 1-3.6 μm wide, appressed to substrate, loosely and irregularly branched; herbarium material greenish to brownish; leaves revoluted when dry, widely spreading when wet; branches of the *Lejeunea*-type (Pl. 4A, B).

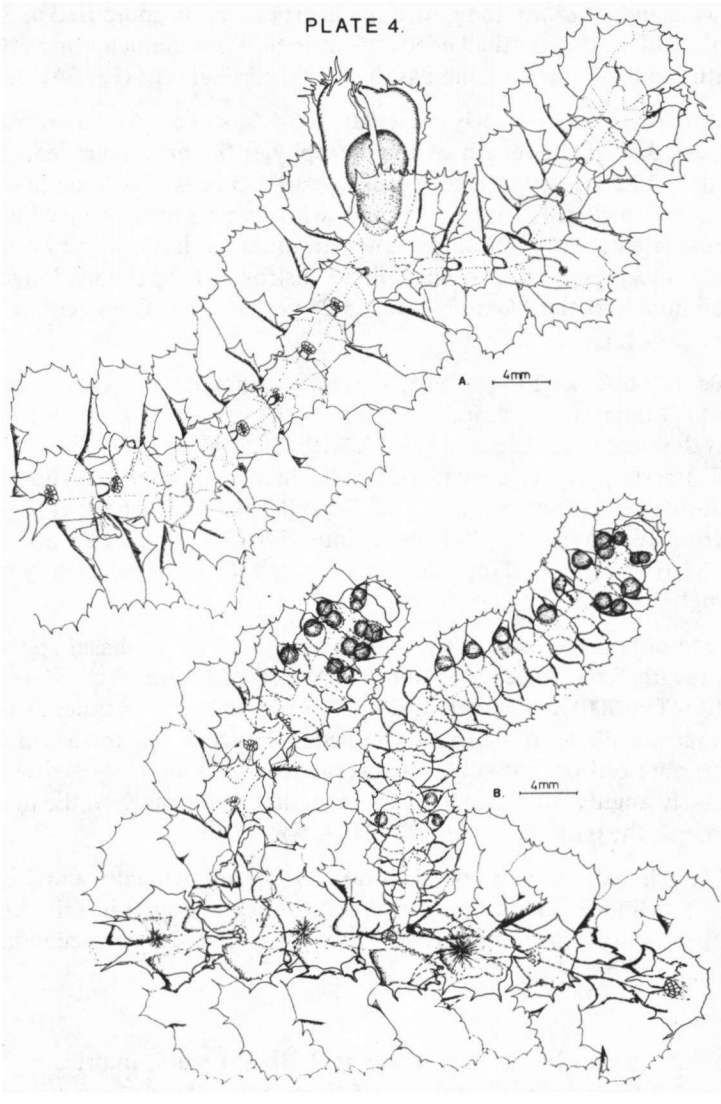


Plate 4. *Odontolejeunea rhomalea* (Spruce) Steph.: A. Habitus ventral of female plant. B. Habitus ventral of male plant. — A from Spruce s.n., Andes. B from Von Lützelburg 22263, Venezuela (type of *O. obversilobula* Herz.).

Stem in cross-section 120-200(-285) μm; cortex in cross section composed of (9-)10-12(-13) cell rows, the cortex cells convex to almost smooth, the cell walls thickened to slightly so; dorsal cortical cells 15-40 μm high, 30-60 μm wide and 35-85 μm long; ventral cortical cells darkened, larger than the dorsal cortical cells, 25-45 μm high,

20-85 μm wide and 30-85 μm long; medulla in cross-section composed of 30-70 cells, the cell walls not or slightly thickened, the cells 6-30 μm diameter and (50-)100-190 μm in length, up to 30 times as small as the dorsal cortical cells (Pl. 5A, B).

Leaf lobe broadly ovate to nearly orbicular, 0.6-1.9 × 0.5-1.8 mm, very imbricate, inserted along 3/4 of the length of the merophyte, the apex rounded, the margin toothed with 10-22 teeth, the teeth consisting of 1-6 cells, the large postical tooth consisting of up to 40 cells; leaf cells broad, with sinuous anticlinal cell walls, 31-44 × 21-36 μm, orientated in latitudinal rows; trigones cordate and very conspicuous; intermediate thickenings broadly ellipsoid to fusiform, 1-2 per each longer cell wall (Pl. 5E); oil bodies of the *Massula*-type, 15-25 per cell (del. Gradstein 6183, French Guyane, Saül, obs. Gradstein).

