

**The Genus *Ceratolejeunea* Jack & Steph.
(Hepaticae: Lejeuneaceae)
in Tropical America**

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ABSTRACT

Abstract. The Genus *Ceratolejeunea* Jack & Steph. (Hepaticae: Lejeuneaceae) in Tropical America. Gregorio Dauphin L. Albrecht-von-Haller-Institut für Pflanzenwissenschaften, Abt. Systematische Botanik, Untere Karspüle 2, D-37073 Göttingen, Germany. gdauphi@gwdg.de. August 2000. A revision of the genus *Ceratolejeunea* (Hepaticae) in Tropical America is presented based on the examination of fresh plant material and about 1000 herbarium specimens and types of the over 100 species names published for the American Continent. Preliminarily, 23 *Ceratolejeunea* species are recognized in two subgenera: subgen. *Ceratolejeunea* (4 spp.) and subgen. *Caduciloba* Schust. (19 spp.). A new species, *Ceratolejeunea minuta* G. Dauphin, is described, and a new combination, *Ceratolejeunea dussiana* (Steph.) Dauphin, is proposed. Morphological descriptions, distributional and ecological data, keys and illustrations of the species are given. A phylogenetic analysis of the relationship between the species is also presented.

INTRODUCTION

The genus *Ceratolejeunea* belongs in the Lejeuneaceae, the most advanced and the most highly specialized family among the leafy Hepaticae (Mizutani 1961). The Lejeuneaceae is also the largest single family of Hepaticae, with about 90 accepted genera (Schuster 1963, Gradstein *et al.* in press). Although generic delimitation within the family has posed problems to many authors, *e. g.* Schuster 1963 (various genera), Piippo 1986 (*Lepidolejeunea*), He 1999 (*Pycnolejeunea*), Grolle & Reiner-Drehwald 1999 (*Harpalejeunea*), Reiner-Drehwald 1999 (*Lejeunea*), the genus *Ceratolejeunea* stands as one of the most natural genera in the Lejeuneaceae (Evans 1905).

Many authors have dealt taxonomically with individual species and species groups of *Ceratolejeunea* (see below), but there has been no work treating the *Ceratolejeunea* species from the Neotropics comprehensively. This study aims to fill the gap in the literature, based on examination of all of the types of the Neotropical taxa published in the genus *Ceratolejeunea*. It also aims at providing a mean of determination of *Ceratolejeunea* species, a phylogenetical hypothesis of the relationship between them, as well as information on their morphology, habitat, ecology and geographical distribution.

HISTORICAL SURVEY

The name „*Cerato-Lejeunea*“ was first introduced by Spruce (1884) for one of the subgenera of his diverse tropical genus *Lejeunea*. The genus *Lejeunea* belonged to the „Schizostipae“, recognized by their bifid underleaves (contrasting with the „Holostipae“, with entire underleaves). The subgenus „*Cerato-Lejeunea*“ was based on the section *Lejeunea* § 3 *Ceratanthae*,

from Synopsis Hepaticarum (Gottsche *et al.* 1845). This section was defined in Synopsis Hepaticarum by its dark color („fuscescens“), the presence of a four-, rarely five-horned perianth, and the presence of utriculi. The sectio *Ceratanthae* was further divided into a. *Genuinae* and b. *Aberrantes*. The latter group, of a more artificial nature, contained different taxa that now belong into different genera, such as *Leptolejeunea*, *Colura* and *Raphidolejeunea* (Reiner-Drehwald 1999). The more natural *Genuinae* group included 17 taxa, 15 of which are still considered within the genus *Ceratolejeunea*: *L. coarina* Gottsche, *L. cubensis* Mont., *L. ceratantha* Nees & Mont., *L. guianensis* Nees & Mont., *L. singaporensis* Lindenb., *L. belangeriana* Gottsche, *L. martiana* Gottsche, *L. brasiliensis* Gottsche, *L. cornuta* Lindenb., *L. variabilis* Lindenb., *L. splitgerberiana* Mont., *L. involvens* Nees & Mont., *L. haeckeriana* Gottsche & Lindenb., *L. longicornis* Gottsche, *L. spinosa* Gottsche and *L. filaria* Taylor ex Gottsche. *Lejeunea fallax* Lehm. & Lindenb. was also included in this section as a „species sedis incertae“. Trevisan (1877) included the above mentioned taxa in the genus *Colura* Dum., giving it the same limits as the sectio *Ceratantha*.

Spruce (1884) included 17 species in the subgenus *Cerato-Lejeunea*, including 5 previously described ones and 12 new taxa. In this acclaimed work, Spruce threw new light about the ecology, and provided more detailed observations on the morphology of the taxa, clearly defining the group of species now included in the subgenus *Caduciloba* Schust. (subg. *Ceratolejeunea* auct.). In subsequent works, Spruce (1890), Stephani (1888, 1890) and Loitlesberger (1894) added further species in the subgenus.

Jack and Stephani (1892) described the holostipous *Ceratolejeunea grandiloba* as a new species. In doing so, they created the new genus *Ceratolejeunea* Jack & Steph. (Art. 42.1). Schiffner (1893) raised the subgenus *Ceratolejeunea* Spruce to generic rank, as *Ceratolejeunea* (Spruce). Even though Spruce (1895) kept *Cerato-Lejeunea* as a subgenus of *Lejeunea*, Schiffner (1893) and Stephani (1895a, 1895b, 1913) subsequently described or combined additional species into *Ceratolejeunea*, treating it as a genus in its own, which contained taxa with bifid and entire underleaves (*C. grandiloba* Jack & Steph. and *C. desciscens* (Sande-Lac.) Steph.).

Evans (1905) included 7 species of *Ceratolejeunea* in his series „Hepaticae of Puerto Rico“ and provided detailed morphological descriptions of the species. He paid special attention to the variation of cytological characters such as thickenings of the cell walls and discussed variability of diagnostic characters of the genus, including ocelli, lobule types (normal, spherical, utriculi) and perianth form. Other vegetative characters, especially underleaf form and leaf lobe dentation, were also considered. He stressed the possibility that many of these characters (wall thickening pattern, occurrence of spherical lobules) might be

influenced by external conditions, making it difficult to determine their taxonomic value. This author also introduced criteria such as the proximal position of the hyaline papilla, the unicellular lobule tooth and perianth morphology to separate holostipous *Ceratolejeunea* from species of *Neurolejeunea* (Evans 1907).

Stephani (1913) recognized 100 species of *Ceratolejeunea*, adding 20 new taxa for the Neotropics (and 12 for the Paleotropics), most of which are here considered synonyms. His work included also 38 new combinations, most of the taxa were previously described by Spruce or himself in the subgen. *Cerato-Lejeunea*. In subsequent years, the addition of new species to the genus decreases and apparently no taxonomic work was done in the group until the thirties.

Zwickel (1932) provided a classification of the ocelli types, based on the distribution of ocelli in the leaf. He reported the occurrence of basal, moniliate, geminate, and aggregate ocelli in species of *Ceratolejeunea*. He discussed the taxonomical value of this character, and state a difference in type of ocelli is frequently enough to separate an individual as a new species (p. 643).

The relationship of *Ceratolejeunea* with other genera in the family Lejeuneaceae was dealt with by Zwickel (1933) and Herzog (1933). The former author transferred *C. scaberula* (Spruce) Steph. to *Prionolejeunea*, *C. anomala* (Lindenb. & Gottsche) Steph. to *Euosmolejeunea*, *C. devexa* (Lindenb. & Gottsche) Steph. to *Neurolejeunea* and described the genus *Cladolejeunea* based on the African *C. aberrans* Steph. Herzog (1933) discussed the relationship between holostipous *Ceratolejeuneas* and *Neurolejeunea* species and combined *C. portoricensis* (Hampe & Gottsche) Evans (= *Physantholejeunea portoricensis* (Hampe & Gottsche) Schust.) and *C. devexa* (Lehm. & Lindenb.) Herz. (= *Neurolejeunea breutelii* (Gottsche) Evans into *Neurolejeunea*. He also suggested that *N. portoricensis* should be placed in a separate subgenus whose affinities with *Ceratolejeunea* should be emphasized.

Further studies in *Ceratolejeunea* focused primarily on cytological characters such as ocelli, cell walls, trigones (*e. g.* Herzog 1942a). Fulford (1944b) defined a *Ceratolejeunea* sporeling type and provided drawings and descriptions of sporelings and vegetative reproduction in 12 taxa. She could not conclude whether these characters were taxonomically informative or not.

The generic treatment of neotropical *Ceratolejeunea* by Fulford (1945) remained the more extensive treatment of the genus in modern times. She treated 41 names, accepting 19 species for the American continent. The distinction of the species is based on perianth and lobe characters which are often variable, however. Maybe because of that and because of the

lack of revision of many of the types, the treatment has been considered not very satisfactory (Schuster (1956), Gradstein *et al.* (in press)).

The African taxa were treated by Vanden Berghen (1951) who accepted 9 species for that continent. He provided a species key and separates the species in four groups based on the orientation of the ocelli („basilaires, dispersés, formant une fause nervure“) and the shape and length of the perianth horns.

In 1953 Bonner listed 120 species names in *Ceratolejeunea* world wide, and published some drawings of *Ceratolejeunea* species by Stephani, including some distributed in the Icones Hepaticarum. Bonner also proposed several lectotypes based on collections in the Stephani Herbarium (G), and a new combination.

Schuster and Hattori (1954) were the first to publish drawings from oil-bodies in *Ceratolejeunea*. They proposed a classification for the oil-body types, and reported two types of oil-bodies in species of *Ceratolejeunea*, one segmented and smooth, the other spherical to ellipsoidal and usually papillose. These authors stressed the isolation of the genus *Ceratolejeunea* within the Schizostipae and suggested that it might be „more nearly allied to the Holostipae“ (p.18).

Infrageneric categories were first included by Schuster (1956), who segregated the *Ceratolejeunea* species with undivided underleaves in the subgenus *Ceratophora*. He also introduced the anatomy of the stem as a character to separate that subgenus from *Neurolejeunea*. This was later supported by the studies of Bischler (1966), who found no differences in stem anatomy among the species of the subgenus *Ceratolejeunea* auct. (=subgen. *Caduciloba* Schust.) and those of the subgenus *Ceratophora* (=subgen. *Ceratolejeunea*). Stem morphology was also studied by Crandall (1969), who also described the utriculi and the development of branches using four taxa.

Schuster (1978) described the new subgenus *Caduciloba* with two species. As previously suggested by Herzog (1933), Schuster also described the new genus *Physantholejeunea* based on *C. portoricensis* (Hampe & Gottsche) Evans, distinguishing it from *Ceratolejeuneas* with entire underleaves based on the greater number of medullary cells in the stem, the lack of wall pigments, the lack of oil-bodies in normal cells and lobule morphology.

In his detailed treatment of the genus *Ceratolejeunea* in North America, Schuster (1980) provided a key to the subgenera, and notes on variation of three North American taxa, *C. cubensis* (Mont.) Schiffn., *C. laetefusca* (Aust.) Schust. and *C. rubiginosa* Steph.

Grolle (1983) dealt with the generic nomenclature of *Ceratolejeunea* (see under generic description) and proposed *C. cubensis* (Mont.) Schiffner as generic lectotype.

Mizutani (1981) treated 7 Asiatic species of *Ceratolejeunea* (2 new), in many cases comparing them with neotropical taxa. Other works on palaeotropic species include those of Miller *et al.* (1983) who reported 11 species from Polynesia, and Udar & Shaheen (1985) reported *C. singaporensis* (Lindenb.) Schiffn. from India. Grolle (1995) and Wigginton & Grolle (1996) listed four species from the East African Islands and 8 species from Sub-Saharan Africa, respectively; *C. belangeriana* (Gottsche) Steph. occurs in Australia (Thiers, pers. comm. 1999). For the Neotropics worth mentioning are the papers of Onraedt (1989) who treated 9 species from French Guyana, provided a key and illustrations for each taxon and that of Gradstein (1989), who gave a key for 8 Caribbean taxa. Gradstein *et al.* (in press) offered a key to the genera of Schizostipae and a generic description emphasizing characters to separate the genus from related ones. The actual number of species in the Neotropics is estimated to be about 20.

A treatment of the holotype species of *Ceratolejeunea* was published by Grolle (1987), who accepted 5 species and two synonyms in the subgenus *Ceratophora* Schust. (= *Ceratolejeunea*). In his key, a wider range of characters are used, including geographical distribution, sexual condition, ocelli number and orientation type, underleaf width proportional to the stem, leaf and female bract shape and dentation, presence or absence of utriculi, lobule shape and plant size. He also discussed the value of the leaf mammillae in *C. grandiloba* Jack & Steph. as a criterion to separate species.

Schuster (1992) described cytological characters including cell shape, size, walls, lamellae, intermediate thickenings, ocelli and oil-bodies in 5 species and one „phenotype“ of *Ceratolejeunea*. This author considers the cytological distinctions between species of „perhaps limited relevance“ but that within limits, a combination of the above characters „prove fairly stable and useful in species discrimination“. A primary division of the schizostipous species in *Ceratolejeunea* based on the orientation of the ocelli is suggested (p. 227).

The total number of species names in *Ceratolejeunea* known from literature records and herbaria is 147. Of these, 109 names are from the New World tropics; some of these are shared with the Old World tropics (G. Dauphin, unpublished data).

MORPHOLOGY AND ANATOMY

Sporelings

First described by Goebel (1930), the development of leafy gametophytes from sporelings in *Ceratolejeunea* was documented in detail by Fulford (1944b). In *Ceratolejeunea* as in other genera of Lejeuneaceae, the spores are shed from the capsule being chlorophyllose. Usually after dispersal, the spore elongates and forms three walls at right angles with the long axis, containing then four cells. A wall, more or less parallel to the long axis in each of the four cells is formed, producing a unistratose thallus of 2 x 4 cells, with a papillose cell wall from the exospore. An apical cell with two cutting faces develops from one of the cells. The activity of this cell produces a secondary thallus with smooth cell walls, which is first two cells wide, but through irregular, almost periclinal division, becomes four cells broad (Figure 1). After several divisions, the apical cell transforms into a an apical cell with three cutting faces, which produces a juvenile leafy shoot (Figure 3). In the juvenile shoot, primary type leaves are followed by the juvenile leaves with enlarged lobuli accompanied by underleaves. Fulford (1944b) provided further descriptions of sporelings in some taxa (12 names), and found several deviations to the *Ceratolejeunea*-type sporeling. *Ceratolejeunea malleigera*, for example, produces a secondary thallus 6 cells broad from which primary type leaves and no underleaves arise (Fulford 1944b).

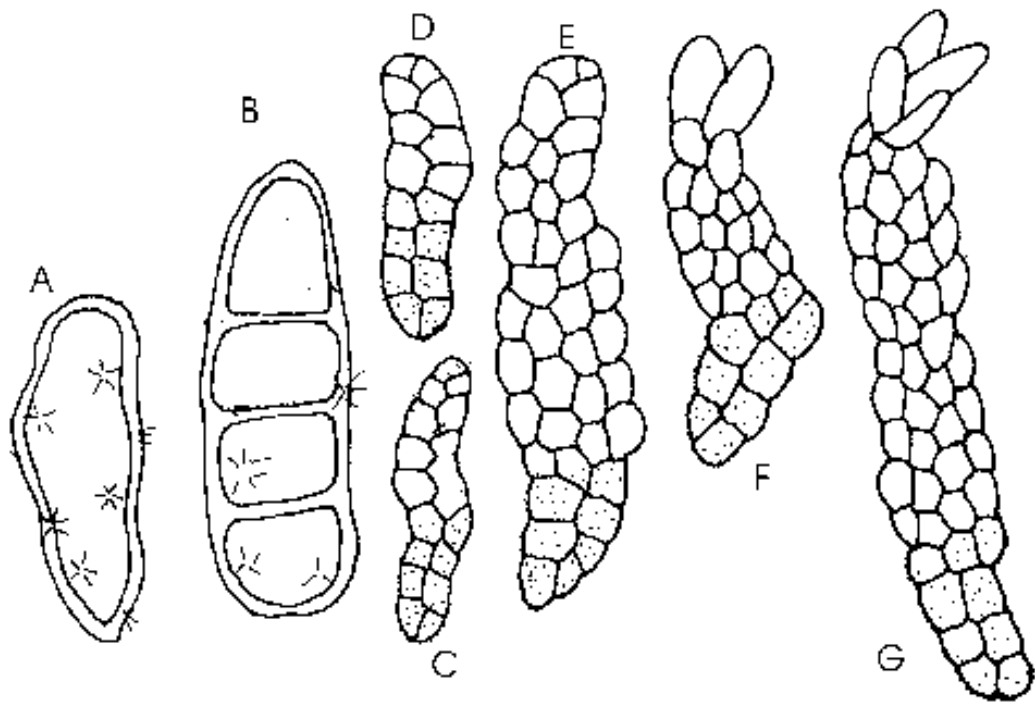


Figure 1. Sporelings. A-B, Spores when sired from capsule. C-D, Eight-celled thalzus within the old exospore (stippled) and secondary thallus. E-G, Early stages of development of the sporeling with early stages of leafy shoot. Redrawn from Fulford 1944h.

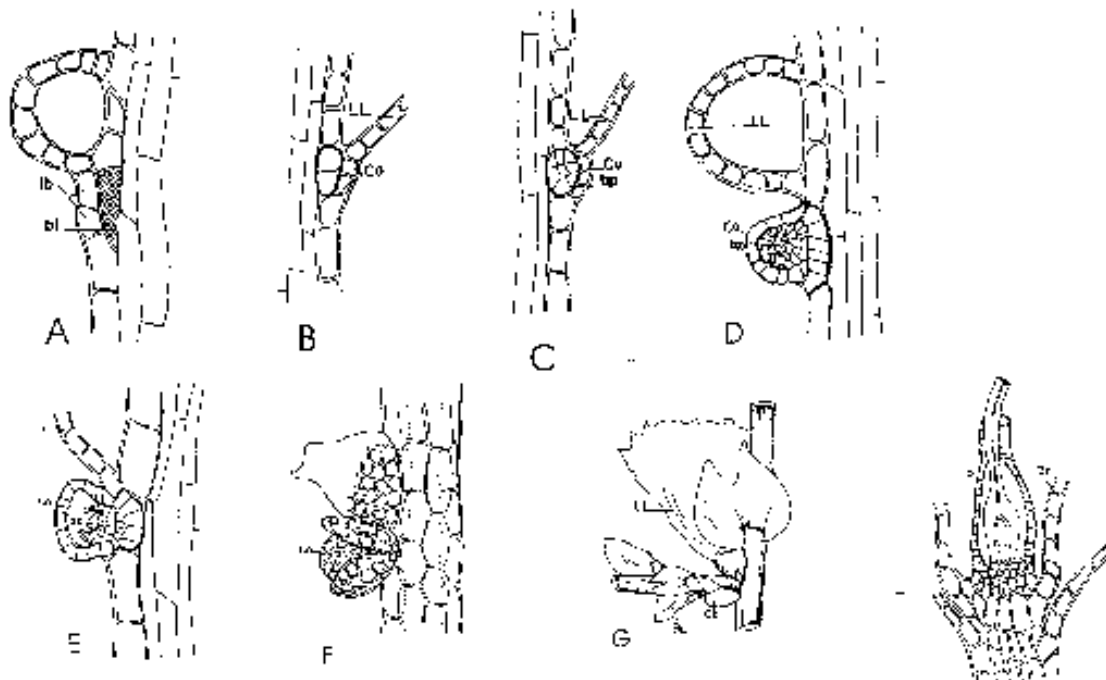


Figure 2. Branch development. A Longitudinal stem section with mass of brace initial cells. B-C, Branch primordium in two developmental stages. D, Young *Lycopodium*-type branch showing apical cell. E, Young branch showing air space, in longitudinal section and surface view. F, Collar enclosing a young branch. G, Young branch out of the broken collar. H, Longitudinal section of female inflorescence. bi: brace cell initials; bl: branch leaf; br: brace; bc: apical cell of the branch; Co: collar; LL: stem leaf; P: perianth. After Crandall (1969), with permission.

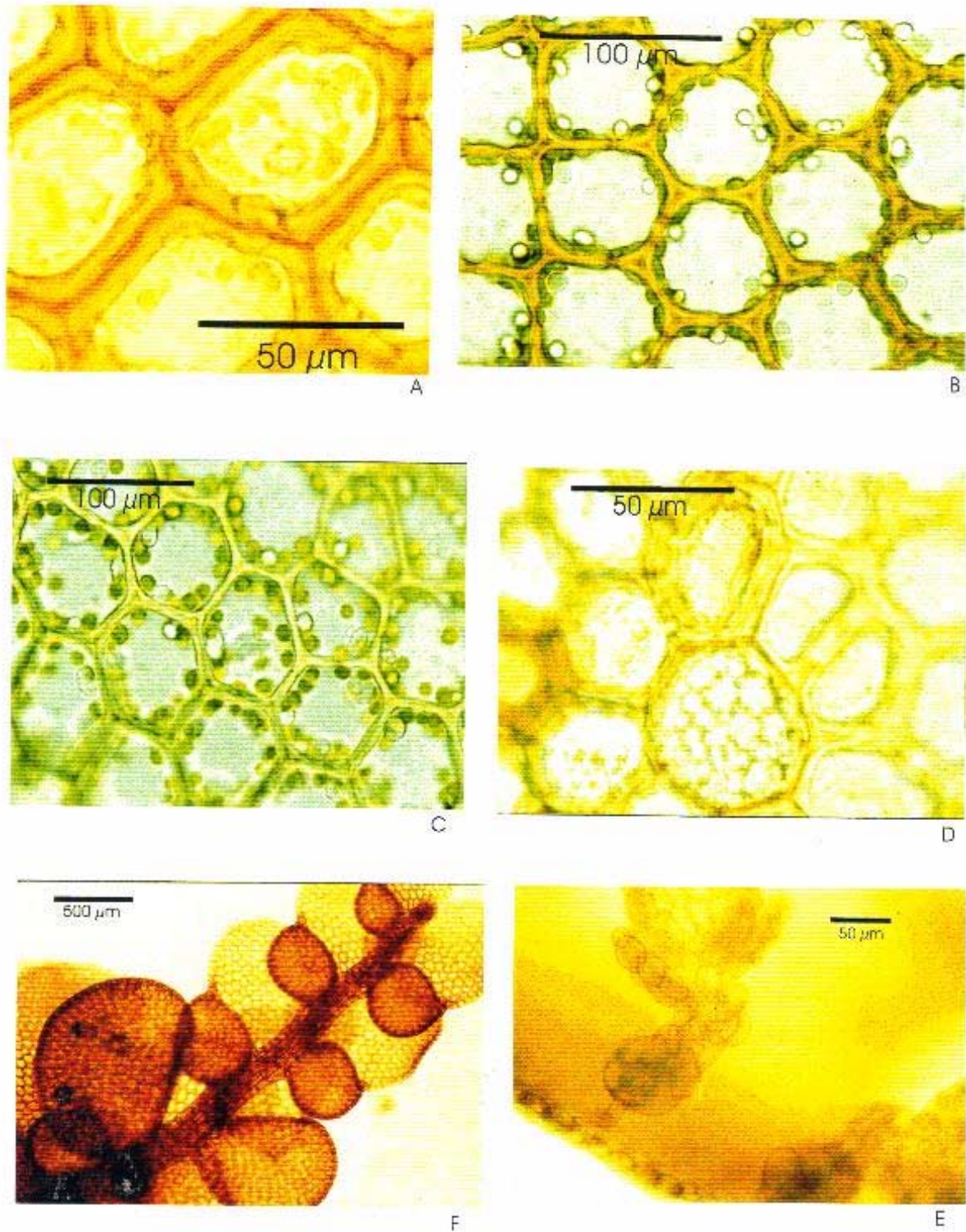


Figure 3. Cells and oil-bodies. A. Cell walls in *Ceratolejeovoa frungens*, Dauphin 2704. B. Oil-bodies in *C. cornuta*, Gradstein s. n., Isla Gorgona, Colombia. C. Oil-bodies in *C. spinosa*, Gradstein s. n., Isla Gorgona, Colombia. D. Laminar ocellus in *C. grandiloba*, Dauphin 2822. E. Sporeling in *C. cornuta*, Dauphin 2715. F. Utriculi and spherical lobuli in *C. cornuta*,

Merophytes

The merophytes originate from three cutting faces of the apical cell. Two lateral merophytes produce leaves (see leaves). A ventral merophyte produces underleaves and rhizoids (see underleaves and rhizoids). The number of ventral epidermal cells in stem width is an important taxonomic character that helps separate species of *Ceratolejeunea* from related genera. Within the genus, this character is constant.

Stem Anatomy

The anatomy of the stem in *Ceratolejeunea* has the typical pattern of the subfamily Lejeuneoideae, as defined by Evans (1935) and Bischler (1966). As in other lejeuneoids, in *Ceratolejeunea* the stems possess seven cortical rows in cross section (2 ventral, 2-3 lateral), and a variable number (4-30) of usually smaller, medullary cells. The cortical cell number is constant, sometimes having an additional cell in cross section, that is assumed to belong to the lobule. Bischler (1966) studied comparatively the stem anatomy in genera of Lejeuneaceae, and separated the family in three groups based on the stem anatomy, *i. e.* number, relative size, wall thickness, pigmentation and trigone size of cortical and medullary cells. The species of *Ceratolejeunea* were considered to have sometimes a slightly variable stem anatomy. At the infrageneric level, the anatomical (stem?) characters were considered too similar to allow the recognition of subdivisions (Bischler 1966, p.668). The number of medullary cells is variable within species, *e. g.* Bischler (1966) reported 10-21 medullary cells in *Ceratolejeunea cubensis* (Mont.) Schiffn. She included 22 species names of *Ceratolejeunea* in her studies, including two species with entire underleaves (subgen. *Ceratolejeunea*), *C. desciscens* (Sande-Lac.) Steph. and *C. portoricensis* (Hampe & Gottsche) Evans (= *Physantholejeunea portoricensis* (Hampe & Gottsche) Schust.). No difference in stem anatomy between the holostipous species (*i. e.* subgen. *Ceratolejeunea*) and those taxa with bifid underleaves (*i. e.* subgen. *Caduciloba*) was found. A general trend within the subfamily of reduction of stem cortical cells and then reduction of medullary cells in the most „advanced“ taxa was signaled by Evans (1935). His hypothesis was supported by Bischler (1966), with some differences regarding the linearity of the reduction pattern. The same trend is seen within the genus *Ceratolejeunea*, where with a constant cortical cell number, smaller plants have fewer medullary cells. The correlation of a

reduced number of medullary cells with other assumed apomorphies has to be established in a cladistic analysis.

Branching

The development of the gyrothecal *Lejeunea*-type branches from a ventral basiscopic cortical cell enclosed by the extended brace cells below the leaf insertion in mature stems, was described in detail by Crandall (1969), using among others *Ceratolejeunea flagelliformis* (Steph.) Fulford (= *C. filaria* (Gottsche) Steph.?) as example (Figure 2). The basiscopic cortical cells do not endure periclinal division, are never displaced, they divide into an ellipsoidal mass of cells, swell and then split into one dorsal and two ventral lobes as the branch grows. For innovations see under Gynoecia.

Leaves

The leaf in *Ceratolejeunea* has the unique kind of insertion found in Lejeuneaceae (Crandall-Stotler 1972): the mature leaf is divided into a dorsal lobe and a ventral lobule (complicate bilobed), being attached to the stem along a J-shaped insertion line. They usually overlap, covering the stem dorsally but in *C. minuta* and *C. laetefusca* the axis can be seen on some branches in dorsal view. At the dorsal end of the leaf insertion, a sometimes caducous, unicellular, hyaline stylus is attached between the stem and the lobe. The leaves are usually glistening, imbricate to shortly distant, spreading to inrolled when dry. In moist condition, they can be plane as in *C. laetefusca* to incurved as in *C. guianensis*, *C. brevinervis*, or *C. grandiloba*. The leaf lobe is ovate to ovate-ligulate or ovate-lanceolate in shape, usually almost symmetrical, to slightly asymmetrical. The apex can be rounded, broadly acute or exceptionally acuminate into an awn (*C. pungens*). In most of the species, the apex is entire, but some show, in variable patterns, teeth. The leaf lobe margin is usually entire, or it can be rarely crenulate by bulging cells as those of *C. dussiana* and *C. oxygonia*. When present, the marginal teeth can appear as just marginal cuticular projections between two neighboring margin cells. A marginal leaf lobe tooth consists usually of one or two conical cells projecting from a one or two-celled base on the margin. A major degree of complexity is attained in the awn of *C. pungens*, which can be up to 15 cells long from a 4-6 celled base (the type). The leaf lobe cells possess many major characters determinant in the taxonomy of the genus *Ceratolejeunea*. Such characters have been considered to be variable within the species of the

genus *Ceratolejeunea* (Evans 1905). The cells are isodiametrical, hexagonal, with rounded, elliptical or almost rectangular lumina, becoming larger and rectangular towards the base. The cuticle is in most of the species smooth, but can be papillose, with a large, rounded papillae like in *C. grandiloba* or finely papillose as in *C. oxygonia*. The cell walls can be evenly thickened or have intermediary thickenings at irregular intervals. The triradiate trigones can be sometimes coalescent, as in *C. patentissima*. The walls and intermediary thickenings have a light-brown pigmentation that becomes darker in the middle lamella (Figure 3, Evans 1905, Schuster 1992). The degree of pigmentation is variable depending on the growth conditions, *e. g.* the plants become darker when growing in extremely wet and submerged habitats. *Ceratolejeunea dussiana* shows a very pale pigmentation in the middle lamellae of the leaf lobes, but the pigmentation is more evident in the stem cross-section.

The oil-bodies are present in the leaf lobe cell, stems, and rarely in underleaves (*C. grandiloba*), prove to be a reliable character for identification of fresh plant material. Their shape is usually elliptical, when viewed along the length axis or rounded when viewed along the width axis. Following the oil-body classification proposed by Gradstein *et al.* (1977), two main types of oil-bodies are found in *Ceratolejeunea*:

- a. *Bazzania*-type: composed of 1-4 segments, with an apparently smooth matrix. This oil-body type is present in the common *C. cornuta* (Figure 3B).
- b. *Jungermannia*-type. The matrix of the oil-bodies appears granulose to botryoidal, depending on the diameter of the spherules. They are in number of 1-5 per cell. This type of oil-body is present in most of the *Ceratolejeunea* species studied and those reported in the literature (Figure 3C, Schuster & Hattori 1954 and Schuster 1992).

Ocelli

The ocelli are a most important classification and identification character in the genus *Ceratolejeunea*. They can be distinguished from other cells by the presence of a single, large, homogeneous oil body and the lack of chloroplasts. In dried material, the content of the oil-bodies seems to be preserved long time. If there are no contents left, the ocelli can still be recognized, for they are pellucid and lack intermediary thickenings as normal cells. The ocelli can occur in different organs such as leaf lobes, stems, underleaves, bracts and perianth body. The used classifications reflect the distribution patterns of the ocelli in leaves. Following Zwickel (1932) and He & Piippo (1999), the following ocelli types are recognized:

- a. Basal. Is the most common type. The cells are arranged in a line or arc, being equidistant from the leaf base, e. g. *C. laetefusca*, *C. cornuta*, *C. spinosa*.
- b. Suprabasal. Is a very rare arrangement in the genus, present sometimes in *C. dussiana*.
- c. Seriate. The cells are oriented in a row towards leaf apex, interrupted by normal, vegetative cells. Plants having this type of ocelli also possess basal ocelli in many leaves. This pattern is typical in *C. fallax*.
- d. Moniliate. The cells are oriented in a continuous row towards leaf apex. This ocelli type is present in *C. brevinervis*. In *C. rubiginosa*, a second row of moniliate ocelli may be present in robust specimens, giving the impression of a vita.
- e. Disperse. The cells are dispersed in the leaf lamina. This seems to occur exclusively in *C. grandiloba* and in *C. malleigera*.

The ocelli are a major classification and identification character, that helps distinguishing the genus *Ceratolejeunea* from related ones (as *Physantholejeunea*), and are major characters in species delimitation. A primary division of the genus *Ceratolejeunea* subgenus *Caduciloba* using ocelli as criteria was proposed by Schuster (1992). See under classification.

Lobules

The lobule displays a notable range of variation in *Ceratolejeunea*, where 4 types of lobules occur:

1. Inflated („normal“): the lobule is inserted to the stem by 4-6 cells on the ventral side and inflated throughout, ovate in shape and narrowed to the opening of the water sac. This lobule type is found in most species of the subgenus *Caduciloba*. In *C. patentissima*, the lobule mouth is strongly constricted and the apical tooth is hidden, which gives the structure the appearance of a bottle (flask-shaped).
2. „Ptychanthoid“: the lower part of the lobule is inflated and the upper part limited by the free margin is flattened, as occurs in the Ptychantheae and in many Lejeuneoideae (Gradstein 1994). In contrast with that subfamily where the lobule may have none or several teeth, in *Ceratolejeunea* the lobule free margin has a single tooth towards the lobule apex. The shape of this lobule type is trapezoid, not narrowed toward the opening. This is typical for the subgen. *Ceratolejeunea*, excepting *C. szyszyłowiczii*.
3. Reduced: in a progressive reduction series, the lobule can have as few as 3 cells at the leaf ventral insertion, which frequently occurs in *C. laetefusca*. This lobule type is apparently restricted to several species of the subgen. *Caduciloba*.

4. Spherical: the lobule is swollen and strongly inrolled, so that the water sac appears as a small sphere at the base of the developed leaf. Spherical lobules are set in series along a branch and might be associated or not with utriculi at the base of the branch. They can be found in *C. cornuta*, *C. coarina*, *C. fallax*, *C. filaria*, *C. pungens* and *C. spinosa*, in main branches, lateral branches and in single innovations (Figure 3).
5. Utriculi: the leaf is unequally divided into a very small dorsal lobe and a large ventral lobule inrolled to form the water sac (Crandall 1969). The utriculi can be rounded or reniform in shape and occur solitary or in pairs at the base of lateral branches (Figure 3).

The leaf lobule cells tend to be more irregular in shape and smaller in size than the leaf lobe cells and are frequently bulging. In some cases, the ocelli are placed under the lobule free margin, but they do not occur in the lobule itself. The keel can be straight or arched, in outline entire or crenulate due to its bulging, mammillose cells. The hyaline papilla is proximal, attached at the base of the apical tooth, frequently bulging upwards or backwards, tending to be laid parallel to the lobule free margin. The lobule tooth can be curved, short or elongated (subgen. *Caduciloba*), sometimes hidden in the constricted lobule mouth (*C. patentissima*) or be scarcely projecting (subgen. *Ceratolejeunea*). The length of the apical tooth has been used by several authors as a distinctive species character (*e. g.* Fulford 1945, Lücking 1995) but it is seemingly variable even in the same plant.

Underleaves and Rhizoids

The underleaves of *Ceratolejeunea* can be put in a linear succession of shapes, sizes and types. It seems that the basic type of underleaf is the entire one. Juvenile plants regenerating from leaf lobe cells show in most cases a first entire underleaf which is then replaced by a mature, bifid underleaf in the subgen. *Caduciloba*. In *C. patentissima*, the juvenile plant regenerating from a leaf lobe cell produces bifid underleaves first (Fulford 1944b), but in shoots of this species, I have seen the youngest underleaves to be practically entire or notched two cells deep. In the same stem, notched underleaves may be replaced by others with deeper underleaf insertion. A plant with bifid underleaves is the more frequent state in *Ceratolejeunea* species. The V-shaped or rarely U-shaped insertion may reach down to half the underleaf length. The underleaf lobes may be somewhat rounded, acute or acuminate. This later state is associated with an ovate underleaf shape. In that case, the lobes are triangular in shape and end with a one or two-celled acumen. The underleaf margin is in most species entire but in several

species, marginal teeth are present at irregular intervals on one or both sides. A particular variation of the underleaf pattern is found in *C. minuta*, where the underleaf incision is U-shaped and the margins bear constantly a single, well developed tooth.

Plants of the subgen. *Ceratolejeunea* may possess entire, truncate, or broad bilobed underleaves (*C. grandiloba*). The underleaves are frequently ovate or orbicular in shape, the margins are entire, and the cells are similar to those of the leaf lobe cells. In the single case of *C. grandiloba*, ocelli have been reported to occur on underleaves (Grolle 1987).

The origin of the underleaves is directly related with that of the rhizoids. Bischler (1968) and Winkler (1968) among others, studied the anatomy of the rhizoid plates in the Lejeuneaceae. The anatomy of the underleaf insertion and the rhizoid disc of *Ceratolejeunea* is likely to follow the plan described for *Drepanolejeunea* by Bischler (1968). The former author studied longitudinal sections of stem at the ventral insertion of the underleaves and recognized cells belonging to the underleaf (i, cellules centrales inférieures), cells belonging both to the underleaf and the stem (y, cellules centrales supérieures) and cells belonging to the stem (tc, cellules corticales ventrales; x, cellules corticales de la tige modifiées).

The superior central cells (y) are „croissant-shaped“ and „connect“ the underleaf to the stem. Above the upper central cells is attached the rhizoid disc (p, paramphigastre), a cell disc developing on the basal part of the underleaf (Bischler 1968). It is not clear whether the rhizoid disc (p) develops from the lower (i) or from the upper central cells (y). From the surface or marginal cells of this rhizoid disc spreading rhizoids or a secondary rhizoid disc (disque adhésif, Haftscheibe) may develop. The presence of a secondary rhizoid disc depends on the substrate, being more developed in epiphyllous plants (Winkler 1970).

In *Ceratolejeunea* the number of lower central cells (i) seems to vary from 2 (e. g., *C. confusa*, *C. patentissima*) to 3 (e. g. *C. cornuta*, *C. globulifera*, *C. szyszyłowiczii*). Judging from the dorsal, surface view, some species tend to be more similar to patterns of Ptychantheae and Brachiolejeuneae as described by Gradstein (1994).

Vegetative reproduction

Evans (1905) first reported vegetative reproduction in species of *Ceratolejeunea*, and Fulford (1944b) studied the vegetative reproduction in eight taxa. Excepting *C. laetefusca* and *C. patentissima*, vegetative reproduction is rare in *Ceratolejeunea*. It consists of direct regeneration of a plant from a leaf lobe median or marginal cell without protonemal intermediates. (see Plates of *C. patentissima* & *C. laetefusca*).

Sex Distribution

The majority of the 23 species of *Ceratolejeunea* treated here are monoicous (35%). Polyicous (22%) and dioicous (22%) species are also well represented. In the remaining species (21%), the sex condition could not be determined due to lack of material. Some species that are usually dioicous may happen to be autoicous in rare occasions, as does in *C. laetefusca*. Due to the rarity of some of the taxa, in many cases it cannot be asserted whether the sex distribution pattern is constant or not.

Androecia

The androecia grow on lateral branches, they can be terminal or intercalary (so that the branch continues producing normal leaves after the androecial spike is formed). The spikes consist of 2-9 (-14) bract pairs. The bracts are hypostatic, *i. e.* they overlap the next, younger bract. Due to the mammillose cells, the bracts are frequently crenulate in outline. The antheridia occur in pairs in the axils of the bracts. The bracteoles follow the same pattern as the underleaves, being entire, notched or bifid. There are usually 1-2 bracteoles per spike. The genus *Ceratolejeunea* seems to be rather homogeneous in androecial characters. Some variation can be seen in the occurrence of intercalary spikes. Such spikes has been seen in 9 species, among which the most frequently collected ones (*e. g.* *C. cornuta*, *C. cubensis*). In *C. minuta*, the androecial branches as a rule seem to produce leaves after the production of males bracts.

Gynoecia

The innovation types in the Lejeuneaceae were first studied by Mizutani (1970, *vide* Grolle 1980); Grolle re-named the described types as „lejeuneoid“ and „pyncnolejeuneoid“. In *Ceratolejeunea* the innovation leaf sequence is pyncnolejeuneoid, with the first appendage being always an underleaf. In the single case of *C. szyszyłowiczii*, in the single specimen known for the species, no innovations were found. The usual gynoecial pattern, seen in 11 species, is a gynoecium with a single, sterile innovation. In some cases, single innovations may be fertile again, producing a cymose pattern, as is seen in *C. ceratantha*, *C. confusa*, *C. globulifera* and *C. grandiloba*. In some common species in which this character also behaves as a polystate

character, paired innovations that become again fertile have been observed. This dichasial pattern has been found in *C. cornuta*, *C. cubensis*, *C. filaria*, *C. fallax* and *C. laetefusca*.

Interestingly, variable gynoecial patterns have been observed in species of which abundant fertile material was available. Many of those recorded as having only a single sterile innovation, however, are known from few collections.

In *Ceratolejeunea* the female bracts have usually an obovate lobe. In concordance with the stem leaves, the lobe margin can be entire or toothed. If toothed, the bract teeth may be larger than those of the stem leaves. In *C. filaria*, the bract teeth reach great development, making the bracts look lacinate. The bract lobule is ovate-lanceolate, the margin is usually entire. In the species of *Ceratolejeunea*, the bracts are connate at the base up to about $\frac{1}{4}$ with the bracteole. The bracteole follows the pattern of the underleaves, being most of the time ovate, entire or bifid. The cells in bracts and bracteoles are similar to those described for the leaf lobes. In robust specimens, ocelli may also be present in bracts, placed in the lower central part, geminate, varying in number from one to six.

The perianth in *Ceratolejeunea* is obconical in shape, its cells are markedly more collenchymatous than those of the leaf lobe, and mammillose. This gives the perianth outline a crenulate appearance, especially on the keels. The keels may be low and rounded, (2 lateral, 2 postical, 0-1 dorsal) as in *C. confusa* and *C. minuta*, or may produce hollow appendages called horns, that can be short or elongated, more or less triangular, terete or bulbous. The horns are usually four per perianth, but very rarely, a fifth horn may develop on a perianth. As an exception, the perianths of *C. malleigera* possess 2, rarely 3 bulbous horns.

The juvenile perianths can appear as small terete horns on a broad, triangular base on the perianth body, or be bulbous on a short stalk. The cells of the perianth horns are much more thin-walled than those of the perianth body. In some specimens the cells appear thin-walled and colorless towards the tips. The cells on the tips of the perianths usually collapse as the horns grow, giving the perianths the appearance of a ripped structure. This is very evident in the horns of *C. spinosa*. In the perianths of *C. dussiana*, the marginal cells of the „ripped“ perianth continue growing, giving the impression that the appendage is branched. A type of branching process has been seen in *C. brevinervis*, whose hollow, terete horns may bifurcate in very robust specimens (Figure 11).

The perianth characters play a preeminent role in the taxonomy of the genus *Ceratolejeunea*. Their variation has led other authors (*e. g.* Vanden Berghen 1951, Grolle 1987) to separate the genus in several coherent groups (see classification).

Sporophyte

As diagnostic in the subfamily Lejeuneoideae, the sporophyte in *Ceratolejeunea* possesses an articulate, hyaline seta, with 12 outer and 4 inner cells in cross section (Mizutani 1961, Figure 4, 14). The capsule splits at maturity into four bistratose, hyaline valves that remain erect at dehiscence (Mizutani 1961). The sporophyte valves have a „Schmetterling“ pattern typical for the subfamily, in which differentiated, thin-walled cells extend from the base up to $\frac{1}{2}$ towards the apex, having an outline comparable to the wings of a butterfly (Weis 1999). The elaters are simple, attached to the valve margins. The spores in the family tend to vary with respect to their ornamentation pattern and tetrad marks (Weis, pers. comm.). The rosettes vary in number per spore and aspect: some might be almost unnoticeable, others conspicuous. They consist of a depression in the spore coat, surrounded by conical projections, here called „teeth“, ordered in one or two circular rows around the rosette depression, the teeth surface can be smooth or adorned. For the purpose of this work, two kind of rosettes are recognized: simple and complex ones (as observed in some specimens with SEM), depending on the number of teeth. Simple rosettes have about 10 teeth, complex ones 10-15 teeth.

Sporophyte characters are useful in classification of higher taxonomic ranks, as family, subfamily and in groups of genera (*e. g.* Weis 1999). Sporophyte characters, excepting for the variation seen in the spores seem to be uniform in the genus *Ceratolejeunea*.