Leaf lobule 170-680 × 200-890 μm, narrowly triangular to almost rectangular, about 2.5-4(-7) times as short and 1.5-2.5 times as narrow as the lobe; free margin inserted on the stem at an angle of 15-45°, with (3-)5(-6) usually incurved teeth consisting of 2 superimposed cells on a 2(-3)-celled base or of mere protruding cells, the anticlinal most teeth often consisting of 3-6 cells; the apex of the free margin 3-9 cells long from keel to first tooth. Lobule sinus (50-)130-180°, lobule apex 150-240°, keel sinus (85-)110-150°, keel insertion on stem 60-150°, the keel slightly rounded to almost straight (Pl. 5G, H).

Underleaves imbricate, centre often convex, frequently long basal spurs up to 12 cells long, length from upper insertion to apex 300-650 μm, from lower to upper insertion 100-700(-800) μm, largest width 430-1500 μm, 3.5-5.5 times as wide as the stem, the margins plane to incurved, toothed, 6-12 teeth, the teeth consisting of 1 sharp protruding cell or consisting of several cells forming a squarrose tooth, the cells irregularly angular in the centre to rectangular at the margin, the insertion line strongly arched, the bases decurrent (Pl. 5I, J, K).

Underleaf attachment in longitudinal section 90-170 μm in length, 1 arched superior central cell, 1 cylindrical modified cortex cell, 3 very seldom 2 inferior central cells (Pl. 5C, D); primary rhizoid disc usually present, giving rise to a secondary rhizoid disc bearing numerous rhizoids.

Plants dioicous.

Androecia 0.8-4.8 mm long; male bracts in 3-20(-35) pairs, imbricate, 450-750 × 300-550 μm, 1-3 times as small and 1.5-3.5 times as narrow as vegetative leaves, the apex obtuse, the margin toothed with 7-12 teeth; bract lobule elongated, ellipsoid, 300-380 × 140-200 μm, 1.5-2.5 times as short and 2-3.5 times as narrow as the bract lobe, without teeth or with 1-2 reduced teeth, the margin usually incurved; hyaline papilla ± marginal, occasionally 1-2 additional hyaline papilla's at the insertion of the lobule and at the insertion of the lobe; keel slightly rounded (Pl. 5F); bracteoles imbricate, 300-460 × 420-670 μm, the margin with 0-3(-14) teeth or if untoothed irregularly sinuate (Pl. 23, d); antheridia 130-145 μm in diameter, the jacket 3-12 μm thick, the stalk 8-18 μm in diameter.

Female bracts 800-1100 × 500-700 μm, the margin toothed with 12-17 teeth, the teeth 2-3 cells long and 3-4 cells wide at the base; bract lobules 175-235 × 70-95 μm,