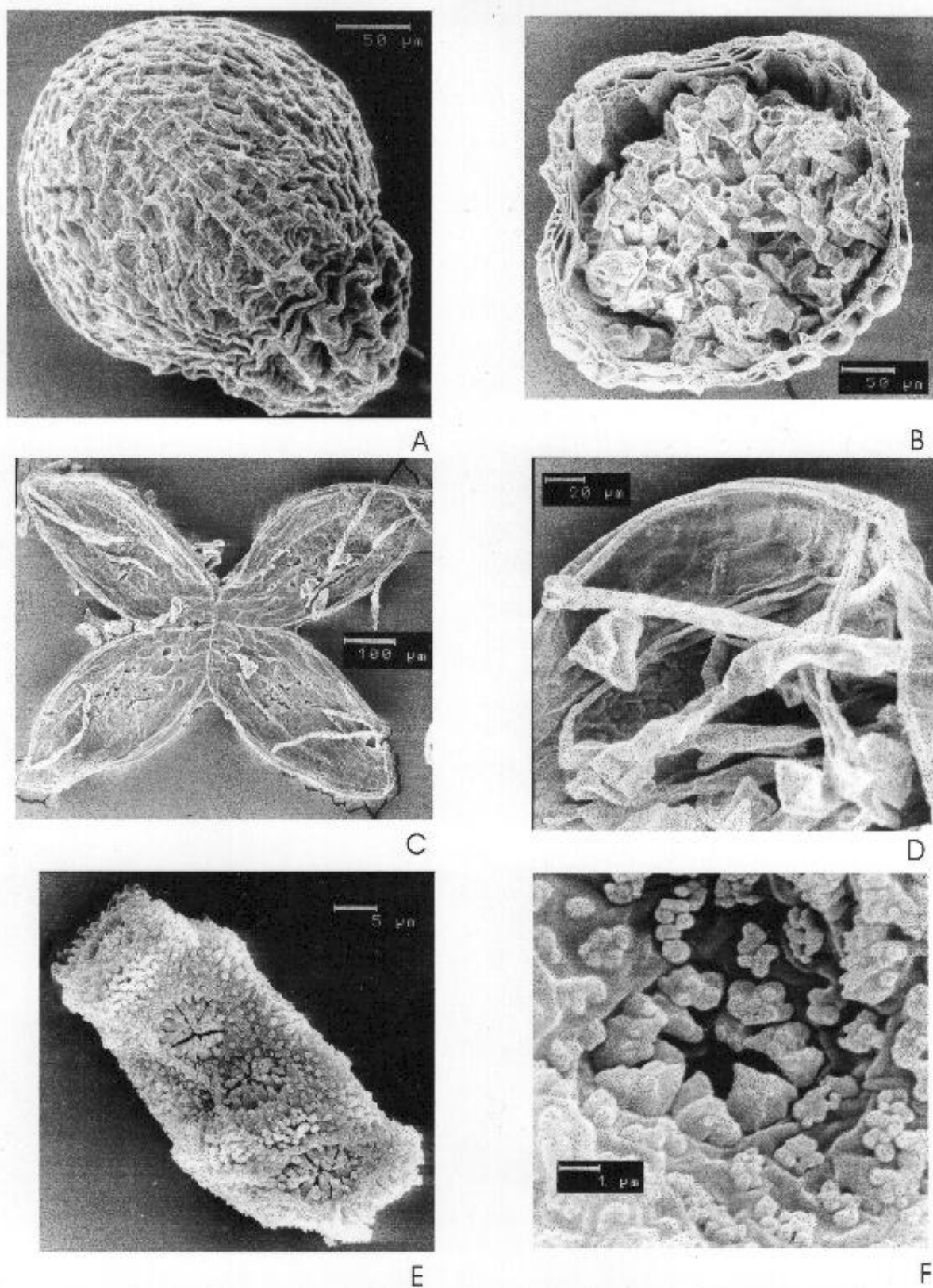


Figure 4. Sporophyte. A. Capsule and foot in *Ceratolejeunea cornuta*, Dauphin 2686. B. Capsule cross section in *C. grandiloba*, Sipman 27205. C. Valves in *Ceratolejeunea cornuta*, Dauphin 2686. D. Elaters and spores in *C. grandiloba*, Sipman 27205. E. Spore from *C. confusa*, the type. F. Rosette in *C. coarctata*, the type.

Growth habit

Following the classification of growth forms in bryophytes by Richards (1983), four types of growth forms occur in *Ceratolejeunea*:

- a. Rough mats. This is the most common growth form found in the genus. Typical for this category is *C. cubensis* (Mont.) Schiffn.
- b. Thread-like forms. Is represented by plants sparingly growing on leaves, e. g. *C. coarina* (Gottsche) Steph.
- c. Tall turfs with projecting or creeping branches. Shown in luxuriant growth conditions by *C. cornuta*, the rough mats produce also more or less vertically oriented branches, that appear entangled, hard to tell apart.
- d. Hanging. This may be just a robust expression of robust mats. The species showing this growth form usually possess strongly thickened cortical stem cells, and the cell pores between them are conspicuous in ventral view. Only two species of *Ceratolejeunea* are known to show this growth form: *C. filaria* (Taylor) Steph. and *C. pungens* (Spruce) Steph.

DISTRIBUTION AND ECOLOGY

The world region with the greatest diversity of *Ceratolejeunea* species is located between the Tropic of Cancer and the Tropic of Capricorn in Tropical America. The Neotropics harbor a wide variety of landscapes and habitats, ranging from deserts to páramos and lowland rainforest. The only common physical factor between the areas appears to be the day length. Other physical parameters such as humidity, elevation and soil are very variable.

Tropical America is here subdivided in 10 different regions, following Gradstein *et al.* (in press) with slight modifications (Figure 5). The distribution and diversity of *Ceratolejeunea* in these regions is as follows:

1. Mexico and South Eastern United States (4 spp.). The southern half of Mexico, is characterized by having the southernmost distributional limits of holartic species, and the northernmost limits of neotropical rainforest species (Gradstein *et al.* in press). To the latter group belong four species of *Ceratolejeunea*: *C. cornuta*, *C. cubensis*, *C. fallax*, *C. filaria*. Not many specimens are available of these species from Mexico, which may indicate that they are rare in the area. *Ceratolejeunea laetefusca* is frequently collected in Southwestern United States, and is the species with the northernmost distribution.
2. Central America (12 spp). This region includes Guatemala, Belize, Honduras, El Salvador, Nicaragua, Continental Costa Rica and Panama. Influenced by the two great subcontinents of South and North America, the Pacific ocean and the Caribbean, Central America shares elements with those areas including widespread species as *C. cornuta*, *C. cubensis*, *C. laetefusca*, *C. coarina*, *C. fallax*, as well as more localized species, *C. dussiana* (lowland Costa Rica and Panamá, Cocos Island Chocó, Amazonia) *C. confusa* (Caribbean, Costa Rica, Chocó, Amazonia), and higher elevation species *C. filaria*, *C. patentissima*, *C. spinosa*. Central America also shares with the Andes *C. globulifera* and with the Caribbean *C. rubiginosa*.
3. Caribbean (14 spp.). This is the region with the highest number of *Ceratolejeunea* species. With two endemic taxa, *C. brevinervis* and *C. dentistipula*, this area holds together with the Northern Andes, the center of diversity of the genus. A subendemic element, *C. oxygonia*, is shared with the latter region. Other species occurring in this area are *C. ceratantha*, *C. coarina*, *C. confusa*, *C. cornuta*, *C. cubensis*, *C. dussiana*, *C. fallax*, *C. filaria*, *C. laetefusca*, *C. patentissima*, *C. rubiginosa* and *C. spinosa*.

4. Chocó (including Cocos Island) (10 spp.). This region is here considered to extend from Guayaquil (Ecuador) to 9 degrees north (Gentry 1980). Several Chocó hepatic species reach Northern Costa Rica (Dauphin *et al.* 1998). Being the region with higher humidity, it holds mostly widespread lowland and middle elevation species, as *C. coarina*, *C. confusa*, *C. cornuta*, *C. cubensis*, *C. fallax*, *C. filaria*, *C. laetefusca*, *C. spinosa*. More localized species are *C. dussiana* and *C. rubiginosa*. A subendemic species, *C. pungens*, is shared with the Northern Andes.

5. Northern Andes (including Galapagos Archipelago?) (12 spp.). This region has several rare or endemic species: *C. szyszyłowiczii* is known from a single collection from this area; *C. globulifera* and *C. grandiloba* are Andean elements; *C. desciscens*, *C. pungens* and *C. oxygonia* are shared with the Amazonia, Chocó and the Caribbean, respectively. Widespread and higher elevation taxa are also present: *C. coarina*, *C. cornuta*, *C. cubensis*, *C. filaria*, *C. patentissima* and *C. spinosa*. Most *Ceratolejeunea* species tend to occur in elevation belts above 500 m that correspond with this region, which may explain the high species number found here (see altitudinal distribution).

6. Central Andes (6 spp.). The presence of *C. globulifera* and *C. grandiloba* indicate affinity of this region with the Northern Andes, though the species number in this area is much more reduced. Probably this is due the drier climate in most of the region. *Ceratolejeunea malleigera*, is endemic and known from a single collection in the Bolivian Yungas. Widespread mountain species also appear in this region: *C. cornuta*, *C. filaria*, and *C. spinosa*.

7. Amazonia (12 spp.). The large surface area may explain the high species diversity of the region. With an area of 5-6 millions square kilometers (Churchill 1998), this is the largest of the ten geographical units in the Neotropics. It extends from sea level up to 800 m (and includes five countries: Bolivia, Brazil, Colombia, Ecuador and Perú (Churchill 1998, Gradstein *et al.* in press). This region includes lowland, widespread taxa such as *C. ceratantha*, *C. coarina*, *C. confusa*, *C. cubensis*, *C. dussiana*, *C. fallax*, *C. guianensis?*, *C. laetefusca*. *Ceratolejeunea cornuta*, seems to be the most common species in the region. Two rare species are shared with the Andes: *C. desciscens* and *C. globulifera* (Napo-Pastaza?). A single taxon, *C. minuta*, is endemic and apparently restricted to an area near the mouth of the Amazon river.

8. Guyana Highland (4 spp.). This relatively small area has a mixture of mountain and lowland species, including *C. cornuta*, *C. grandiloba*, *C. guianensis* and *C. patentissima*.

9. Brazilian Planalto (3 spp.). This region presents widespread species more tolerant to dryer conditions, as *C. cornuta*, *C. cubensis* and *C. laetefusca*.

10. Southeastern Brazil (7 spp.). Widespread, lowland species are typical for this region: *C. ceratantha*, *C. coarina*, *C. cornuta*, *C. cubensis*, *C. fallax*, *C. laetefusca* and *C. rubiginosa*. This area shows no particularity in its species composition, and is the southernmost limit of the species of *Ceratolejeunea*.

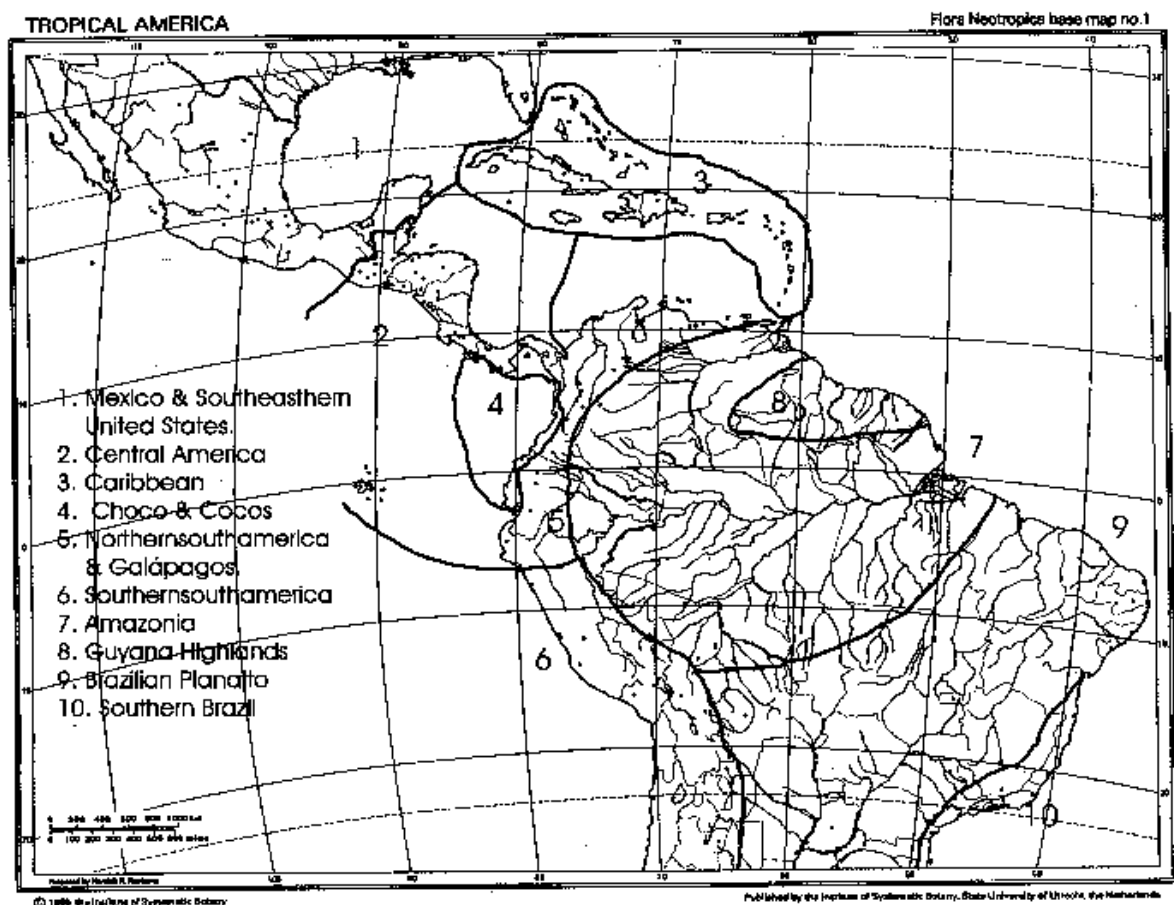


Figure 5. Regions of Tropical America. Following Gradstein *et al.* (in press).

Table 4 resumes the distribution, altitudinal range and habitat for the neotropical species of *Ceratolejeunea*. The Caribbean stands out as the area with the greater species diversity, having almost 60% of the species known from Tropical America. With two endemic species, *C. brevinervis* and *C. dentistipula*, this area is also the major center of endemism.

The Caribbean shares a sub-endemic element with the Northern Andes (*C. oxygonia*), which is the second diversity center for *Ceratolejeunea* in the Neotropics.

Table 4. Neotropical *Ceratolejeunea* species:
Distributional range (by neotropical region), altitude and habitat.
For explanation of numbers of neotropical regions see text and Figure 5.

Species	Range	Alt (m)	Main habitat
<i>Ceratolejeunea brevinervis</i>	3	1400-1700	Submontane, montane forest.
<i>C. ceratantha</i>	3,7,10	640-900	Canopy in lowland and submontane forests.
<i>C. coarina</i>	2-7,10	0-1400	Primary & secondary lowland to submontane forests.
<i>C. confusa</i>	2-4,7	0-250	Primary & secondary lowland forests.
<i>C. cornuta</i>	1-10	0-2000	Primary & secondary lowland to montane forests.
<i>C. cubensis</i>	1-4, 7,9,10	0-1000	Primary & secondary lowland wet and seasonal forest to submontane.
<i>C. dentistipula</i>	3	300-650	Lowland rainforests.
<i>C. desciscens</i>	5,7	0-1400	Primary & secondary lowland wet forest to submontane.
<i>C. dussiana</i>	2,3,4,7	100-1200	Wet lowland & submontane forests.
<i>C. fallax</i>	1-4, 7,10	200-1600	Wet lowland to lower montane forests.
<i>C. filaria</i>	1-7	650-2900	Primary & secondary submontane forest to montane
<i>C. globulifera</i>	2,5,6,7	1200-1900	Primary wet submontane forest to montane
<i>C. grandiloba</i>	5,6,8	1500-3100	Primary & secondary wet submontane forest to montane
<i>C. guianensis</i>	1,7,8?	0-900	Primary & secondary lowland forests.
<i>C. laetefusca</i>	1-4, 7,9,10	0-1300	Hammocks, primary & secondary lowland forests.
<i>C. malleigera</i>	6	2000	Montane wet forest.
<i>C. minuta</i>	7	-	Lowland wet forests.
<i>C. oxygonia</i>	3,5?	?	Submontane forest?
<i>C. patentissima</i>	2,3,5,8	450-300	Wet submontane forest to lower páramo.
<i>C. pungens</i>	4,5	200-650	Wet submontane forests.
<i>C. rubiginosa</i>	2,3,4,10	0-900	Lowland to lower montane forests.
<i>C. spinosa</i>	2-6	250-2000	Wet submontane and montane forests.
<i>C. szyszyłowiczii</i>	5	?	?

Altitudinal distribution

The distribution pattern of the species in the different regions of the Neotropics is also determined by the presence of the different altitudinal belts. The recognition of the different forest belts follows Frahm & Gradstein (1991).

1. Tropical lowland forest (0-500 m). Dense bryophyte masses are generally lacking in this type of forest, except in the canopy where a high cover of *Ceratolejeunea cornuta* or *C. cubensis* can be present. *C. coarina* occasionally covers the surface of leaves, especially on understory palms and ferns. In dryer areas, the abundant *C. cornuta* tends to be replaced by *C. cubensis* and *C. laetefusca*. About 60% (15) of the species of *Ceratolejeunea* occur in this elevation belt and throughout the Neotropics. A single species, *C. confusa*, seems to be confined to this belt.
2. Tropical submontane forest (ca. 500-1400 m). This elevation belt has the highest species diversity of *Ceratolejeunea* in the Neotropics, with ca. 80 % (19) of the species occurring in this belt. The species in this areas are corticolous, and not as common as in the lowlands, even though the highest species diversity of the genus is to be expected in this areas.
3. Lower tropical montane forest (ca.1450-2000 m). The number of *Ceratolejeunea* species drastically decreases at this elevation, with ca. 45% (11) of the species present. The Bolivian *C. malleigera* has been recorded only for this elevation belt.
4. Upper tropical montane forest (2050-3000 m). Only 25% (6) of the *Ceratolejeunea* species occur in this belt. These are usually robust corticolous specimens, that may also grow facultatively as epiphylls or on litter. This belt may include the „elfin forest“ were *C. cornuta* and *C. patentissima* are ubiquitous (Fulford *et al.* 1971b).
5. Tropical subalpine forest. Only *C. patentissima* and *C. grandiloba* have been reported from over 3000 m. Schuster (1978) reported the occurrence of the former in a lower páramo area, growing on soil (as *C. andicola* Schust.).

Ceratolejeunea species are apparently absent in the highest elevations of the Andes and Central America, corresponding to the open páramo and superpáramo habitats. Even though a greater diversity of hepatics in the tropics is found in the upper montane forest (Gradstein 1995). The pattern of diversity show by the genus *Ceratolejeunea* in the different elevations and forest belts clearly coincides with that of the Lejeuneaceae in general, which are most diverse and frequent in lowland and submontane forest (Gradstein 1995). The species of *Ceratolejeunea* are particularly abundant in lowland rain forests, where *C. cornuta* and *C. cubensis* may cover copiously the bark of trees in old secondary growth and forest canopies. *Ceratolejeunea coarina* is a frequent epiphyll in this habitat type. In submontane and lower montane forests, the species

of *Ceratolejeunea* become less abundant, but their overall species diversity seems to increase here. At higher elevations, above 2000 m, the species become scarce, at the same time the plants become more robust.

Substrate

The present data depend on the interpretation of the information written on the specimen labels and the field observations of the author. The substrate types in which *Ceratolejeunea* species occur are shown in Table 5.

Table 5. Substrate preference of the neotropical species of *Ceratolejeunea*

Substrate type	# of species	remarks
Artificial	1	<i>C. cornuta</i> on plastic ribbon (Reese 14875, NY)
Bark	20	including trunk base, trunk, branches, twigs, pendent and lianas.
Leaves	10	
Rocks	5	
Rotting bark	8	

The genus *Ceratolejeunea* is primarily corticolous and occurs secondarily on other substrates: almost half of the examined specimens (48%) have been collected on bark, while 8% were epiphylls, 2.9% grew on rocks, 2.6% on rotting bark and only 1.9% were terrestrial (rest unknown).

Based on the observations of Winkler (1968), the species of *Ceratolejeunea* appear to be facultative epiphylls. No *Ceratolejeunea* species has been found as leaf colonizer. According to Winkler (1968), obligate epiphylls are usually found as leaf colonizers. Other species apparently grow only on leaves where other epiphyllous already grow, producing thus a succession. Our species are frequent elements in the epiphyllous flora: Lücking (1995) found *C. coarina*, *C. cornuta* and *C. cubensis* growing on 42, 35 and 13 of 68 host plants respectively. No substrate nor host specificity has been found, the successful growth of *Ceratolejeunea* species on artificial substrates (Reese 14875, NY) suggests that they may grow in any smooth surface.

The species tend to grow in well illuminated places, and are particularly common on canopy branches, twigs and on exposed trunks.

Some species are frequent in riparian and submerged habitats (*e. g. C. fallax, C. cornuta*).

Growth on rotting bark is rare (just as terrestrial and saxicolous growth) and is mostly seen at higher elevations.

CONSERVATION

The widespread *Ceratolejeunea* species may commonly occur in old secondary vegetation and woody crop plantations and are not threatened. On the other hand, endemic species occur very localized in upper elevation areas of the Caribbean and in submontane forests in the Northern Andes. These are major centers of species diversity also in *Ceratolejeunea*, on which conservation should focus (Myers *et al.* 2000).

CLASSIFICATION AND PHYLOGENY

Generic relationships

The genus *Ceratolejeunea* has generally been recognized as a natural entity (e. g. Evans 1905, Schuster 1980) since its first description by Spruce in 1884. It is defined within the subfamily Lejeuneoideae by the presence of dark pigmentation, horns on the perianth, ocelli and utriculi. The ranking of *Ceratolejeunea* and its taxonomic placing by different authors is shown in Table 1.

By its sporophyte and stem morphology *Ceratolejeunea* clearly belongs in the subfamily Lejeuneoideae; affinities of the genus and holostipous Lejeuneaceae are mentioned in the literature. Within the Lejeuneoideae, Schuster (1963) treated *Ceratolejeunea* as a separate „genus complex“, signaling affinities with the „*Stictolejeunea-Neurolejeunea* complex“ and the „*Cladolejeunea* complex“.

The genera *Stictolejeunea* and *Neurolejeunea* belong in the Tribe Brachiolejeuneae (Gradstein 1994). Their bearing ocelli, entire underleaves and their dark color relate them to *Ceratolejeunea* subgen. *Ceratolejeunea*. The former genera are easily separated from holostipous *Ceratolejeunea* whose merophyte is only two cells wide, in contrast with *Stictolejeunea* and *Neurolejeunea* whose ventral merophytes are 4-18 and 4-6 (-10) cells wide respectively. The Tribe Brachiolejeuneae possesses also genera whose ventral merophytes are two cells wide, such as *Dicranolejeunea*, *Odontolejeunea* and *Acanthocoleus*. The latter genera show more than one tooth at the leaf lobule margin, and can be separated by the single apical tooth on the leaf lobule apex of *Ceratolejeunea*. All members of Brachiolejeuneae can be separated from *Ceratolejeunea* and other members of the Lejeuneoideae by the thicker seta.

Table 1. Taxonomical placement of the genus *Ceratolejeunea* by different authors

Taxon rank B	Spruce 1884	Schiffner 1893	Mizutani 1961	Schuster 1956, 1963, 1978; Herzog 1958 <i>(fide Schuster 1963)</i>	Grolle 1983	Schuster 1984	Gradstein 1994, Gradstein <i>et al.</i> in press	Dauphin 2000
Family		Jungermanniaceae	Lejeuneaceae	Lejeuneaceae	Lejeuneaceae	Lejeuneaceae	Lejeuneaceae	Lejeuneaceae
Subfamily			Lejeuncoideae			Lejeuncoideae	Lejeuncoideae	
Tribe		Jubuloideae-Lejeuneae		Schizostipae			Lejeunae	?
Genus	<i>Lejeunea</i> Lib.	<i>Ceratolejeunea</i> (Spruce) Schiffn.	<i>Ceratolejeunea</i>	<i>Ceratolejeunea</i> (Spruce) Schiffn. ¹	<i>Ceratolejeunea</i> (Spruce) Schiffn	<i>Ceratolejeunea</i> (Spruce) Schiffn	<i>Ceratolejeunea</i>	<i>Ceratolejeunea</i> Jack & Steph.
	Schizostipae							
Subgenus	<i>Cerato-Lejeunea</i> Spruce			<i>Ceratophora</i> Schust. <i>Ceratolejeunea</i> auct. <i>Caduciloba</i> Schust.				<i>Ceratolejeunea</i> <i>Caduciloba</i> Schust.

¹ Excluding in 1963 *Cladolejeunea* Zwickel and *Physantholejeunea* Schust. in 1978.

The Caribbean genus *Physantholejeunea* was segregated from *Ceratolejeunea* by Schuster (1978). The lack of pigmentation in the cell walls and middle lamellae, and the ventral merophyte structure (4 cells wide) clearly separate *Physantholejeunea* from *Ceratolejeunea* subgen. *Ceratolejeunea*.

The lack of ocelli, utriculi, and dark pigmentation in the cell walls and middle lamellae segregate the African genus *Cladolejeunea* from *Ceratolejeunea*. *Cladolejeunea* is characterized by the perianth with four low horns and the gynoecia on a short branch without innovation (Zwicker 1933, Schuster 1963).

Plants of *Pycnolejeunea* and *Lepidolejeunea* with a similar stem structure, divided underleaves, pycnolejeuneoid innovations and ocelli resemble *Ceratolejeunea* species without horns. But the lack of pigmentation in the cell walls and middle lamellae, and the utriculi, separate them from *Ceratolejeunea* (Piippo 1986, He 1999).

Species of the complex genus *Lejeunea* represent the basic structural scheme of the subfamily. The lack of pigmentation in the cell walls and middle lamellae, ocelli, and utriculi help separate *Lejeunea* from *Ceratolejeunea* species that lack perianth horns (Schuster 1963, 1980).

Dark colored plants of *Cheilolejeunea* and *Cyclolejeunea*, finally, have frequently been determined as *Ceratolejeunea*. A closer look at the specimens of *Cheilolejeunea* reveals the lack of pigmentation in the middle lamellae of leaf lobe cells, and the distal papilla of the leaf lobule (Gradstein *et al.* in press). The presence of gemmae and the absence of pigmentation in the middle lamellae clearly separate *Cyclolejeunea* from *Ceratolejeunea*.

Phylogenetic Analysis

This analysis aims at providing a hypothesis about the phylogenetical relationships among the neotropical species of *Ceratolejeunea*. Twenty three species were included, using *Physantholejeunea portoricensis* (Hampe & Gottsche) Schust. (*vide* Schuster 1978, 1980) and *Lejeunea flava* (*vide* Mizutani 1961, Schuster 1980) as outgroups. The choice was based on the close relationship between *Lejeunea* and *Ceratolejeunea* (S. R. Gradstein, pers. comm.) The genus *Physantholejeunea* was segregated from *Ceratolejeunea* by Schuster (1978). This analysis includes 19 morphological, gametophytical characters and a spore character (rosette type). The characters and character states used for the analysis are presented in Table 2. The character states assigned to the taxa are given in Table 3.

Table 2. Characters and character states for the cladistic

analysis of Neotropical *Ceratolejeunea* Jack & Steph. For explanation see text.

1. Sex distribution: 0= autoicous, 1= dioicous.
2. Plant width: 0=<1.5 mm, 1=>1,5 mm.
3. Stem diameter: 0= <100 μm , 1= >100 μm .
4. Flagelliferous branches: 0= absent, 1= entire leaflets, 2= dentate leaflets.
5. Caducous leaves: 0= absent, 1= present.
6. Mean leaf length: 0= <600 μm , 1= >600 μm .
7. Leaf teeth on antical margin: 0= absent, 1= distal half, 2= all over.
8. Ocelli: 0= absent, 1= basal, 2= geminate, 3= seriate, 4= moniliate, 5= scattered.
9. Leaf lobe cells: 0= smooth, 1= papillose, 2= mammillose.
10. Lobule/ leaf lobe length prop.: 0= <0.3, 1= >0.3.
11. „Normal“ lobule type, 0= inflated throughout, 1= inflated lower part, 2= flask shaped.
12. Spherical lobules: 0= absent, 1= present.
13. Reduced lobules: 0= absent, 1= present.
14. Underleaf type: 0= entire, 1= bifid.
15. Underleaf shape: 0= longer than wide, 1= wider than long, 2= orbicular.
16. Underleaf teeth: 0= absent, 1= present.
17. Female bract margin: 0= entire, 1= toothed.
18. Perianth horn type: 0= absent, 1= terete, 2= bulbous, 3= erose dentate.
19. Rosette type: 0= simple, 1= complex.
20. Dark pigmentation: 0= absent, 1= present.

Table 3. Data matrix of species and characters states for the cladistic analysis of species of *Ceratolejeunea* Jack & Steph.

Taxon	111111112											
	1	2	3	4	5	6	7	8	9	10	11	12
Physantholejeune	1	0	0	0	1	0	5	1	1	0	0	1
Lejeunea flava	0	0	0	0	0	0	0	0	0	0	1	0
brevinervis	1	1	1	0	1	4	0	2	0	1	1	1
ceratantha	0	0	0	0	1	3	0	1	0	1	1	0
coarina	0	0	0	0	1	2	1	0	1	1	1	1
	2											
confusa	0	0	0	0	0	1	0	0	0	1	1	0
cornuta	0	0	0	0	0	1	0	0	0	1	1	1
	1	1									1	
	2											
	3											
cubensis	0	0	0	0	1	1	0	1	1	0	1	1
	1		2								1	
dentistipula	0	0	1	0	1	2	4	0	0	0	0	1
desciscens	0	0	0	0	1	0	4	0	1	1	0	0
dussiana	0	0	0	0	1	0	0	0	1	1	1	1
	1								1			3
fallax	0	0	2	1	0	1	1	0	0	0	0	1
	1											3
globulifera	0	0	1	0	0	1	2	4	0	1	1	0
grandiloba	1	1	1	0	0	1	1	0	0	0	1	0
	5											
guianensis	1	0	0	0	0	0	1	0	1	0	0	1
laetefusca	0	0	0	0	1	0	1	0	0	1	1	0
	1											1
malleigera	0	0	0	0	0	5	0	1	1	0	0	2
minuta	1	0	0	0	0	0	1	0	0	1	1	0
oxygonia	1	0	0	0	0	0	0	1	0	0	0	1
	1											
patentissima	1	0	0	1	0	1	0	1	2	0	1	1
	2											
	1											
pungens	1	1	1	0	1	2	4	0	0	1	0	1
rubiginosa	0	0	0	0	0	2	4	0	1	0	0	1
spinosa	1	1	1	0	1	2	1	0	1	0	1	1
	2											
szyszlowiczii	1	1	1	0	1	0	5	0	1	0	0	0
filaria	1	0	1	1	1	0	0	0	1	0	1	1

The analysis of the data was performed using Paup 3.1 (Swofford 1991). All characters were treated as unordered. A heuristic search with simple addition sequence was used. A set of 3 trees is presented (Figure 6). A most parsimonious tree was found when using *Physantholejeunea* as outgroup (Tree A, length 70, CI 0.39, HI 0.61, RI 0.63). That analysis places the subgenus *Ceratolejeunea* as a more apomorphic group and the species related to

Ceratolejeunea cornuta (with broad underleaves) in an early diverging clade. In Tree B both *L. flava* and *Physantholejeunea* are used as outgroups. In this case, the subgenus *Ceratolejeunea* appears as an early diverging clade that also contains *C. malleigera* as related taxon. The third hypothesis (Figure 6.C) presented is a strict consensus of 12 trees (length 71, CI 0.39, HI 0.61, RI 0.63) using *Physantholejeunea* as outgroup.

In all cases, the genus *Ceratolejeunea* shows two clear lineages, a clade including the subgenus *Ceratolejeunea* (perianths with bulbous horns), and another clade with the subgenus *Caduciloba*. Those results support the assumption that the subgenus *Ceratolejeunea* is a natural group within the genus.

Among the species of the subgenus *Caduciloba* there is no clear evolutionary trend shown. As in the strict consensus tree, species with broad underleaves tend to be lumped together in a late diverging clade (when *Physantholejeunea* is used as outgroup). Also *C. laetefusca* and *C. patentissima* appear as most closely related, because of the shared caducous leaves, which is here regarded as an homoplasy.

The high Homoplasy Index (HI) and low Consistency Index (CI) of the above analysis do not allow to use the tree hypothesis as a basis for an evolutionary classification of the species within the subgenera. Therefore they are presented in alphabetical sequence (see below).

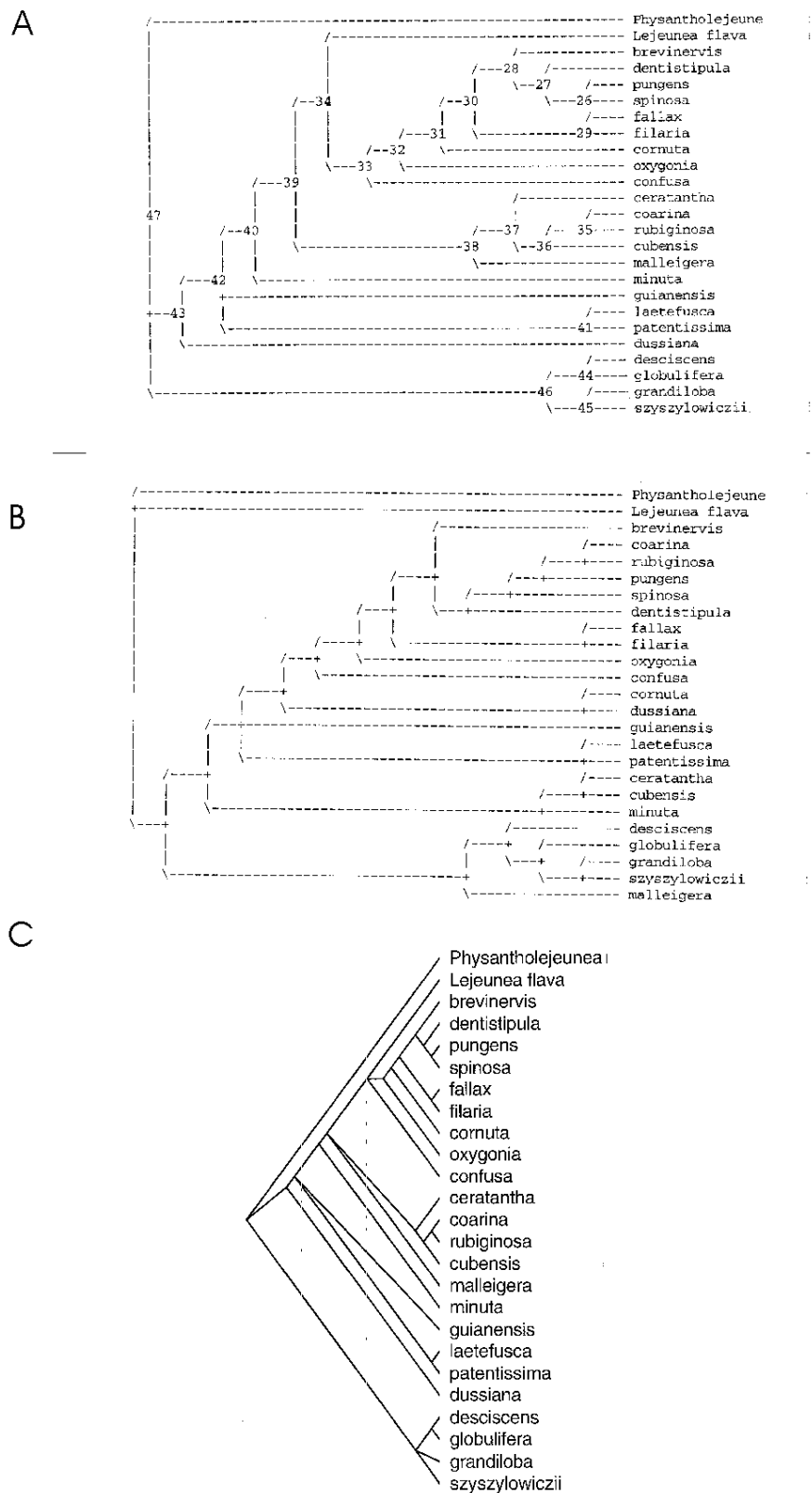


Figure 6. Phylogenetic trees. A. Most parsimonious tree, using *Physantholejeunea* as outgroup. B. Tree using *Physantholejeunea* and *Lejeunea flava* as outgroups. C. Strict consensus tree. For explanation see text.

The gametophytic characters allow segregation and identification of the species, but do not provide enough information for a well-founded evolutionary classification. The use of a broader range of characters in the phylogenetic analysis of the genus *Ceratolejeunea* is urgent. New characters should include analysis of secondary metabolites and sequences of nucleic acids. Although flavonoids and terpenoids have been studied in many genera of Lejeuneaceae (Gradstein *et al.* 1988), nothing has been published about the chemical contents of plants of *Ceratolejeunea* (Mues, pers. comm., Asakawa, pers. comm.).

Also, the use of ultrastructural attributes has been encouraged by Duckett & Renzaglia (1988). The study of the fine structure of organs such as the oil-bodies may also help find more characters relevant to phylogeny.

Proposed classification (assessed by the cladistic analysis)

Conspectus

Genus *Ceratolejeunea* Jack & Steph.

Subgenus *Ceratolejeunea*

Leaf lobule inflated in the lower part, reduced lobules absent. Underleaves entire. Perianth horns bulbous.

1. *C. desciscens* (Sande-Lac.) Steph.
2. *C. globulifera* Herz.
3. *C. grandiloba* Jack & Steph.
4. *C. szyszyłowiczii* (Loitl.) Steph.

Subgenus *Caduciloba* Schuster

Leaf lobule inflated throughout, reduced lobules present. Underleaves bifid. Perianth horns not bulbous.

1. *C. brevinervis* (Spruce) Evans
2. *C. ceratantha* (Nees & Mont.) Schiffn.
3. *C. coarina* (Gottsche) Schiffn.
4. *C. confusa* Schust.
5. *C. cornuta* (Lindenb.) Steph.
6. *C. cubensis* (Mont.) Schiffn.
7. *C. dentistipula* Gottsche ex Steph.
8. *C. dussiana* (Steph.) G. Dauphin
9. *C. fallax* (Lehm. & Lindenb.) Bonner
10. *C. filaria* (Taylor ex Lehm.) Steph.
11. *C. guianensis* (Nees & Mont.) Steph.
12. *C. laetefusca* (Aust.) Schust.
13. *C. malleigera* (Spruce) Steph.
14. *C. minuta* G. Dauphin
15. *C. oxygonia* Gottsche ex Steph.
16. *C. patentissima* (Hampe & Gottsche) Evans
17. *C. pungens* Spruce ex Steph.
18. *C. rubiginosa* Steph.
19. *C. spinosa* (Gottsche) Schiffn.

SYSTEMATIC TREATMENT

Ceratolejeunea Jack & Steph., Hedwigia 31: 16. 1892. Type. *C. grandiloba* Jack & Steph.

Ceratolejeunea (Spruce) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 125. 1893, *nom. illeg.*; *Lejeunea* subgen. *Cerato-Lejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 198. 1884. Lectotype (Evans 1920). *Ceratolejeunea plumula* (Spruce) Steph.

Plants autoicous or dioicous, pale, yellowish, green or brown to almost black, shiny when dry, creeping to hanging, growing in mats or turfs stems with leaves 0.3-2.5 mm wide, sparsely to profusely branched, irregularly pinnate to plumose; stems in cross section 30-185 μm in diameter, with 7 epidermal (=cortical) cells, cells thin-walled, rarely thick-walled, walls to ca. 5 μm thick, and 4-30 medullary cells, cells thick-walled, walls ca. 4 μm thick, with two ventral rows of cells in surface view, and 2-3 dorsal rows, cells quadrate to rectangular, sometimes more or less transversally elongate. Branches *Lejeunea*-type, basal collars three-lobed, flagelliferous branches occasional, its leaves entire or toothed. Stylus unicellular, hyaline, frequently deciduous. Leaves complicate-bilobed, stem leaves imbricate to distant, usually overlapping the stem dorsally, convex or plane; leaf lobe ovate, ligulate or lanceolate, more or less symmetrical or asymmetrical, lobe margins entire, crenulate by projecting cells or toothed along the antical margin or teeth restricted to the distal half or apex, apex rounded, acute, or acuminate, incurved or plane; median leaf cells isodiametrical, elliptical or variously shaped; marginal cells quadrate to rectangular, basal leaf cells rectangular or long hexagonal, thin-walled; cell walls regularly thickened, pale brown, with or without intermediate thickenings, middle lamellae pale to dark brown, trigones almost absent to medium-sized, radiate; oil-bodies smooth, finely granular to botryoidal, septate when smooth, elliptical; ocelli long-hexagonal to rounded, basal, rarely suprabaasal, moniliate, seriate or disperse in the leaf lamina, rarely in underleaves, contiguous or isolate, with a single, homogeneous (granulose in *C. grandiloba*?) oil-body almost filling the cell lumen; lobules inflated, reduced or spherical, 0.1-0.6 the leaf length, free margin involute or plane, when inflated ovate in shape, constricted before the mouth, apical tooth with unicellular, frequently curved, hyaline papilla proximal, bulging. Utriculi absent, solitary or in pairs at the base of lateral branches, more or less globular or reniform. Underleaves ovate, orbicular or reniform, sometimes lanceolate, notched, bifid or entire, when bifid lobes more or less rounded or a acuminate, sinus V-shaped

or U-shaped, base slightly decurrent, sometimes cordate, lobes absent or with rounded auricles. Vegetative reproduction by caducous leaves occasional and rarely by gemmae. Androecia intercalary on main stems or intercalary or terminal on lateral branches, in spikes of 2-9 (-14) bract pairs, bracts hypostatic, cells frequently mammillose; male bracteoles entire, notched or bifid, 1-2 per spike.

Gynoecia on lateral branches or on main stems with 1-2 sterile or repeatedly fertile innovations, innovations *Pycnolejeunea*-type; female bracts obovate, margins entire, dentate throughout or only distally; bract lobule ovate, ovate-lanceolate, or obovate, margins entire, apex acuminate or rounded, rarely with one to several ocelli in a central basal group; bracteoles ovate, bifid to $\frac{1}{4}$, lobes short to long acuminate, margins entire, connate at the base with the bracts. Perianth almost immersed or emergent to ca. $\frac{1}{2}$, obconic to more or less globose, cells frequently mammillose, rarely with 1 ocellus per face??; horns 4 (-5) conical, triangular or bulbous inserted laterally on the perianth body, or with 4-5 rounded keels (2 lateral, 2 postical, 0-1 dorsal).

Sporophyte seta articulate, short or elongate, colorless or rarely tinged with brown, with 4 inner and 12 outer cell rows. Capsule globose, hyaline or rarely tinged with brown, splitting up to 0.7 of its length into 4 valves, the valves ovate to elliptical, erect at dehiscence, bistratose, tristratose towards the base, outer layer median cells rhomboidal, fusiform towards the base, marginal ones quadrate to short rectangular, uniformly thickened or with intermediate thickenings and more or less nodulose trigones. Elaters with a single spiral, 4-5 per valve, colorless or rarely tinged with brown, papillose. Spores long rectangular or irregularly shaped frequently with precocious germination, usually strongly papillose, papillose-tuberculate; rosettes poorly or clearly defined, with 10 to ca. 20 „teeth“.

Distribution. Pantropical. Ubiquitous genus in tropical and subtropical regions in America, also present in Africa, Asia, Australia and the Pacific Islands. In the Neotropics found from Southeastern United States to South Brazil, from sea level to about 3000 m, from lowland to páramo areas, in wet and dry habitats, predominantly in forest canopies, clearings or old secondary growth areas, commonly corticolous but also occurring on leaves, rocks, logs, artificial substrates and rarely terrestrial.

This genus has been previously cited as *Ceratolejeunea* (Spruce) Steph. (*e. g.* Bonner 1953, 1963, Bonner *et al.* 1961), as *Ceratolejeunea* (Spruce) Schiffn. (*e. g.* Evans 1920, Fulford 1945,

Schuster 1956, 1980, Grolle 1983, Engel 1984), or as *Ceratolejeunea* Jack & Steph. (e. g. Grolle 1983, Engel 1989).

According to Zijlstra (1982) and Grolle (1983), there is no valid generic name *Ceratolejeunea* in Stephani (1890). Grolle (1983), calls the attention to the first valid establishment of the generic name *Ceratolejeunea* by Jack and Stephani (1892).

Grolle (1983) suggests rejection of *Ceratolejeunea* Jack & Steph. against *Ceratolejeunea* (Spruce) Schiffn., arguing that the type species differs from typical species described by Spruce (1884) in his subgenus *Cerato-Lejeunea*. His proposal serves his opinion on nomenclatural stability (Grolle pers. comm. 1997), considering the possibility that holostipous *Ceratolejeuneas* may belong in another genus. As considered in this work (see below), holostipous *Ceratolejeuneas* (including *C. grandiloba* Jack & Steph.) are congeneric with the schizostipous species, there is no threat for the nomenclatural stability of the genus. Therefore, according to the Code (Art. 11.3), the name *Ceratolejeunea* Jack. & Steph. should be kept.