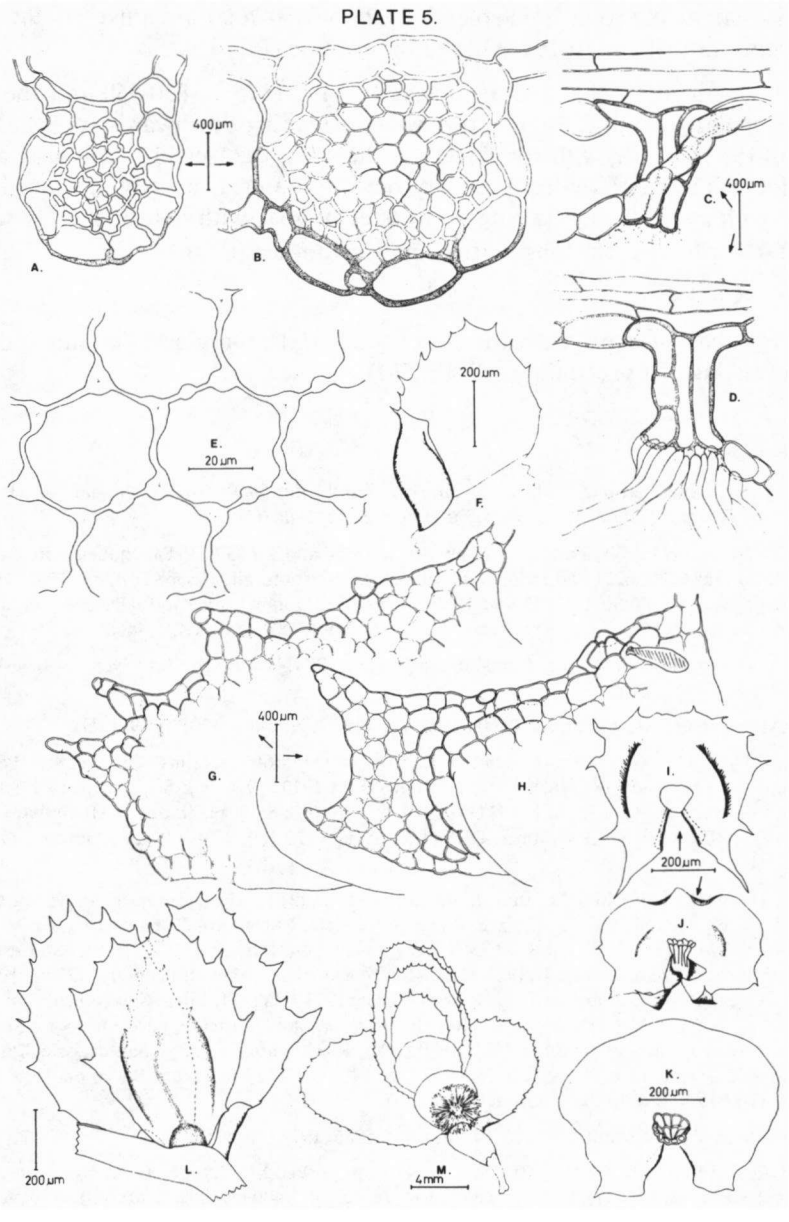


Plate 5. *Odontolejeunea rhomalea* (Spruce) Steph.: A, B. Stems in cross section. C, D. Underleaf attachment in longitudinal section. E. Leaf cells. F. Male bract. G, H. Leaf lobules. I, J, K. Underleaves. L. Female bracts and bracteole. M. Cladium. — A, F, G, H, I from Von Lützelburg 22263, Venezuela (type of *O. obversilobula* Herz.). B, D from Allioni 6466, Ecuador (type of *O. grandiloba* Steph.). C from ORSTOM 3923, French Guiana. E, K, M from Spruce s.n., Ecuador (type of *O. rhomalea* (Spruce) Steph.). J from Harling 2214, Ecuador. L from Spruce s.n., Andes.

reduced to a narrow fold; bracteoles 700-925 × 650-700 μm, convex in the centre, the margins toothed, up to 15 teeth, the apex obtuse (Pl. 5L).

Perianth emergent for 1/3-1/2 of its length, 1450-1575 × 850-950 μm, the lateral wings irregularly shaped, 3-6 cellrows wide, extending downwards for 1/3-1/2 the length of the perianth, with 10-15 teeth at the apex, the teeth 1-6 cells long and 1-3 cells wide at the base; ventral keel very bluntly rounded, usually unwinged, occasionally with a short wing bearing up to 6 teeth; apex with non or slightly recessed beak of 4-7 cells long, the longer beaks may be toothed (Pl. 4A).

Sporophyte not seen.

Cladia few; basal leaves ovate, the apex rounded, the margins with numerous small teeth consisting of 1 protruding cell (Pl. 5M).

Specimens seen

GUATEMALA: Alta Verapaz, Cubilguitz, alt. 350, Türckheim 5060, 5063, 5066 and s.n., 1906 (BM, G, NY); Alta Verapaz, Coban, alt. 1550 m, Türckheim 5080, 1906 (G).