Ceratolejeunea grandiloba Jack & Steph. and other members of the subgenus *Ceratolejeunea* (=subgen. *Ceratophora* Schust.) are characterized by their entire underleaves, their lobule structure and bulbous horns. In other morphological (diagnostic) respects such as pigmentation, stem structure (Bischler 1966), presence of ocelli, utriculi, and sporophyte structure, this species group agrees with the *Ceratolejeuneas* with bifid underleaves. This sharing of diagnostic morphological characters, suggests that both species groups should be kept in one genus. The placing of holostipous species within *Ceratolejeunea* and their relationship with other genera such as *Neurolejeunea* and *Physantholejeunea* has been previously discussed by several authors, including Stephani (1888), Evans (1907), Herzog (1933), Schuster (1956, 1978, 1980). The species of *Ceratolejeunea* can be separated of *Neurolejeunea* by their proximal papillae and the presence of a single, unicellular lobule tooth. The stem morphology also helps separating them: the ventral merophytes in species of *Neurolejeunea* are 4 or more cell rows wide (Gradstein 1994), not 2 as in *Ceratolejeunea* and *Physantholejeunea*. Also the seta in *Neurolejeunea* has 16 outer cell rows (Gradstein 1994), in contrast with the 12 outer cell rows in *Ceratolejeunea*. The lack of cell wall pigments and oil-bodies in vegetative cells, the presence of a 1-2 celled apical lobular tooth and the elongated, linear cells bordering the free lobule margin, clearly separate the monotypic *Physantholejeunea* from *Ceratolejeunea* species.

The genus *Ceratolejeunea* is thus a natural, well defined genus that stands isolated among the Lejeuneoideae. Schuster and Hattori (1954) suggested that this genus may be „more nearly allied to the Holostipae“ (p. 18), because of the secondary dark pigmentation and the

oil-body types. The question of placement of this genus should be dealt with in a broader generic analysis. By now it must be pointed out that not alone *Ceratolejeunea* but also other genera within the Lejeuneoideae, such as *Cheilolejeunea*, *Cyclolejeunea*, *Lepidolejeunea* have species with entire and bifid underleaves (Gradstein 1985). From those related genera, *Ceratolejeunea* differs by showing difference in combinations of at least two of its diagnostic characters: brown pigmentation, presence of ocelli, utriculi and perianths with horns (see under Classification).

Key to the subgenera of *Ceratolejeunea*

1. Underleaves entire. Perianths with bulbous horns.....subgen. *Ceratolejeunea*
1. Underleaves bifid. Perianths without bulbous horns (except *C. malleigera*)
.....subgen. *Caduciloba*

Ceratolejeunea* subgenus *Ceratolejeunea

Ceratolejeunea subgen. *Ceratophora* Schust., Journ. Elisha Mitchell Soc. 72: 224. 1956. Type. *C. desciscens* (Sande-Lac.) Schiffn., *syn. nov.*

The subgenus *Ceratolejeunea* has four species in the Neotropics. Excepting *Ceratolejeunea desciscens* (Sande-Lac.) Steph., that grows in the Amazonia, the species in this subgenus are montane taxa, occurring at middle and high elevations in the Andes and the Guyana Highlands, with one species, *C. globulifera* Herz. reaching Costa Rica.

The members of this subgenus are characterized by their entire underleaves, their leaf lobule typically inflated in the lower part and plane towards the free margin (except *C. szyszyłowiczii* (Loitl.) Steph.), and the perianths with bulbous horns. They are medium-sized or robust plants, with frequently incurved leaves. Series of spherical lobules are lacking in this subgenus. The ocelli might be dispersed in the leaf lamina (*C. grandiloba* Jack & Steph., *C. szyszyłowiczii* (Loitl.) Steph.) or in a basal row oriented towards leaf apex (*C. desciscens* (Sande-Lac) Schiffn., *C. globulifera* Herz.). A key to the species of this subgenus was previously published by Grolle (1987).

Members of this subgenus can be confused with members of the Ptychantheae and Brachiolejeuneae (Gradstein 1994), which also have entire underleaves and frequently a dark pigmentation. The merophyte in ventral view has usually 4 or more cells rows in the latter groups, which easily separate them from *Ceratolejeunea* which has only two. *Physantholejeunea portoricensis* (Hampe & Gottsche) Schust. could be mistaken for a holostipous *Ceratolejeunea*, but lacks dark pigmentation in the middle lamellae and has elongated cells at the lobe apex, which is not found in species of *Ceratolejeunea*.

Key to the species of *Ceratolejeunea* subgenus *Ceratolejeunea*

1. Ocelli scattered in the leaf lamina and in short basal row.....2
 2. Lobules inflated in the lower part, free margin plane. Ocelli present in underleaves3. *C. grandiloba*
 2. Lobules inflated throughout, free margin plane or slightly involute. Ocelli absent in underleaves4. *C. szyszyłowiczii*
1. Ocelli not scattered in the leaf lamina3
 3. Antical leaf margins with teeth throughout. Ocelli moniliate 1-2. Underleaves 1-2 x the stem width.....2. *C. globulifera*
 3. Antical leaf margins entire or with teeth restricted to the apical region. Ocelli moniliate (1-) 2-6 in a row. Underleaves 1-4 x the stem width1. *C. desciscens*

1. *Ceratolejeunea desciscens* (Sande-Lac.) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1(3): 126. 1893; *Lejeunea desciscens* Sande-Lac., Syn. Hep. Jav.: 107. 1857. Type. Surinam. Without locality, Focke s. n. (holotype, L). Figure 7.

Ceratolejeunea arhexia Spruce, Mem. Torrey Bot. Club 3: 124. 1890, *nom. nud.* Material. Ecuador. Mt. Tungurahua, Spruce s. n. (MANCH), *syn. nov.*

Ceratolejeunea lechleriana Steph., Hedwigia 34: 235. 1895. Type. Peru. Tatanara, Lechler s. n. (holotype, G), *syn. nov.*

Ceratolejeunea paradoxa Herz., Beih. Bot. Centralbl. B 61: 579. 1942. Type. Brazil. „Amazonasgebiet“, Frank s. n. (holotype, JE; isotype, B).

Plants autoicous, brown, stems to 3.5 cm long, with leaves 0.8-1.5 cm wide; profusely branched. Stems in cross section 70-120 µm in diameter, medullary cells 11-16, thick-walled,

ventral stem cells quadrate to rectangular, 25-45 x 25-55 μm . Leaves imbricate, ovate-falcate, 350-500 x 580-720 μm , leaf lobes with margins entire to slightly crenulate, apex rounded, incurved or plane; median leaf cells with rounded to elliptic lumina, 15-25 x 15-50 μm ; marginal cells subquadrate or rectangular, 7-20 x 15-30 μm ; ocelli 25-35 x 35-55 μm , 2-6 per leaf lobe, moniliate, row 85-230 μm long; oil-bodies in all cells, 3-6 per cell, ellipsoid, vaguely papillose, colorless (*vide* Gradstein 9901); lobules inflated in the lower part, ovate-rectangular?, 0.5-0.6 the leaf lobe length, free margin plane, reduced lobules not seen, apical tooth sometimes scarcely projecting. Utriculi not seen. Underleaves entire, distant or slightly imbricate, subquadrate, 170-300 x 175-290 μm , margins entire and plane.

Androecia in spikes of 4-7 bracts pairs, spikes 750-1300 μm long, bracteoles entire, 100 x 150 μm , 1-2 per spike.

Gynoecia on lateral branches with 1 sterile innovation or on main stems without innovation; bract lobe obovate-falcate, 500 x 860 μm , margins entire; bracteole obovate, 410 x 600 μm , margins entire, connate at the base with the bracts. Perianths ovoid, 350-440 x 500-600 μm , with four bulbous horns, 120-150 μm long.

Sporophyte not seen.

Illustrations. Bonner 1953, p. 185; Fulford 1945, p. 400; Onraedt 1989, p. 124.

Distribution. A northern South American species, growing mostly in lowland Amazonian rainforests but also reaching middle elevations (up to 1400 m) in the Northern Andes. Usually epiphyte on tree trunks, in open habitats, and probably canopies.

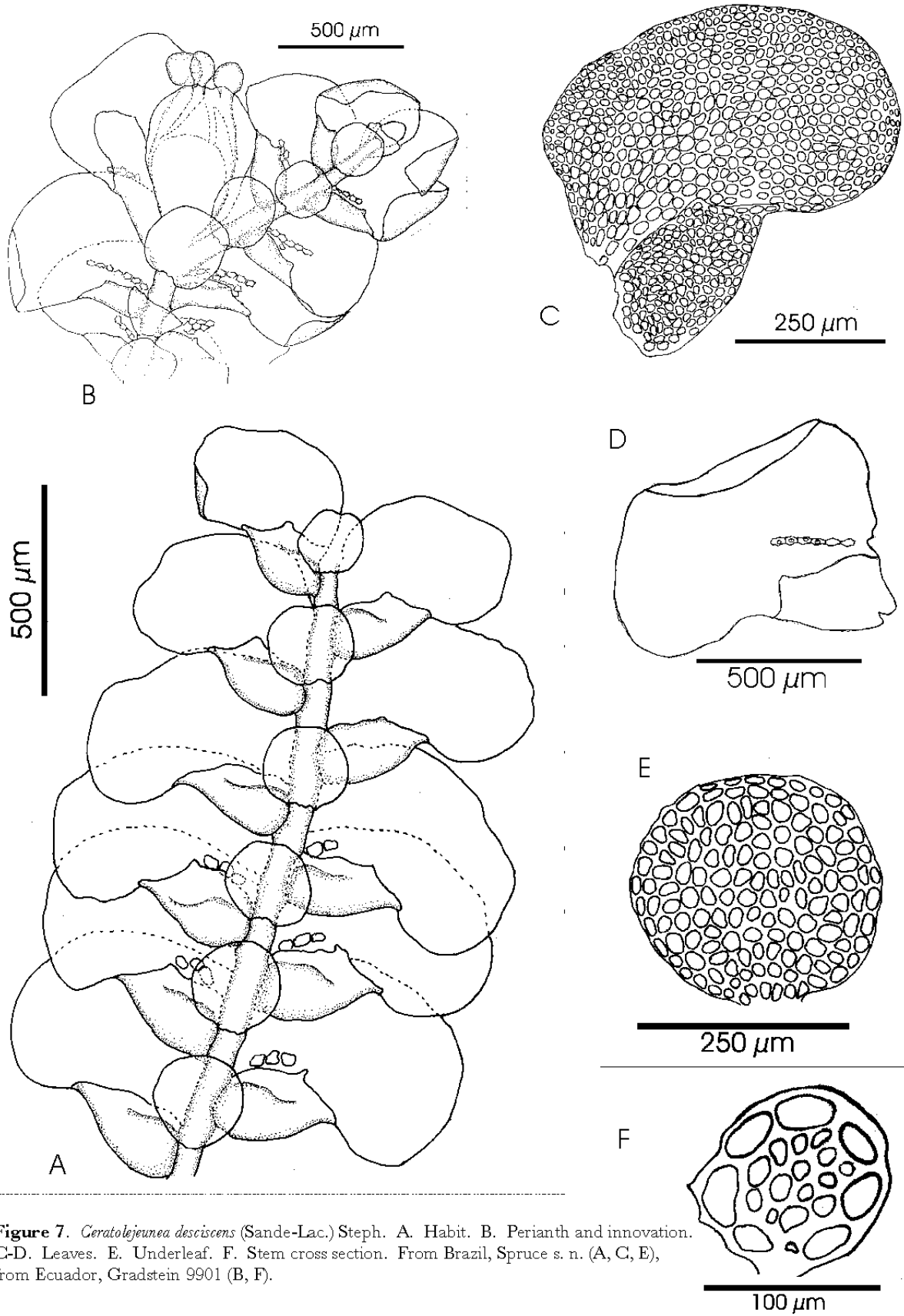


Figure 7. *Ceratolejeunea desciscens* (Sande-Lac.) Steph. A. Habit. B. Perianth and innovation. C-D. Leaves. E. Underleaf. F. Stem cross section. From Brazil, Spruce s. n. (A, C, E), from Ecuador, Gradstein 9901 (B, F).

Specimens examined. COLOMBIA. **Vaupés:** Rio Kananari (affluent of Rio Isibukuri), Evans Schultes & Cabrera, 13254 (NY).

GUYANA. Essequibo River, Moraballi Creek, near Bartica, Richards 813 (BM).

SURINAM. Road between Moengotapoe and Grote Zwiebelzwamp, Lanjouw & Lindeman 523 (GOET, PC, U); Brownsberg plateau, Gradstein 4681 (GOET, U).

FRENCH GUIANA. **Brokopondo:** Brownsberg plateau, Gradstein 4681 (GOET, U). Essequibo River: Moraballi Creek near Bartica, Richards 813 (BM). Montagne de Kaw, 2 km N of Camp Kaiman, Cornelissen & ter Steege 337 (GOET, U). Road from Cayenne to St. Laurent, pk 180, without collector, Herbier du Centre Orstom 7862, 7863 (GOET, U). **Without locality**, the type.

ECUADOR. **Pichincha:** Minde, Gradstein 9901 (GOET). **Without department:** material of *Ceratolejeunea arhexia* Spruce.

PERU. Type of *Ceratolejeunea lechleriana* Steph.

BRAZIL. **Amazonas:** Manaus, Vital 4338c (JE); San Gabriel, Spruce s. n. (MANCH, G); Rio Negro, Spruce s. n. (MANCH, G, JE, BM); type of *Ceratolejeunea paradoxa* Herz.

C. desciscens is the most frequently collected species of the subgenus *Ceratolejeunea*. It can be recognized by its ocelli in rows of (1-) 2 to 6 cells, its broad underleaves and frequently entire leaf margins. Utriculi are apparently absent in this species. *C. desciscens* could be confused with *C. globulifera*, but the latter has no more than 2 moniliate ocelli and the antical leaf margins are toothed throughout.

2. *Ceratolejeunea globulifera* Herz., Rev. Bryol. Lichénol. 13: 23. 1942. Type.

Colombia. El Cauca: La Galera, Micay Valley, Cord. Occid., 1400-1500m, 19/20.VI.1922, Killip 7789 (isotype, G). Figure 8.

Ceratolejeunea ecuadorensis S. Arnell, Svensk Bot. Tidskrift. 56: 336. 1962. Type. Ecuador.

Napo-Pastaza: Canelos, path to Vera Cruz, campamento militar (Chontóa), 1100 m, Harling 3253 (holotype, S; isotype, UPS). (Grolle 1987).

Plants autoicous, dull-brown, with leaves 0,9-1.8 mm wide, profusely branched. Stems in cross section 70-165 μm in diameter, medullary cells 9-20, ca. 2-4 μm thick, ventral stem cells quadrate to short-rectangular, 20-50 x 20-80 μm , dorsal stem cells variously shaped, 15-50 x 25-65 μm . Flagelliferous branches not seen. Leaves imbricate, leaf lobe ovate, slightly falcate, 270-690 x 430-940 μm , margins toothed, with 5-8 antical and 0-2 postical teeth, teeth one cell long projecting from a 2-celled base, 10-30 μm long, apex incurved; median cells leaf lobe

rhomboidal to elliptical or subquadrate, 15-35 x 15-50 μm , marginal leaf lobe cells 10-20 x 10-25 μm ; ocelli, 20-35 x 35-60 μm , moniliate, (1-) 2 per leaf, row 80-115 μm ; oil-bodies not seen; lobules inflated in the lower part, 0.4-0.5 the length of the leaf lobe, free margin plane, apical tooth sometimes scarcely projecting. Utriculi absent or single at the base of lateral branches. Underleaves entire, 120-320 x 125-280 μm , mostly wider than long, to 2 times the stem width, margins entire and plane.

Androecia in spikes of 2-6 bract pairs, 260-750 μm long, bracteole entire, ca 90 x 80 μm .

Gynoecia on lateral branches with 1 sterile innovation or on main stems with 1 fertile innovation; bract lobe obovate, margins toothed at the apex; bracteole ovate, 325-380 x 425-480 μm , margins entire, connate at the base with the bracts. Perianths obconic, 350-450 x 520-720 μm , horns bulbous, sometimes appearing laterally compressed, 4 per perianth, 140-250 μm long.

Sporophyte not seen.

Illustrations. Herzog 1942, p. 22.

Distribution. Costa Rica to Bolivia. Epiphytic on tree trunks, or epiphyllous in middle elevations (1000-1850 m) in wet, forested mountain areas.

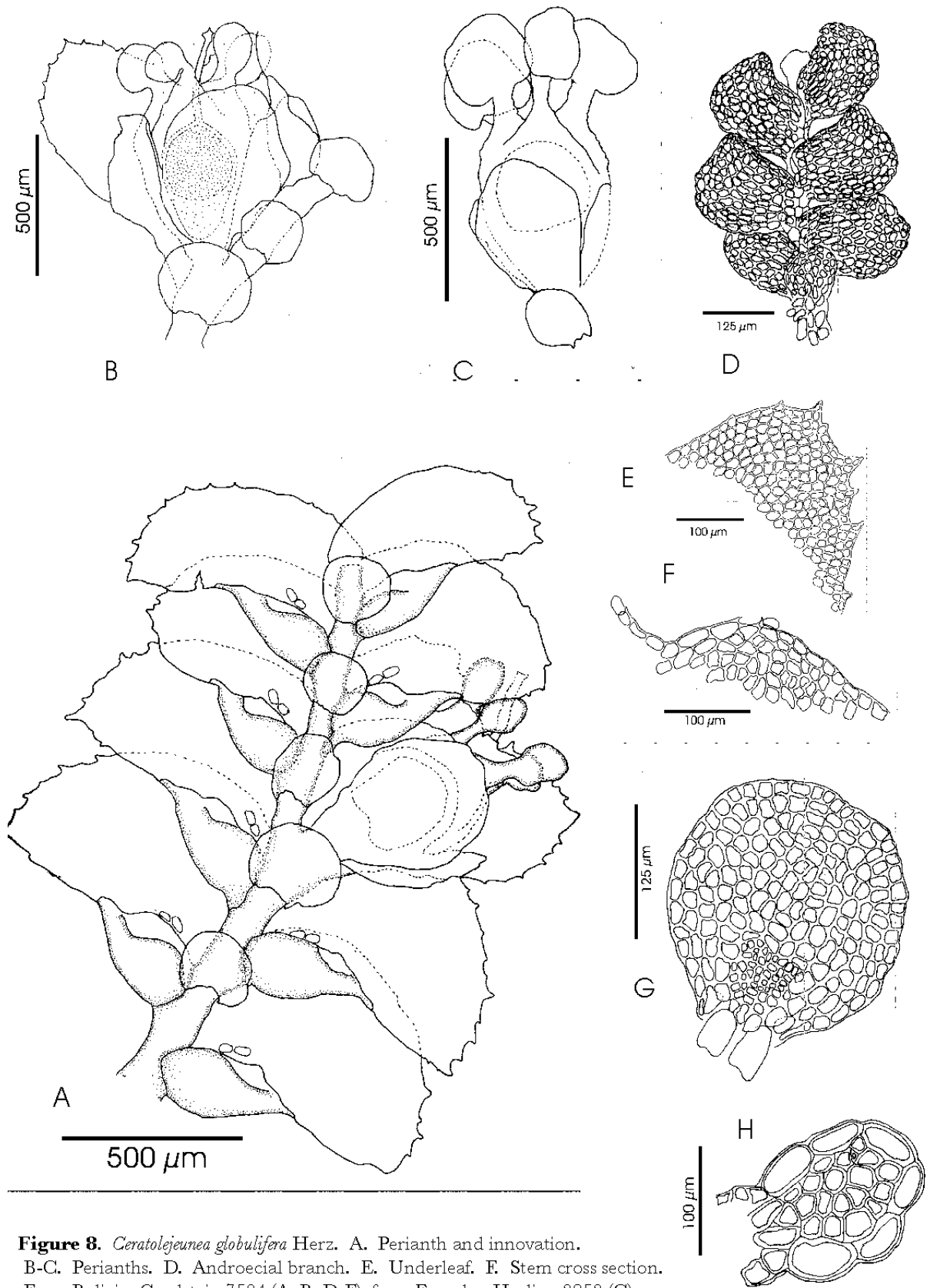


Figure 8. *Ceratolejeunea globulifera* Herz. A. Perianth and innovation. B-C. Perianths. D. Androecial branch. E. Underleaf. F. Stem cross section. From Bolivia, Gradstein 7584 (A, B, D-F), from Ecuador, Harling 3253 (C).

Specimens examined. COSTA RICA. Cartago: Refugio de Fauna Silvestre Tapantí, Morales 2137pp (USJ).

COLOMBIA. The type.

ECUADOR. Type of *Ceratolejeunea ecuadorensis* S. Arnell.

BOLIVIA. **Cochabamba:** Chapare, road Cochabamba-Villa Tunari, Gradstein 7584 (GOET, U).

A seldom collected species, *C. globulifera* can be distinguished from the close *C. desciscens* by its distant, smaller underleaves always less than twice the stem width. The leaf lobes in *C. globulifera* are frequently toothed along the antical margin, whereas in *C. desciscens* the teeth are restricted to the apex. The ocelli are moniliate in both species, but in *C. globulifera* their number is restricted to two (occasionally one or three), while *C. desciscens* may have up to 6 ocelli in a row.

3. *Ceratolejeunea grandiloba* Jack & Steph., Hedwigia 31: 16. 1892. Type. Colombia. Antioquia: Páramo de Sonson, 10000 ft., 1872, Wallis *s. n.* (holotype, G; isotypes BM, FH, G, W). Figure 9.

Plants dioicous, dull-brown, stem with leaves 1.0-2.5 mm wide, profusely branched. Stems in cross section 100-190 μm in diameter, medullary cells 11-22, thick walled, ca. 4 μm thick, ventral cells 20-65 x 20-65 (-90) μm , dorsal cells, quadrate or irregularly shaped, 40-65 x 35-65 μm . Flagelliferous branches not seen. Leaves imbricate, leaf lobe strongly concave, ovate, 400-1125 x 520-1300 μm , apex rounded to acute, margins entire, irregularly crenulate or with 1-4 teeth at the apex, teeth mostly single-celled, to ca. 20 μm long; median leaf lobe cells isodiametrical, 10-35 x 10-50 x 12.5-30 μm , smooth or conspicuously mammillose, intermediate thickenings frequent; oil-bodies apparently lacking in normal cells; ocelli rounded, 25-45 x 25-55 μm , 1-21 per leaf, scattered in leaf lobe, or rarely moniliate at leaf lobe base, row 80-95 μm , ocellar oil-bodies botryoidal, rounded, gray, filling the lumen; lobule inflated in the lower part, elongate, never reduced?, 0.4-0.6 the leaf lobe length, free margin plane, lobule tooth sometimes scarcely projecting. Utriculi absent, single or in pairs at the base of lateral branches. Underleaves 240-870 x 300-750 μm , 1.5-4 x stem width, margins entire and plane, apex entire or emarginate, lobes rounded, occasionally with scattered ocelli in the lobe.