COSTA RICA: Rio Naranjo, Tonduz 3075 pp, 3082, 15504 and 15605 (G); Talamanca, forest de Tsaki, alt. 200 m, Tonduz 6230, 6231 and 15542 (G); Talamanca, Shirores, alt. 100 m, Tonduz 15581, 1895 (NY, G); forest de Boruca, Tonduz 15505 and 15506, 1891 (G); Domingo de Golfo Dulce, Tonduz 15564, 15579 and 15604, 1896 (G, NY, S, YU; Puerto Viejo, Biolley 15583, 1892 (G).

GUYANA: Upper Mazaruni River, Kamakusa, Long 9, 1922 (NY); Essequibo River, Bartica, Richards 313, 1929, (BM, YU).

SURINAME: Kabalebodam area, alt. 2500 m, Bekker 1684, 1690C and 1709A, 1981 (U).

FRENCH GUIANA: River Comté between Belizon and Jalbot, Degelius s.n., 1958 (UPS); Saül, Gradstein 6107, 6114 and 6183, 1986 (U); Saül, ORSTOM 3923, 1976 (U); Saül, Aptroot 15301g, 1985 (U); Saül, piedmont of Mt Galbao, ORSTOM 3939/b, 1976 (U); Saül, piedmont of Mt Galbao, Cremers 3941/b, 1976 (JE); near River Arataye, ORSTOM 5526, 1979 (U); along River Marauini, ORSTOM 4965, 1977 (U).

BRAZIL: Oyapock, Salto Manõa, Lützelburg 20199, 1927 (JE); Rio Casiquiare, Playa da Candela, Lützelburg 22262, (JE, S); Rio Cassiquiare, Playa da Candela, Lützelburg 22263, lectotype of *Odontolejeunea obversilobula* Herz. (JE, S); Rio Cassiquiare, Solano, Lützelburg 22269 (JE, S); Rio Cassiquiare, Playa da Froya, Lützelburg 22354, 1928 (JE); Rio Negro, San Isabel, Lützelburg 22366, 1928 (JE); Roraima, Uaicá, Prance, Dobzhansky & Ramos 19960, 1973 (NY, U); Silva Amazonica, San Gabriel, Spruce s.n. (BM, G, MANCH); Amazone, Rio Bombonasa, San Gabriel, Spruce s.n. (NY); Serra Curicuraira, Rio Negro, alt. 450 m, Buck 2427, 1979 (NY); Rio Uatumã, Igarapé Santa Luzia, Buck 2881, 1979 (NY); Rio Juruá, Juruá Miry, Ule 550 and 552, 1900 (G, L); Rio Juruá, Bucco do Tejo, Ule 551, 1901 (BM, G); Rio Negro, Manáos, Ule 580, 1910 (G).

COLOMBIA: El Valle, Cordoba, alt. 50-100 m, Killip 5086, 1922 (JE, NY).

ECUADOR: Rio Verde, fl. Pastasa affluens, alt. 4500 m, Spruce XL78, type of *Odontolejeunea rhomalea* (Spruce) Steph. (MANCH); Sylva Canelos, Rio Verde, alt. 1400 m, Spruce s.n. (G); Azuay, Paramo del Matango, alt. 3200 m, Allioni 6466, 1909, type of *Odontolejeunea grandiloba* Steph. (G); Napo-Pastaza, El Topo, alt. 1250 m, Harling 3409, 1958 (S); Napo-Pastaza, Rio Napo, Harling 3611/d, 1958 (JE); Napo-Pastaza, Rio Napo, Almana, Harling 3645 pp, 1958 (S); Napo-Pastaza, Tena, Harling 3675, 1958 (S); Napo-Pastaza, Santa Bárbara de Sucumbios, alt. 2700 m, Harling 4144, 1959 (S); Napo-Pastaza, Rio Pastaza, Mera, alt. 1160 m, Harling 3234, 1958 (S); Esmeraldas, Rio Grande, Harling 4629 pp, 1959 (NY, S); Esmeraldas, Rio San Miguel, alt. 70 m, Harling 4701, 1959 (S); Zamora-Chinchipe, alt. 800-900 m, Harling 5886, 1959 (S); Santiago-Zamora, Méndez, alt. 700 m, Harling 968, 2214, 2222 and 2223, 1947 (JE, S, UPS); Azuay, Gualaquiza, Allioni 6549, 6554, 6590, 6594, 6597, 6598 and 6599, 1909 (G).