Androecia lateral on main branches or terminal on secondary branches, in spikes of 4-8 bract pairs, 100-1500 μm long; bracteoles, 125-150 x 150-180 μm , 2 per spike, apex entire.

Gynoecia on short lateral branches or on main branches with one sterile or repeatedly fertile innovation; bract lobe obovate, ca. 600 x 1000 μm , margins entire or crenulate, bract lobule ligulate, ca. 230 x 670 ; bracteole obovate, ca. 550 x 700 μm , apex entire. Perianth obconic, 450-625 x 750-1000 μm , surface strongly mammillose, with four bulbous horns, 200-450 μm long.

Elaters, 15 x 450-550 μm . Spores irregularly shaped, mostly rectangular, 20-40 x 45-70 μm , greenish-brown, papillose-tuberculate; rosettes complex, aperture ca. 7 μm in diameter with ca. 15 teeth.

Illustrations. Bonner 1953, p. 198.

Distribution: A mostly Andean species, found at middle and high elevations in wet, frequently degraded, montane forests of Colombia, Venezuela, Peru and Bolivia, it has been collected also in the Guyana Highlands. This species grows on bark mixed with other bryophytes and occasionally on leaves, from 1400 to about 3000 m elevation.

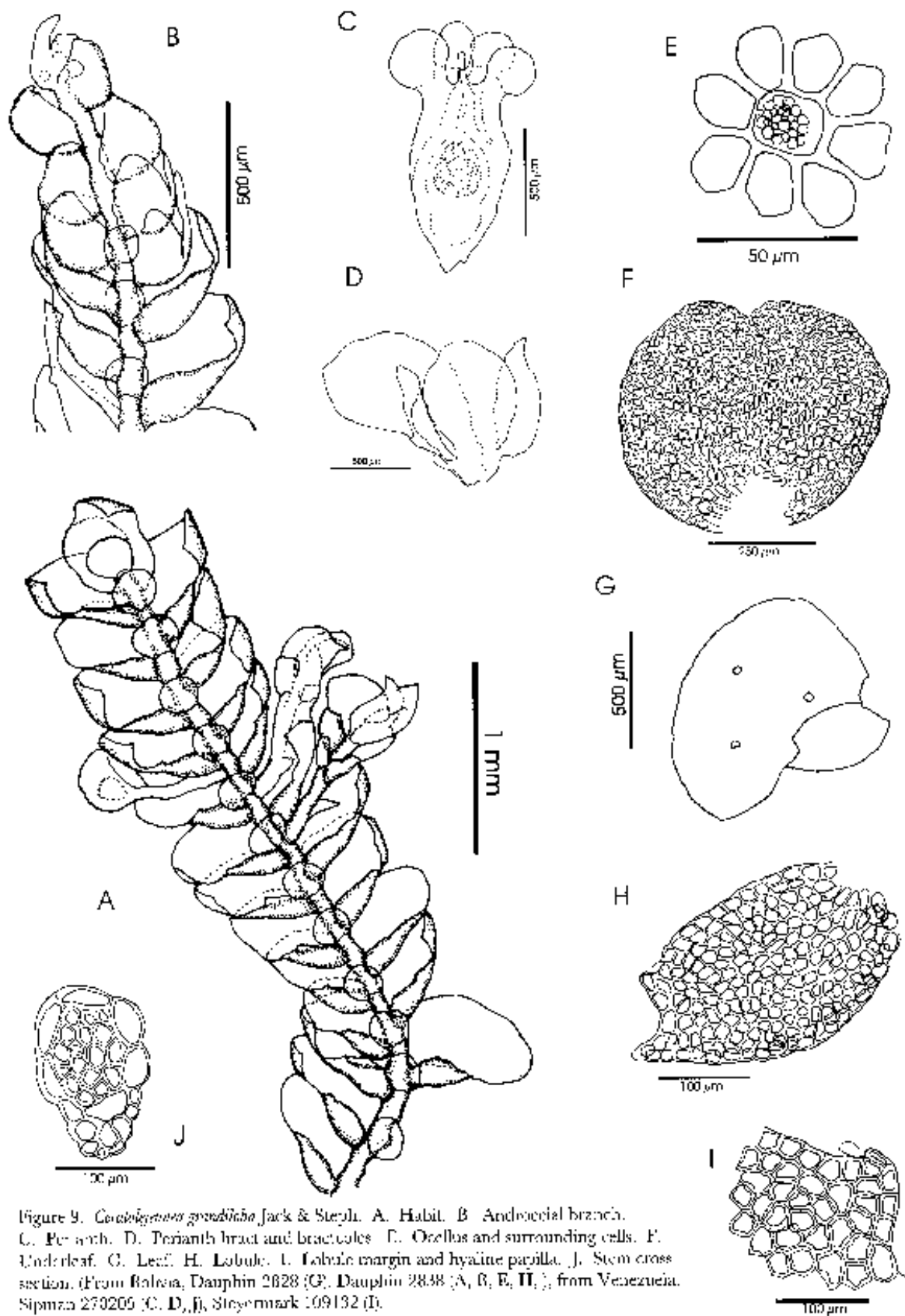


Figure 9. *Conobryopsis gyrodicha* Jack & Steyerl. A. Habit. B. Androecial branch. C. Perianth. D. Perianth bract and bracteoles. E. Ocellus and surrounding cells. F. Underside of leaf. G. Leaf. H. Lobule. I. Lobule margin and hyaline papilla. J. Stem cross section. (From Bolivia, Dauphin 2628 (G, Dauphin 2838 (A, B, E, H)), from Venezuela, Sipanza 279205 (C, D, J), Steyermark 109132 (I).

Specimens examined. COLOMBIA. **Antioquia:** the type.

VENEZUELA. **Bolívar:** Cerro Guaiquinima, Sipman 27154 (B, U), 27250 (B); Meseta de Java, Cerro Sarisañama, Steyemark *et al.* 109132, 109221 (US).

PERU. **San Martín:** Rioja, Frahm *et al.* 650 (JE, U), 811 (B, JE, NY, U).

BOLIVIA. **Cochabamba:** Chapare, El Limbo, Dauphin *et al.* 2822, 2838 (GOET, USJ); Tablas Monte, Gradstein 7481 (GOET, U). **La Paz:** road La Paz-Coroico, Gradstein 7055 (GOET, U).

Distinguished by the ocelli scattered in the leaf lobe and sometimes present in underleaves (unique in the genus!) and gynoeical bracts. The distal half of the leaf lobes is frequently strongly incurved. A very distinctive species, it can be hardly mistaken by any other in the genus. Mizutani (1981) described *Ceratolejeunea inflata* from Java, whose description and drawings agree with those of *C. grandiloba* and might belong here. The type of the Asiatic species must be examined in order to verify its identity.

4. *Ceratolejeunea szyszyłowiczii* (Loitl.) Steph., Sp. Hep. 5: 443. 1913; *Lejeunea* (*Ceratolejeunea*) *szyszyłowiczii* Loitl., Diss. Cl. Math. Phys. Acad. Litt. Cracow 29: 233. 1894. Type. Peru. Tambillo, Jelski 527 (holotype, W; isotypes G, U). Figure 10.

Plants dioicous?, dull-brown, stem with leaves 1.0-1.6 mm wide, sparsely to profusely branched. Stems in cross section 100 μm in diameter, medullary cells 13-17, ca. 4 μm thick, ventral cells in surface view quadrate to rectangular, 25-55 x 30-60 (-95) μm , dorsal cells mostly quadrate, 30-50 x 25-50 μm . Flagelliferous branches not seen. Leaves imbricate, leaf lobe ovate, slightly asymmetrical, 290-630 x 450-850 μm , apex rounded or broadly acute, margins entire and plane, median leaf lobe cells isodiametrical, elliptical towards base, 15-25 x 20-40 μm , marginal leaf lobe cells 10-20 x 15-25 μm , intermediate thickenings present; oil-bodies not seen; ocelli scarcely differentiated from normal leaf cells, 3-4? per leaf, 20-30 x 30-40 μm , scattered in the leaf lamina or seriate, row 110 μm ; lobules inflated throughout, elongate, 0.4-0.6 the leaf lobe length, free margin plane or slightly involute, apical tooth scarcely projecting. Utriculi not seen. Underleaves orbicular, 190-410 x 200-375 μm , margins entire and plane, apex entire or slightly emarginate.

Androecia not seen.

Gynoecea on short lateral branch of main stem, without innovation, bracts with entire margins; bracteoles 390 x 570 μm , obovate, margins entire. Perianth 260-520 x 390-970 μm , horns bulbous, 4 per perianth, 125 μm long.

Sporophyte not seen.

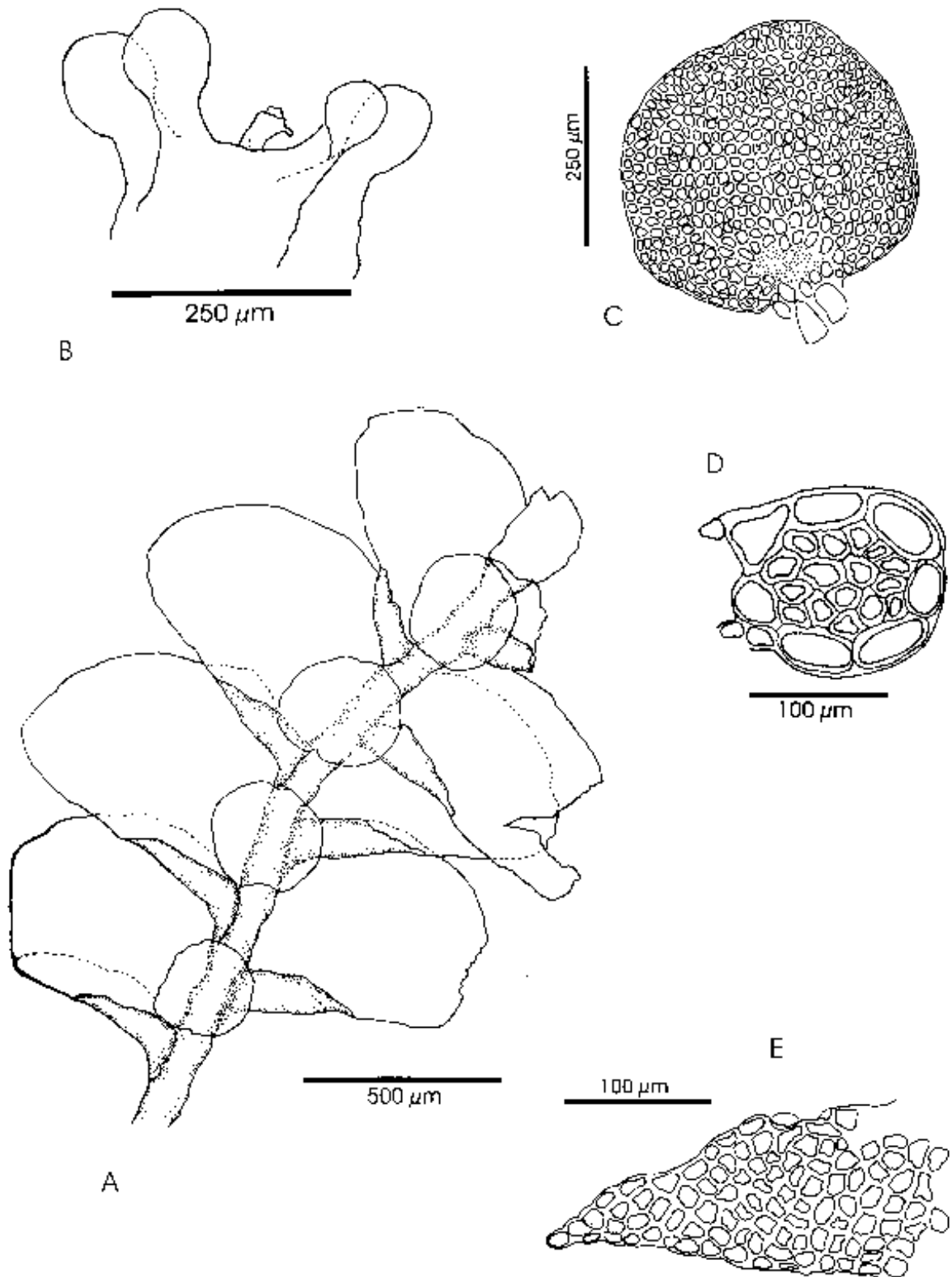


Figure 10. *Combigeomys squyziosus* (Loid.) Steph. A. Habit. B. Perianth horns. C. Undeveloped leaf. D. Stem cross section. E. Lobule. From Peru, the type.

Distribution: Peru. Known only from the type locality in the Northern Andes. Substrate and habitat unknown.

Specimen examined. PERU. The type.

Ceratolejeunea szyszyłowiczii is distinguished from other species in the subgenus *Ceratolejeunea* by its lobules, that are uniformly inflated with a sometimes involute free margin. The leaf lobe is plane and not incurved as in the other members of the subgenus. This species resembles *C. grandiloba* in the distribution of the ocelli, which may be scattered or moniliate at the leaf lobe base, but the lobule and leaf lobe characters (plane in *C. szyszyłowiczii*, strongly concave in *C. grandiloba*) separate these taxa.

***Ceratolejeunea* subgenus *Caduciloba* Schust.,**

Phytologia 39: 430. 1978. Type. *C. patentissima* (Hampe & Gott.) Evans.
Ceratolejeunea subgen. *Ceratolejeunea* auct. (e. g. Schuster 1978, 1992).

The subgenus *Caduciloba* Schust. is probably the most diverse subgenus in the family after the subgenus *Lejeunea*. It contains 19 species distributed all over the Neotropical continent and also in the Paleotropics.

Typical for this subgenus are the bifid underleaves, inflated lobules with an unicellular projecting apical tooth and the perianth with four, rarely five horns or four to five keels. The ocelli are in most of the species basal, but some have also moniliate or seriate ones and in *Ceratolejeunea malleigera* the ocelli are scattered in the leaf lobe.

Initially, the subgenus *Caduciloba* Schust. contained only two species, *C. patentissima* and *C. andicola* (= *C. patentissima*). In this treatment, subgen. *Caduciloba* is treated in a broad sense, including also the species assigned previously to the subgenus *Ceratolejeunea* auct.

Schuster (1978, 1980) delimited the subgenus *Caduciloba* based on the flask-shaped lobule structure, edentate female bracts and leaves and absence of utriculi. The lobule structure of *C. patentissima* shows a range of variation including flask-shaped to „normal“ inflated lobules typical for most of the species now contained in the subgenus. The leaves in *C. patentissima* are entire, but lobe of the female bracts may be toothed near the apex, which is a variable character in the subgenus. The utriculi may be present or absent in the specimens of *C. patentissima*. On this basis, the species is not considered to be a separate subgenus.

Key to the Neotropical species of *Ceratolejeunea* subgen. *Caduciloba* Schust.

1. Ocelli scattered in the leaf lobe. Perianth with 2 (-3) horns.....*C. malleigera*
1. Ocelli not scattered in the leaf lobe. Perianth with 4 horns or 4-5 keels.....2
2. Ocelli moniliate or seriate, forming a row towards leaf apex.....3
3. Ocelli seriate. Antical margin of leaf lobes entire, teeth restricted to the apex of leaf lobes.....4
4. Underleaves ovate, distant. Utriculi if present, single. Plants small
.....*C. ceratantha*
4. Underleaves wide ovate to reniform, distant to imbricate. Utriculi if present, in pairs. Plants robust.....*C. fallax*
3. Ocelli moniliate. Teeth restricted to the apex of leaf lobes or present along the antical leaf lobe margin.....5
5. Underleaves reniform. Plants robust.....6
6. Teeth restricted to the leaf lobe apex. Plants dark-brown. Leaf apex strongly incurved. Underleaf margins entire. Restricted to higher mountain areas in the Caribbean.....*C. brevinervis*
6. Teeth present along the antical margin of the leaf lobe. Underleaves margins crenulate or distally toothed. Known from lowland forest in Cuba and Guadeloupe.....*C. dentistipula*
5. Underleaves ovate. Plants robust or small7
7. Plants dioicous, robust. Antical margin of leaf lobe strongly dentate, teeth multicellular. Colombia and Ecuador.....*C. pungens*

7. Plants monoicous, small. Antical margin of leaf lobe weakly dentate, teeth mostly unicellular.....*C. rubiginosa*
2. Ocelli basal, suprabasal, geminate, absent or rarely seriate not forming a row towards leaf apex.....8
8. Leaf lobe antical margin and apex weakly to strongly toothed, teeth at least in some leaves.....9
8. Leaf lobe antical margin and apex completely devoid of teeth14
9. Teeth present along the leaf lobe antical margin and apex.....10
9. Teeth restricted to the leaf apex.....11
10. Plants dioicous, robust, corticolous. Antical leaf lobe margin strongly toothed, teeth multicellular.....*C. spinosa*
10. Plants monoicous, small, epiphyllous or corticolous. Antical leaf lobe margin weakly to strongly toothed, teeth mostly unicellular.....*C. coarina*
11. Underleaf lobes acuminate, sinus frequently U-shaped. Plants rare*C. oxygonia*
11. Underleaf lobes acute, sinus V-shaped. Plants common.....12
12. Underleaves on main stems ovate, base never auriculate.....*C. cubensis*
12. Underleaves wide ovate to reniform, base sometimes auriculate.....13
13. Flagelliform branches with toothed leaves present. Oil-bodies granular. Underleaf insertion U-shaped, base frequently auriculate. Montane, in middle to high elevation areas (700-ca. 3000 m).....*C. filaria*
13. Flagelliform branches absent. Oil-bodies smooth. Underleaf insertion slightly curved not or rarely auriculate. Lowlands to middle elevation areas.....*C. cornuta*

14. Underleaf margins constantly bearing with a tooth per side, sinus U-shaped.....*C. minuta*
14. Underleaf margins entire, sinus V-shaped15
15. Plants pale-brown colored. Perianth horns erose-dentate. Ocelli basal or suprabasal.....*C. dussiana*
15. Plants brown to almost fuscous. Perianth with terete horns or rounded keels. Ocelli basal.....16
16. Underleaves on main axis wide ovate to reniform. Utriculi present.....17
16. Underleaves on main axis orbicular to ovate, never reniform. Utriculi absent or sometimes present18
17. Perianth with 5 rounded keels. Utriculi single. Series of spherical lobules lacking.....*C. confusa*
17. Perianth with 4 terete horns.. Utriculi in pairs. Series of spherical lobules occasional.....*C. cornuta*
18. Leaf lobule frequently flask-shaped. Ocelli usually single, basal. Plants from wet areas at middle and high elevations in Central America, Chocó northern Andes and the Guyana Highlands. Caducous leaves frequently present.....*C. patentissima*
18. Leaf lobule inflated throughout. Ocelli usually in pairs. Plants occurring usually in low and middle elevations, widespread. Caducous leaves present or absent.....19
19. Flagelliferous branches with rounded leaflets present. Leaves strongly incurved. Underleaves orbicular, lobes frequently connivent. Caducous leaves absent*C. guianensis*
19. Flagelliferous branches absent. Leaves plane or incurved. Underleaves ovate, lobes spreading.....20
19. Perianth with horns. Plants usually autoicous.....*C. cubensis*
19. Perianth without horns. Plants usually dioicous.....*C. laetefusca*

1. *Ceratolejeunea brevinervis* (Spruce) Evans, Bull. Torrey Bot. Club 32: 282. 1905; *Lejeunea (Cerato-Lejeunea) brevinervis* Spruce, Journ. Linn. Soc. London 30: 342. 1895. Type. Guadeloupe. „ad arbores, *Lejeuneae filiformi* consociata“, L'Herminier B31 (lectotype (*vide* Evans 1905), MANCH). Figure 11.

Plants dioicous, dark brown, stems with leaves 1.0-2.0 mm wide, sparsely to profusely branched. Flagelliferous branches not seen. Stems in cross section 80-150 μm in diameter, epidermal cells thick-walled, walls to ca. 5 μm thick, medullary cells 11-29, thick-walled, walls ca. 3 μm thick, ventral cells quadrate to rectangular, 30-50 x 45-85 μm , dorsal cells quadrate to rectangular, 30-65 x 40-70 μm . Stem leaves imbricate, ovate, 410-875 x 450-1200 μm , leaf lobe margin entire or toothed at the apex, apex usually strongly incurved, rounded; median leaf lobe cells isodiametrical to elliptical, 15-35 x 25-55 μm , smooth; marginal cells quadrate, 10-25 x 20-40 μm ; oil-bodies variable, 1-3 per cell, paramecioid or spherical to ovoid, 3-5 x 4.8-7.5 μm , granular-botryoidal (Schuster 1992); ocelli 30-60 x 30-75 μm , 1-8 per leaf, moniliate, row 100-300 μm long; lobules like in the genus, somewhat flask-shaped on secondary branches, 0.1-0.5 the leaf lobe length, free margin involute, apical tooth usually hidden. Utriculi 1-2 at the base of lateral branches. Underleaves ovate to reniform, 130-480 x 160-380 μm , bifid to ca. $\frac{1}{2}$, lobes acute or rounded, margins entire, base frequently cordate. Androecia lateral on main stem, in spikes of 2-3 bract pairs, 600-750 μm long, bracteoles bifid, 130-170 x 140-200 μm , 2 per spike.

Gynoecia on lateral branches with one sterile innovation; bracts more or less ligulate, 650-850 x 900-1040 μm , apex rounded to acute, bract lobe entire, strongly toothed at the apex, rarely with 2 ocelli on the lower central part; bracteoles more or less ovate, 620-740 x 790-100 μm , bifid to $\frac{1}{2}$, lobes rounded to acute, margins entire, connate at the base with the bracts. Perianth obconic, 490-650 x 750-920 μm , horns inflated, elongate, 270-800 μm long, sometimes shortly branched.

Capsule valves 220 x 460 μm . Elaters ca. 200 μm long. Spores long rectangular or irregularly shaped, 25-40 x 60-75 μm , verruculose-tuberculate, rosettes complex, aperture ca. 8 μm in diameter, with ca. 11 teeth.

Illustrations. Bonner 1953, p. 172; Fulford 1945, p. 374.

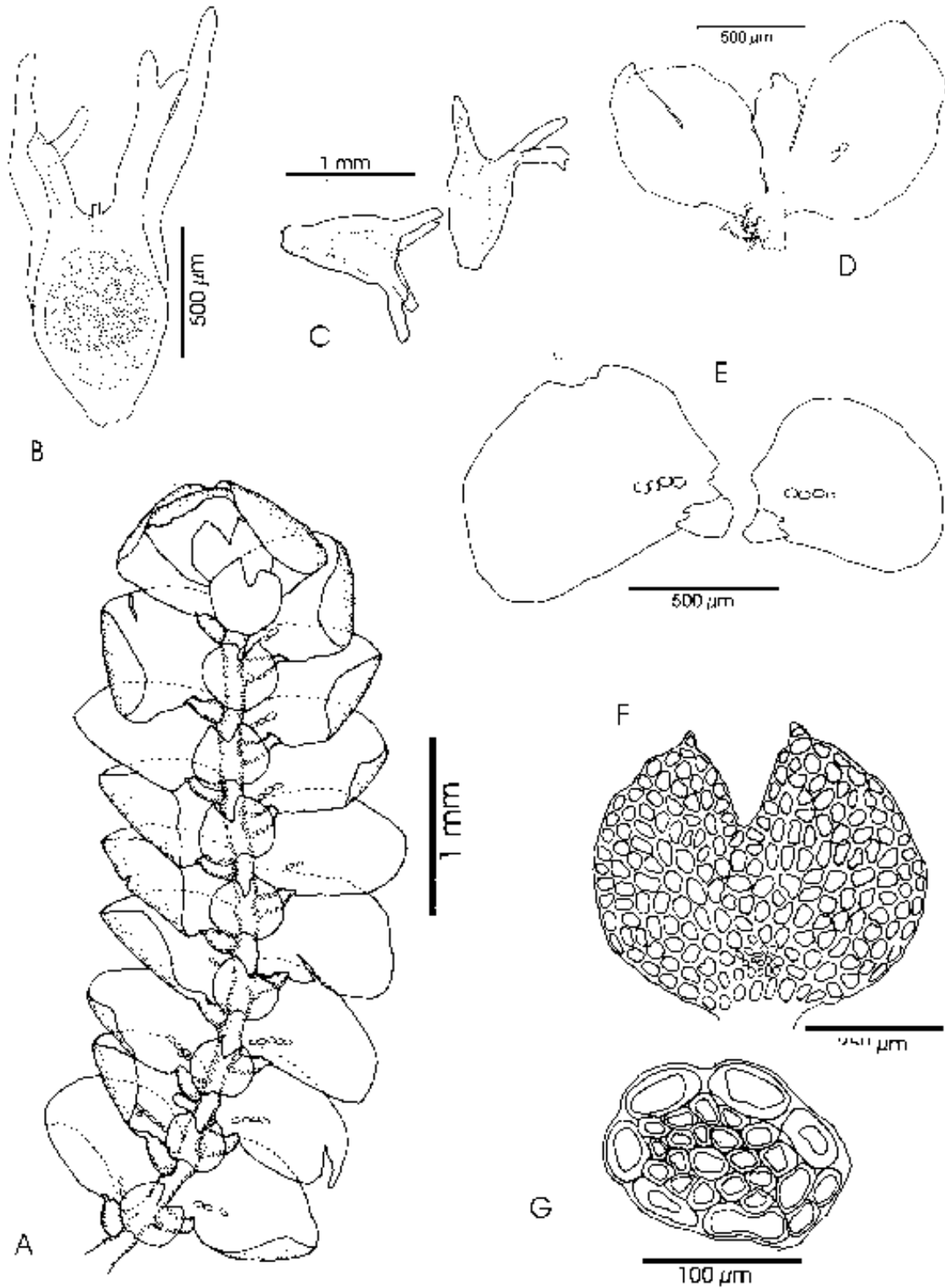


Figure 11. *Caratolinia bresinensis* (Spruce) Evans. A. Habit. B-C. Perianths. D. Perianth bracts and bracteoles. E. Leaves. F. Underleaf. G. Stem cross section. From Dominica, Elliot 681.

Distribution. Caribbean species growing at high elevations in the Greater and Lesser Antilles, as epiphyte on tree trunks or on logs in moist, submontane or montane forests, up to 1700 m altitude.

Specimens examined. JAMAICA. Blue Mountains, Evans 232 (NY, US). **Cinchona:** John Crow Peak., Britton 217 (NY), Evans 89 (NY, U), Underwood 646 (NY). **St. Andrew Parish:** trail to Mt. Horeb, SE of Hardwar Gap, Gradstein 6347 (GOET, U).
DOMINICAN REPUBLIC. **San Rafael:** Sierra de Neiba, along Haitian border, line between San Rafael and Independencia provinces, Norris B6845b (NY).
DOMINICA. Mt. Micotrin, Elliot 67 (MANCH); Mt. Diablotin, Elliot 681 (MANCH).
GUADELOUPE. The type.

Ceratolejeunea brevinervis can be distinguished from robust *C. cornuta* by its ocelli in a row of 1-6 cells towards the leaf lobe apex, rarely forming a second parallel row. The plants have a dark brown color and the leaf lobes are usually incurved. The horns of the perianth are sometimes very long and may even produce short lateral horns. This species is known from a few localities in high elevations in the Caribbean, and is probably widespread in similar habitats in the region, it may probably occur in Cuba and other major Caribbean islands.

The Caribbean *C. dentistipula*, known from Cuba and Guadeloupe, also has moniliate ocelli as *C. brevinervis*, but both can be easily distinguished by the toothed leaf and underleaf lobe margins in the latter.

2. *Ceratolejeunea ceratantha* (Nees & Mont.) Schiffn., Bot. Jahrb. 23: 582. 1897;
Lejeunea ceratantha Nees & Mont., in Montagne, Ann. Sci. Nat. ser. 2. Bot. 14: 335. 1840.
Type. French Guiana. „ad cortices in sylvis humidis circa Cayennam“, Leprieur 271
(holotype, PC; isotypes, MANCH, PC). Figure 12.

Ceratolejeunea poeppigiana (Nees) Steph., Sp. Hep. 5: 433. 1913; *Jungermannia thymifolia* Nees var. b**, in Martius, Flor. Bras. I: 359. 1833; *Lejeunea ceratantha* Nees & Mont. var. *poeppigiana* Nees, in Gottsche, Lindenberg & Nees, Syn. Hep.: 396. 1845; *Lejeunea poeppigiana* (Nees) Steph., Hedwigia 29: 92. 1890. Type. Brazil. Without locality, „ad filicum frondes“, Poeppig *s. n.* (isotypes, G, W), *syn. nov.*

Plants autoicous, dark-green to brown, stem with leaves 0.6-1.4 mm wide, sparsely branched. Stems in cross section 60-80 µm in diameter, medullary cells 9-18, ventral cells rectangular, 20-45 x 20-75 µm, dorsal rectangular, 25-40 x 25-55 µm. Branches sometimes attenuate towards the tips, appearing flagelliferous. Leaves imbricate, to shortly distant, leaf lobe ovate,

200-450 x 340-600 μm , margins entire, irregularly crenulate or with 1-7 teeth at the apex, teeth 1-2 cells long on a 1-2 celled base, 10-30 μm long, apex rounded to acute, plane; median leaf lobe cells isodiametrical, 10-30 x 15-40 μm , intermediate thickenings frequent, marginal leaf lobe cells quadrate to rectangular, 10-15 x 15-30 μm ; oil-bodies not seen; ocelli 25-35 x 20-60 μm , seriate, 1-3 per lobe, row 115-155 μm long; lobules inflated or reduced, 0.2-0.4 the leaf lobe length, free margin plane. Utriculi absent, single or in pairs at the base of lateral branches. Underleaves ovate, slightly longer than broad, 110-280 x 140-300 μm , bifid to $\frac{1}{2}$, lobes acute, ending in a 1-2 cells tip, margins entire, plane or rarely recurved.

Androecia on main branches or intecalary on secondary branches, in spikes of 5-7 pairs of bracts, 830-950 μm long; bracteole obovate, 90 x 105 μm , bifid.

Gynoecia on lateral branches with one sterile or repeatedly fertile innovation, bracts obovate, entire, dentate distally; bracteole ovate, 275-650 x 400-900, bifid to $\frac{1}{2}$, dentate distally, teeth to 25 μm long, connate at the base with the bracts. Perianth emergent to $\frac{1}{2}$, obconic, 340-500 x 570-750 μm , with four inflated horns, 70-110 μm long.

Spores irregularly shaped, mostly rectangular, 17.5-25 x 45-75 μm , greenish-brown, papillose-tuberculate, rosettes apparently absent.

Distribution: Known from the Caribbean, Amazonia and Southeastern Brazil. A rarely collected species, grows on bark in canopies of lowland and submontane forests, up to 600 m elevation.

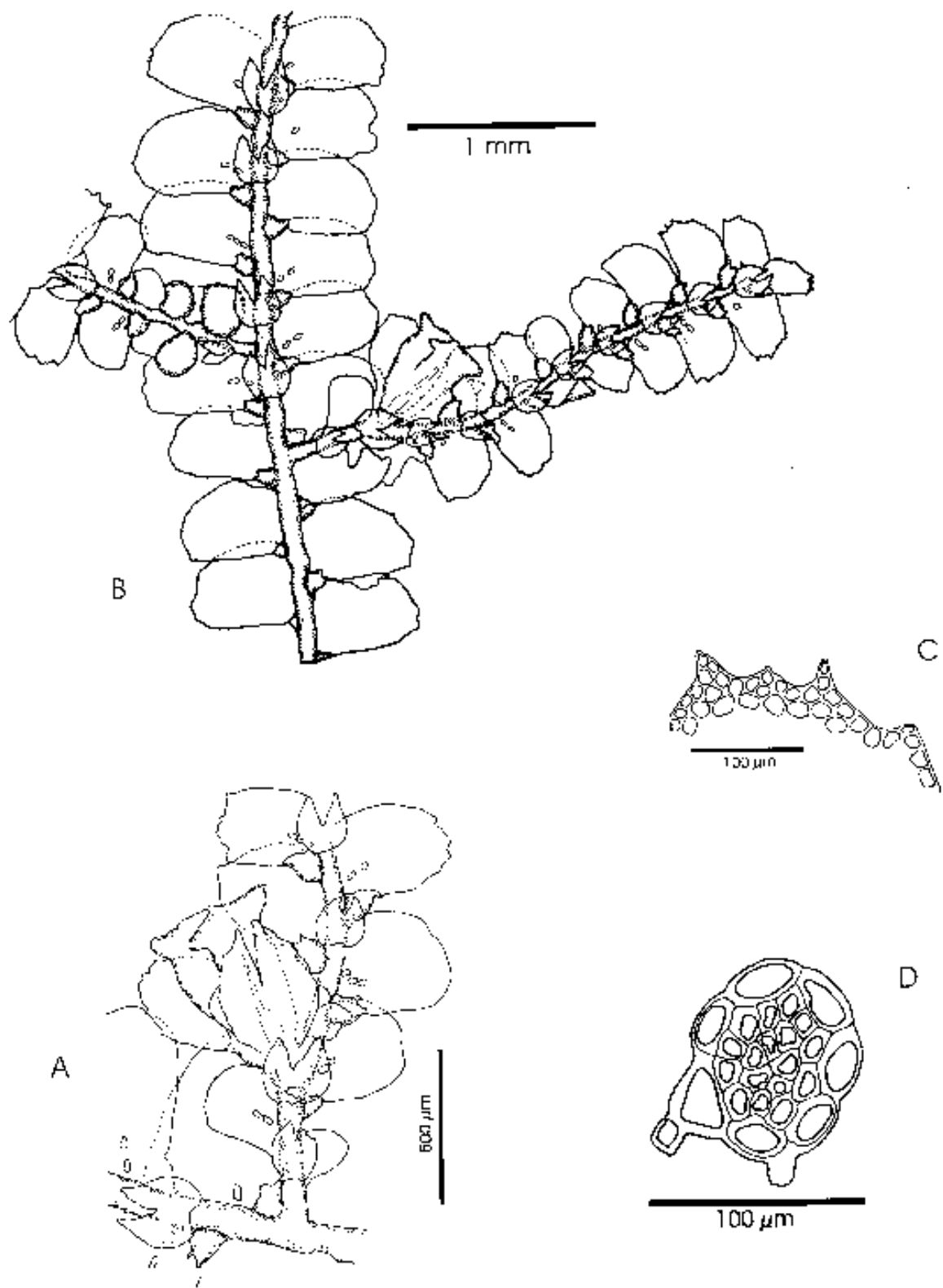


Figure 12. *Ceratopteris caratensis* (Nees & Mont.) Steph. A. Perianth and innovation. B. Habit. C. Leaf lobe margin. D. Stem cross section. From French Guiana, the type.

Specimens examined. CUBA. **Holguín:** Sierra de Nipe, sendero la Sofia, Vicario & Motito 16839 (HABE). **Santiago de Cuba:** Sierra del Cobre, Vicario & Mustelier 9381 (HABE).
FRENCH GUIANA. The type.
BRAZIL. **Rio de Janeiro:** Silva Jardim, Poço das Antas Biological Reserve, Costa *et al.*, 2089 (GOET).
Without locality: type of *Ceratolejeunea poepiggiana* (Nees) Steph.

Ceratolejeunea ceratantha is recognized by the seriate ocelli in most of the leaves or single ocelli in some of them. Typically, the underleaves do not exceed twice the width of the stem and their lobes are acute. According to the original description (Montagne 1840), the perianths of *Ceratolejeunea ceratantha* may rarely bear 5 horns, but I have not been able to confirm this observation.

The description of this species by Stephani (1913) is erroneous and refers to *C. cornuta* (Lindenb.) Steph. (*e. g.* „Amphigastria caulina magna, caule quadruplo latiora“), being apparently based on a specimen of the latter species mixed in with the isotype in G.

This species may be confused with the common *Ceratolejeunea cubensis*, from which it can be distinguished by the seriate ocelli in most of its leaves, the former usually having 1-2 basal or up to 7 geminate ocelli. *C. ceratantha* can also be confused with *C. rubiginosa* Steph., which has moniliate ocelli. The presence of small teeth throughout the antical leaf margin in *C. rubiginosa*, definitely separates it from *C. ceratantha*, which has the teeth restricted to the leaf apex.

3. *Ceratolejeunea coarina* (Gottsche) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 125. 1893; *Jungermannia thymifolia* var. *b* Nees, in Martius Flor. Bras. I: 359. 1833, *nom. inval.*; *Lejeunea coarina* Gottsche, in Gottsche, Lindenb. & Nees, Syn. Hep.: 395. 1845. Type. Brazil. „ad Coari“, Martius s. n. (isotype, G). Figure 13.

Ceratolejeunea kegelii (Lindenb. & Gottsche) Steph., Sp. Hep. 5: 420. 1913; *Lejeunea kegelii* Lindenb. & Gottsche, Linnaea 24: 635. 1851. Type. Surinam. Paramaribo, Kegel 535 (isotypes, G, GOET), *syn. nov.*

Ceratolejeunea plumula (Spruce) Steph., Sp. Hep. 5: 433. 1913; *Lejeunea (Cerato-Lejeunea) plumula* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 201. 1884. Type. Brazil. Amazonas: „Fl. Uaupés, in foliis viridis“, Spruce L311 (lectotype (*fide* Grolle *in sched.*), MANCH; isolectotypes, MANCH), *syn. nov.*

Ceratolejeunea monticola (Spruce) Steph., Sp. Hep. 5: 427. 1913; *Lejeunea* (*Cerato-Lejeunea*) *monticola* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 204. 1884. Type. Peru. Monte Guayrapurina, „ad cortices vetustas“, Spruce s. n. (holotype, MANCH; isotype, G), *syn. nov.*

Ceratolejeunea connata Steph., in Urban, Symb. Ant. 2: 471. 1901. Type. Guadeloupe. „Sur les feuilles de *Danaea nodosa*“, Sofoia, Ravine Chaude, 245-700 m, Duss 44 (isotype, NY), *syn. nov.*

Ceratolejeunea remotistipula Steph., Sp. Hep. 5: 437. 1913. Type. Surinam. Without locality, without collector (holotype, G), *syn. nov.*

Plants autoicous, pale-green to reddish-brown, stem with leaves 0.5-1.5 (-1.8) mm wide, profusely and irregularly branched (plumose). Stems in cross section 65-90 (-125) μm in diameter, medullary cells 10-21, ventral cells in surface view quadrate to rectangular, 15-40 (-65) x 30-50 (-85) μm , dorsal cells subquadrate to rectangular, 20-40 (-55) x 25-60 (-80) μm . Flagelliferous branches common, with leaves 0,3 mm wide; lobes of leaflets on flagelliferous branches with rounded apices, 90-120 x 180-230 μm , lobules 0.7 the leaflet lobe length. Leaves imbricate, lobe asymmetric-ovate, frequently patent, 250-540 (-650) x 420-680 (-920) μm , antical margin entire, crenulate or finely to roughly toothed, with 0-30 teeth, 5-25 (-35) μm long, postical margin usually entire or with 2 teeth; median leaf cells with rounded to short-elliptic lumina, 10-25 (-35) x 15-50 μm ; walls thin, intermediate thickenings rare; ocelli 25-50 x 40-75 μm , basal or geminate, 1-4 (-7) per leaf; oil-bodies smooth (Dauphin 2691 (GOET)); lobules inflated, spherical or rarely reduced, 0.2-0.5 the leaf lobe length, free margin involute or plane, apical tooth projecting, curved. Utriculi frequent, solitary or in pairs at the base of lateral branches. Underleaves distant to subimbricate, ovate, 120-400 x 110-400 μm , bifid to 2/3, lobes rounded or acute, ending in a one-celled tip, margins entire, crenulate or with a tooth, plane.

Androecia lateral or terminal on main stems, in spikes of 2-4 (-8) bracts pairs, 340-650 (-800) μm long, bracteole single, ovate, 65-181 x 75-180 μm , bifid to 1/2.

Gynoecia on lateral branches, with one sterile innovation; bracts obovate, 300 x 450-550 μm , margins entire, toothed distally; bracteoles ovate to ligulate, 200-620 x 350-780 μm , bifid to 1/4, margins entire or sparsely toothed. Perianth, 330-450 x 430-650 μm , with four inflated, erect horns, 110-200 (-600) μm long.

Elaters 12.5 x 265-330 μm ; spores irregularly shaped, mostly rectangular, 15-25 x 40-70 μm , surface verruculose, rosettes?.

Illustrations. Fulford 1945, p. 378 (as *C. plumula* (Spruce) Steph.).

Distribution. Known from Amazonia, Chocó, Costa Rica and the Caribbean, commonly epiphyllous or corticolous, this species is confined to primary or secondary lowland rainforests to submontane forests, from sea level to ca. 1000 m altitude.

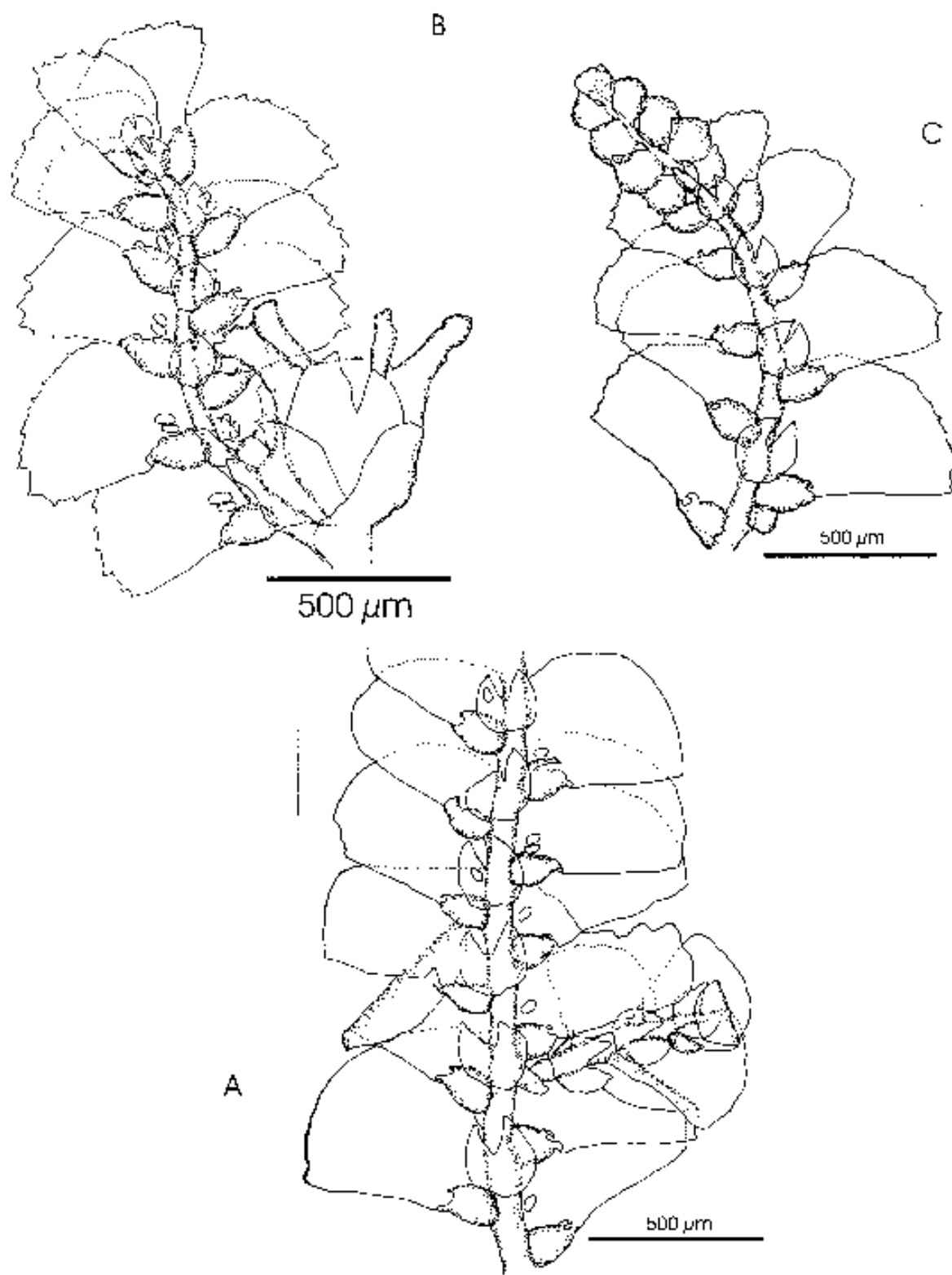


Figure 13. *Graptobalanus caribea* (Goussier) Steph. A. Habit, margin entire. B. Perianth and innovation. C. Androecial branch. From Brazil, the type (A), from Guadeloupe, Duss 44 (B-C).