PERU: Huanuco, alt. 700 m, Weberbauer 3677, 1903 (G); Tarapota, Spruce s.n. (MANCH); Rio Bombonasa, Spruce s.n. (MANCH); Rio Amazonas, Ule 604, 1902 (G); Riga, San Martin, alt. 1500 m, Frahm et al. 97, 1982 (U); Loreto, San Antonio, alt. 110 m, Killip & Smith 29323, 29454, 29626 and 29654, 1929 (JE, NY, S); Junín, Rio Paucartambo, alt. 700 m, Killip & Smith 25257, 1929 (JE).

Excludenda

Lejeunea subg. *Odontolejeunea accedens* (Gott.) Steph. (1888)
= *Cyclolejeunea accedens* (Gott.) Evans (Evans 1904: 201).

Lejeunea subg. *Odontolejeunea berteroana* Gott. ex Steph. (1888)
= *Rectolejeunea berteroana* (Gott.) Evans (Evans 1906: 12).

Odontolejeunea contractilis (Mitt.) Steph. (1913)
= *Caudalejeunea renistipula* (Gott.) Steph. (Verdoorn 1934: 60).
orthogr. err. pro *C. reniloba* (Gott.) Steph., fide Miller, Whittier & Whittier (1983: 241).

Odontolejeunea convexistipa (Lehm. & Lindenb.) Schiffn. (1897)
= *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) Evans (Evans 1904: 198).

Lejeunea subg. *Odontolejeunea glaziovii* Spruce ex Besch. & Spruce (1889).
= *Brachiolejeunea phylloriza* (Nees.) Kruijt & Gradstein (1986).

Odontolejeunea hanningtonii (Mitt.) Steph. (1912)
= *Caudalejeunea hanningtonii* (Mitt.) Schiffn. (Schiffner 1893: 129).

Odontolejeunea integerrima Steph. (1905)
= *Cyclolejeunea integerrima* (Steph.) Steph. (Stephani 1913: 195).

Odontolejeunea minimula Steph. (1896)
= *Cyclolejeunea mimula* (Steph.) Steph. (Stephani 1913: 192).

Odontolejeunea mirabilis Steph. ex Goebel (1898), nom. nud.
= *Cyclolejeunea peruviana* (Lehm. & Lindenb.) Evans (Evans 1904: 205).

Lejeunea subg. *Odontolejeunea papillata* Steph. ex Duss (1904), nom. nud.
= *Trachylejeunea papillata* (Mitt.) Steph., Stephani (1913: 316).

Odontolejeunea paulina Steph. (1896)
= *Cyclolejeunea paulina* (Steph.) Steph. (Stephani 1913: 186).

Odontolejeunea peruviana (Lehm. & Lindenb.) Schiffn. (1893)
= *Cyclolejeunea peruviana* (Lehm. & Lindenb.) Evans (Evans 1904: 196).

Lejeunea subg. *Odontolejeunea scalpellifolia* Besch. et Spr. (1889)
= *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) Evans fide Grolle (1984: 760).

Odontolejeunea stachyclada (Spruce) Steph. (1896)
= *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) Evans fide Stephani (1896).

Odontolejeunea subbifida Steph. (1896); Stephani (1902: 277)
= *Cyclolejeunea chitonia* (Tayl.) Evans (Evans 1904: 194).

Lejeunea subg. Odontolejeunea surinamensis (Mont.) Spruce (1884)
= *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) Evans (Evans 1904: 198); Grolle (1984: 760).

Lejeunea subg. *Odontolejeunea truncatula* Spruce (1884)
= *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) Evans fide Grolle (1984: 760).

Dubious names

Odontolejeunea caledonica Steph. ex Paris (1910), nom. nud.

Odontolejeunea grandistipula Steph. (in Icon.) ex Herz. (1957), nom. nud.

Odontolejeunea octoplicata Steph. ex Paris (1910), nom. nud.

Odontolejeunea sumatrensis Steph. ex Herz. (1957), nom. nud.

Lejeunea subg. *Odontolejeunea tacoriensis* Steph. ex Duss (1904), nom. nud.

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RATA:

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