Specimens examined. COSTA RICA. **Limón:** Braulio Carrillo National Park, Quebrada Gónzales, Bernecker-Lücking 92-218, 92-230 (hb Bernecker-Lücking). **Puntarenas:** Osa Peninsula, Rincón, trail Boscosa to Cerro Chocuaco, Gradstein & Dauphin 9315 (GOET).

GUADELOUPE. Type of *C. connata* Steph.

COLOMBIA. **Chocó:** Nuqui, amargal at the Pacific Coast SW of Arusi, Gradstein 8817, 8861 (GOET, U). **Santander del Norte:** Catatumbo, Puerto Barco, borde del Río Catatumbo, Bischler 2622 (GOET, U)

VENEZUELA. **Amazonas:** along Rio Mawarinuma, outside Cañón Grande, vicinity of Neblina Base Camp, Buck10956, 11247 (NY); Río Negro, along SE of Town, Halling 4373 (NY)

TRINIDAD. North Range, Welch 21215 (GOET, U)

GUYANA. **Upper Demerara-Berbice:** Mabura Hill, DTL Concession Warabuta Compartment, 3 km transect from road to Essequibo River., Kennedy & Pulles 4739a (GOET). Upper Mazaruni: Mazaruni river, 2 km below its junction with Kamarang River, Robinson 85-0085 (US).

SURINAM. **Wanica:** Paramaribo, type of *C. kegelii* (Lindenb. & Gottsche) Steph.. **Without locality:** type of *C. remotistipula* Steph.

FRENCH GUIANA. **Maroni:** Saint Laurent, Benoist s. n. (PC).

ECUADOR. **Esmeraldas:** Río Grande, Harling 4628pp (NY); San Lorenzo, ca. 5km on the main road, Dauphin 2691, 2696pp (GOET, USJ). **Without locality,** Leprieur 1394 (MANCH).

PERU. **Loreto:** Maynas, near Iquitos, Río Momon, 3 km above junction with Río Nanay, Timme 4784 (NY), above junction with Río Momoncillo, McDaniel 13647 (NY). **San Martín:** Lamas, road Yurimaguas-Tarapoto, km 107, Frahm et al. 2070 (GOET, U), km 56, Frahm *et. al.* 1578 (GOET, NY). Without department: type of *C. monticola* (Spruce) Steph.

BRAZIL. **Acre:** 15 km E of Rio Branco, along road to Abuña, Reese & Mc Pherson 13157a (GOET, U); Cruzeiro do Sus, Estrada Alemanha, Maas *et. al.* 2773 (NY). **Amapá:** Oyapok River, Salto Trois Sants, Lützelberg 149 (GOET, U, US). **Amazonas:** Coari, the type; along E shore of Rio Uatumã at junction of Rio Pitinga, Buck 3170 (GOET, U, US), along N shore of Rio Pitinga, ca. 4km from junction of Rio Uatuma., Buck 3195 (NY); along Rio Cauburi between Rio Negro and Cachoeira do Carangueijo, Schuster 79-10-280pp (NY); Manaus, Campus of the Instituto Nacional de Pesquisas da Amazonia, Griffin III *et. al.* I-45 (GOET, U), along the road Manaus-Itacoatiara, km 30, Estação Agrícola (CEPLAC), Vital *et. al.* 3820 (GOET, U), Igapó de Curuçae Autaz-Mirim, Vital *et. al.* 4378, (GOET, U), Manaus-Caracarai road, km 115, Griffin III *et. al.* 845 (GOET, U); NW of São Gabriel, near mouth of Rio Uaupés, Schuster 79-20-1059, 79-20-1061 (NY), type of *C. plumula* (Spruce) Steph. **Maranhão:** Turiaçu, 8 km NW from Maranhãozinho, Vital 2955a (GOET, U). **Pará:** **Without locality,** Spruce s. n. (NY), Traill s. n. (NY). **Without department:** without locality, Ule 214 (BM).

Ceratolejeunea coarina has been frequently confused in herbaria with *C. cubensis* (Mont.) Schiffn. and *C. cornuta* (Lindenb.) Steph. It can be distinguished by its usually epiphyllous habit, its profusely branched habit (plumose), its patent, asymmetrical leaves, its frequently arcuate antical leaf margin that can be entire, crenulate, finely or roughly toothed. The ocelli usually appear in groups of three contiguous cells, but some individuals may show 1 up to 4 ocelli per leaf in different arrangements parallel to the leaf base.

Epiphyllous forms of *Ceratolejeunea cornuta* (Lindenb.) Steph. with a plumose habit and abundant utriculi and underleaves with non-cordate bases, may be hard to separate from *C. coarina*. Both species can be distinguished by the asymmetrical leaf shape and the marginal leaf teeth that extend along the antical leaf margin in the latter, but when teeth are present, they are restricted to the apical leaf region in *C. cornuta*.

Spruce (1884) treated this taxon under the monoicous *Ceratolejeuneas* with wide underleaves. Judging from his description and specimens identified and distributed by him under *C. coarina* Gottsche (*e. g.* Silva Amazonica, Rio Negro, „in truncis inundatis“, Spruce s. n. (BM 92274)), he refers to forms of *Ceratolejeunea cornuta* (Lindenb.) Steph. with relatively patent leaves on secondary stems.

4. *Ceratolejeunea confusa* Schust., Journ. Elisha Mitchell Soc. 72: 313. 1956. Type. Trinidad. Caroni: north bank road, Britton *et al.* 581 (holotype, NY; isotype, hb Schuster (*vide* Schuster (1956))). Figure 14.

Plants autoicous, light yellowish-brown, stems with leaves 0.7-1.5 mm wide, profusely branched, stems in cross section 50-95 μm in diameter, medullary cells 10-15, ventral cells in surface view quadrate to rectangular, 20-45 x 20-60 μm , dorsal cells, quadrate to rectangular, 30-35 x 35-50 μm . Flagelliferous branches not seen. Stem leaves imbricate to strongly imbricate, lobe ovate from a wide base, 300-600 x 450-720 μm , margins entire, apex rounded, plane; median leaf lobe cells isodiametrical to elliptical or long-hexagonal, 15-30 x 20-40 μm , cell walls regularly thickened, intermediate thickenings rare; marginal cells quadrate to rectangular, 10-20 x 15-20 μm ; oil-bodies not seen; ocelli rectangular, 25-30 x 50-55 μm , 1-2 (-3) per leaf, basal or rarely seriate (2 cells); lobules, 0.2-0.3 the leaf lobe length, free margin plane, apical tooth short; spherical lobules not seen. Utriculi occasional, solitary at the base of lateral branches. Underleaves orbicular, 280-520 x 260-450 μm , lobes acute, ending in a one or two-celled tip.

Androecia lateral on main branches, terminal or intercalary on lateral branches, in spikes of 2-4 (-8) bract pairs, spike 370-1125 μm long; bracteole orbicular, 150-250 x 160-250 μm , bifid to 1/3.

Gynoecia on lateral branches with 1 sterile or fertile innovation; female bracts obovate, 400 x 550 μm , margins entire or crenulate, bract lobule lanceolate-acuminate, 250-300 x 450-650 μm , margins entire; bracteoles ovate, 370-450 x 500-650 μm , bifid to 2/3, lobes acuminate,

margins strongly crenulate, sometimes distally toothed, connate at the base with the bracts.

Perianth obconic, 450-560 x 800-880 μm , with five rounded, mammillose keels.

Elaters 17,5 μm wide. Spores long rectangular to irregularly shaped, 25-30 x 45-70 μm , low papillose, rosettes complex.

Distribution. Known from Costa Rica, Trinidad, Chocó and Amazonia, this species grows in dry and moist lowland forest habitats, from sea level to 200 m altitude. Apparently well adapted to temporarily dry environments, this species grows on bark of trees, from the base to the outermost canopy branches.

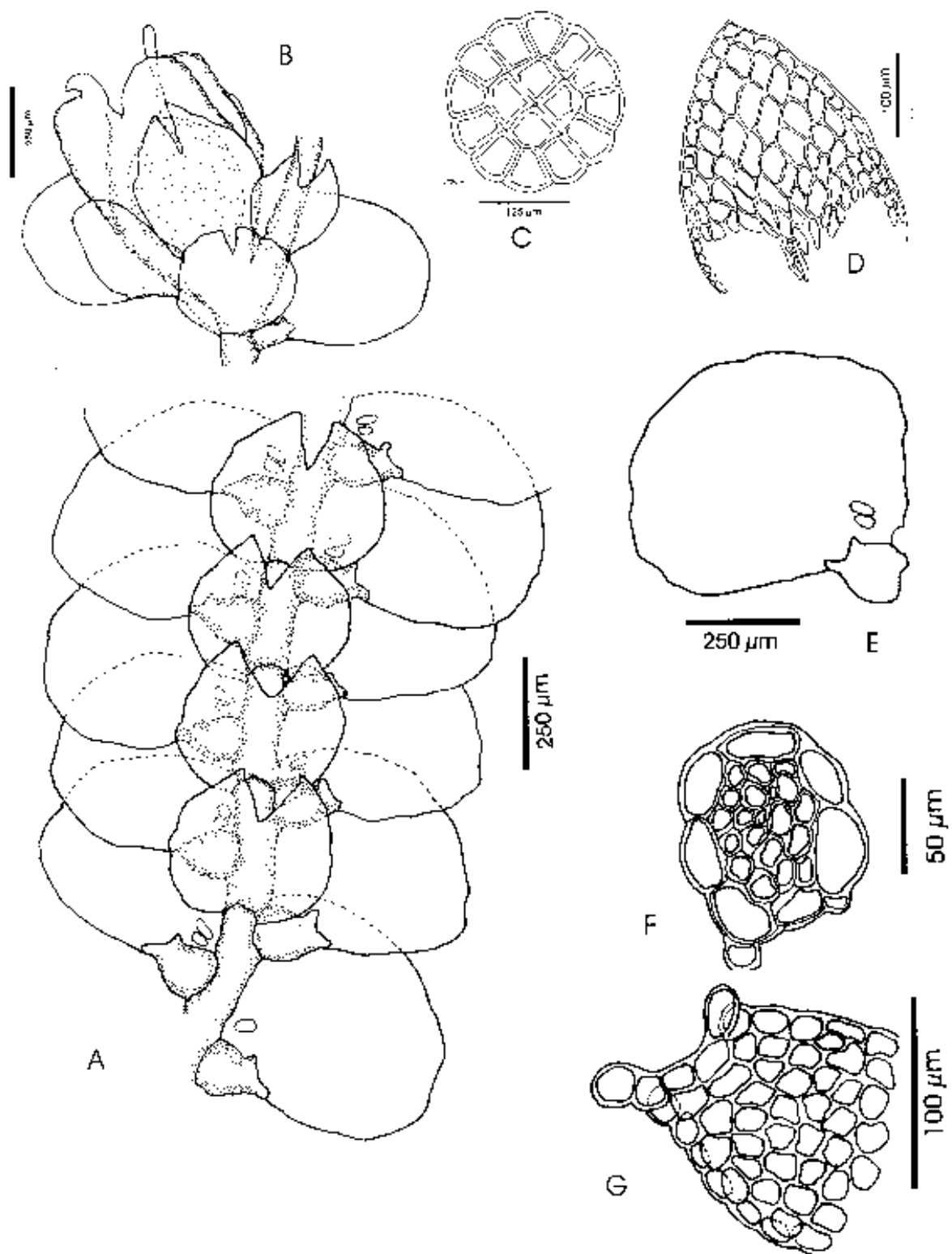


Figure 14. *Utricularia confusa* Schust.. A. Habit. B. Perianth. C. Sporophyte foot. D. Sporophyte capsule valve. E. Leaf. F. Stem cross section. G. Lobule. From Trinidad, the type.

Specimens examined. COSTA RICA. **Limón:** Punta Uva, Dauphin & Rodríguez s. n. (NY).
Puntarenas: Cocos Island, Dauphin 1080 (USJ).
COLOMBIA. **Chocó:** road Santa Cecilia-Tadó, 40 km W of St. Cecilia, Gradstein 8721 (GOET, U).
TRINIDAD. **Caroni:** the type.
GUYANA. Mabura Hill: 180 km SSE of Georgetown, Cornelissen & ter Steege 564, 718, 748, 818, 819, 820 (GOET, U).
SURINAM. Road to Afoebaka, near road to NW-Koffie Kamp, km 106, Bekker 1022a (GOET, U).
FRENCH GUIANA. **Saül:** 2 km SW of town, “Sentier Limonade”, Montfoort & Ek 447 (GOET, U).
BRAZIL. **Amazonas:** Manaus, Griffin III *et al.* 810 (GOET, U).
BOLIVIA. **Beni:** Beni Forest Reserve, Gradstein 9936 (GOET, U, USJ).

Ceratolejeunea confusa may be hard to separate from *Ceratolejeunea cornuta* when sterile. In *C. confusa*, the leaf lobes are always entire, the utriculi are occasional and single, whereas in *C. cornuta*, the leaf lobes may be entire or toothed at the apex, and the utriculi usually appear in pairs, in addition the presence of series of spherical lobules in some branches clearly distinguishes *C. cornuta* from *C. confusa*. Both species differ in perianth type. *C. confusa* lacks horns and has a perianth with five low crested keels; in addition, the spores are low papillose with well developed rosettes. *C. cornuta* has usually four well developed short or long horns and the spores are verruculose-tuberculate and the rosettes are simple.

5. *Ceratolejeunea cornuta* (Lindenb.) Steph., in Engler, Pflanzenwelt Ost-Afrikas...Theil CC: 65. 1895; *Jungermannia cornuta* Lindenb., Nova Acta Caes Leop. Carol. 14 Suppl.: 23. 1829; *Lejeunea cornuta* (Lindenb.) Lindenb., in Gottsche, Lindenberg & Nees, Syn. Hep.: 399. 1845; *Colura cornuta* (Lindenb.) Trevis., Mem. Ist. Lomb. Sci. Mat. Nat., Ser. 3, 4: 402. 1887. Type. Jamaica. Without locality, on *Grammitis serrulatus*, Swartz s. n. (holotype, W). Figure 15.

Ceratolejeunea involvens (Nees & Mont.) Steph., Sp. Hep. 5: 419. 1913; *Lejeunea involvens* Nees & Mont., Ann. Sci. Nat., Bot. Ser. 2, 14: 336. 1840. Type. French Guiana. Mt. Serpent, Leprieur 287 (holotype, PC; isotype, MANCH), *syn. nov.*

Ceratolejeunea splitgerberiana (Mont.) Steph., Sp. Hep. 5: 443. 1913; *Lejeunea splitgerberiana* Mont., Ann. Sci. Nat. Bot. ser 2, 16: 112. 1841. Type. Surinam. Without locality, Splitberger s. n. (holotype, PC), *syn. nov.*

Ceratolejeunea haeckeriana (Gottsche & Lindenb.) Steph., Sp. Hep. 5: 417. 1913. *Lejeunea haeckeriana* Gottsche & Lindenb. in Gottsche, Lindenberg & Nees, Syn. Hep.: 401. 1845. Type: Peru; "In cortice Cinchonae (China rubrae)", Haecker s. n. (isotype, G), *syn. nov.*

Ceratolejeunea martiana (Gottsche) Steph., Sp. Hep. 5: 421. 1913. *Lejeunea martiana* Gottsche, in Gottsche, Lindenberg & Nees, Syn. Hep.: 398. 1845. Type. Brazil. Without locality, „circa flumen Amazonum Brasiliae“, Martius s. n. (isotypes, G, S), *syn. nov.*

Ceratolejeunea variabilis (Lindenb.) Schiffn., in Engler & Prantl., Nat. Pflanzenfam. 1, 3: 125. 1893; *Lejeunea variabilis* Lindenb., in Gottsche, Lindenberg & Nees, Syn. Hep.: 399. 1845, Trans. & Proc. Bot. Soc. Edinburgh 15: 206. 1884. Type. Saint Kitts. Without locality, Breutel s. n. (lectotype (*fide* Grolle in sched. 1974), W; isolectotypes, BM, G, S), *syn. nov.*

Lejeunea (*Cerato-Lejeunea*) *variabilis* Lindenb. var. *subserrata* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 207. 1884. Type. Brazil. Rio Negro, Spruce s. n. (*lectotypus nov.*, MANCH), *syn. nov.*

Spruce (1884) indicated no type or localities for this taxon. The lectotype was chosen among the material identified under that name by Spruce in MANCH.

Lejeunea (*Cerato-Lejeunea*) *variabilis* Lindenb. var. *saproxylophila* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 207. 1884. Type. Brazil. Uaupés, Spruce 328 (*lectotypus nov.*, MANCH). Peru: Mt. Guayrapurina, „in trunco putrido“, Spruce L154 (syntype, MANCH), *syn. nov.* Spruce (1884) indicated the above cited type localities for this variety. The lectotype was chosen based on a fertile, more abundant specimen.

Ceratolejeunea fuliginosa (Spruce) Steph., Sp. Hep. 5: 413. 1913; *Lejeunea* (*Cerato-Lejeunea*) *fuliginosa* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 208. 1884. Type. Brazil. Amazonas: Rio Negro, „Rupes ad fl. Negro cataractas“, Spruce s. n. (*lectotypus nov.*, MANCH; isolectotype, G); „Fl. Uaupés cataractas, Spruce L35 (syntype, MANCH); „Ad Fl. Negro et Uaupés“, Spruce s. n. (syntype, MANCH), *syn. nov.*

Spruce (1884) indicated the above cited type localities for this species. The lectotype provided has also a duplicate in G.

Ceratolejeunea grandibracteolata Fulford, Bull. Torrey Bot. Club 71: 637. 1944; *Ceratolejeunea subserrata* Spruce, *nom. herb.* Type. Brazil. Rio Negro, „in cortice foliisque“, Spruce s. n. (*lectotypus nov.*, BM; isolectotypes, G, US), *syn. nov.*

Fulford (1944a) indicated no type for her new taxon, but obviously based herself on the material distributed to different herbaria in the Hepaticae Spruceanae. The lectotype corresponds to this material.

Ceratolejeunea hylophila (Spruce) Steph., Hedwigia 34: 238. 1895; *Lejeunea* (*Cerato-Lejeunea*) *hylophila* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 209. 1884. Type. Brazil. Pará: „lacum Quiriquiry fluvii Trombetas“, Spruce L236 (*lectotypus nov.*, MANCH), *syn. nov.*

Spruce (1884) indicated several localities for this taxon, in MANCH there are also several specimens from a single locality (e. g. Pará). The chosen lectotype is the only sample from that locality also cited in the protologue.

Lejeunea (*Cerato-Lejeunea*) *hylophila* Spruce var. *subdenticulata* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 209. 1884. Type. Brazil. Amazonas: San Carlos, Spruce s. n. (*lectotypus nov.*, MANCH), *syn. nov.*

Spruce (1884) indicated several localities for this taxon, the lectotype fits his description.

Ceratolejeunea maritima (Spruce) Steph., Sp. Hep. 5: 423. 1913; *Lejeunea* (*Cerato-Lejeunea*) *maritima* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 210. 1884. Type. Brazil. Caripi, „prope Pará, in saxis maritimis“, Spruce s. n. (holotype, MANCH; isotypes, BM, US), *syn. nov.*

Ceratolejeunea megalophysa (Spruce) Steph., Sp. Hep. 5: 425. 1913; *Lejeunea* (*Cerato-Lejeunea*) *megalophysa* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 202. 1884. Type. Brazil. Amazonas: „San Gabriel, in foliis palmarum“, Spruce s. n. (*lectotypus nov.*, MANCH; isolectotypes, BM, US, W); Rio Negro, Spruce s. n. (syntype, MANCH), *syn. nov.*

Two type localities were mentioned in the protologue (Spruce 1884). The lectotype has more abundant material.

Ceratolejeunea microrhegma (Spruce) Lacout., Rev. Bryol. 35: 113. 1908; *Lejeunea* (*Cerato-Lejeunea*) *microrhegma* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 209. 1884. Type. Ecuador. Canelos, Spruce L558 (holotype, MANCH; isotype, MANCH), *syn. nov.*

Ceratolejeunea rufo-pellucida (Spruce) Steph., Sp. Hep. 5: 439.1913; *Lejeunea* (*Cerato-Lejeunea*) *rufo-pellucida* Spruce Trans. & Proc. Bot. Soc. Edinburgh 15: 207. 1884. Type. Brazil. „Ad San Carlos del Rio Negro, in arborum foliis“, Spruce s. n. (holotype MANCH; isotype G)

Ceratolejeunea spruceana Zwickel, Annal. Bryol. 6: 108. 1933. Type. Brazil. Amazonas: „Rio Negro, in palmarum foliis“, Spruce s. n. (holotype, M), *syn. nov.*

Ceratolejeunea miradorensis (Steph.) Steph., Sp. Hep. 5: 426. 1913; *Lejeunea brasiliensis* Gottsche var. δ , in Gottsche, Lindenberg & Nees, Syn. Hep.: 398. 1845; *Lejeunea* (*Cerato-Lejeunea*) *miradorensis* Steph., Hedwigia 29: 93. 1890. Type. Mexico. Mirador, Liebmann s. n. (Lectotype (Bonner 1953), G), *syn. nov.*

Ceratolejeunea andicola Steph., Hedwigia 34: 234. 1895 (*non* Schust. 1978). Type. Ecuador. Manabi, Wallis s. n. (holotype, G), *syn. nov.*

Ceratolejeunea peruviana Steph., Hedwigia 34: 236. 1895. Type. Peru. Tatanara, Lechler s. n. (holotype, G; isotype, G), *syn. nov.*

Ceratolejeunea schwaneckeii Steph., Hedwigia 34: 237. 1895; *Lejeunea ceratantha sensu* Hampe & Gottsche, Linnaea 25: 356. 1852 (*non* *Lejeunea ceratantha* Nees & Mont. 1840). Type. Puerto Rico. Without locality, Schwanecke s. n. (holotype, G; isotype, G), *syn. nov.*

Ceratolejeunea sintenisii Steph., Hedwigia 34: 237. 1895. Type. Puerto Rico. Without locality, Sintenis 125 (holotype, G), *syn. nov.*

Ceratolejeunea valida Evans, Bull. Torrey Bot. Club 32: 280. 1905. Type. Puerto Rico. El Yunque, on bushes, Evans 91 (holotype, YU; isotype, JE), *syn. nov.*

Ceratolejeunea brevicornuta Steph., Sp. Hep. 5: 398. 1913. Type. Peru. St. Gavan, Lechler s. n. (holotype, G), *syn. nov.*

Ceratolejeunea bullatiloba Steph., Sp. Hep. 5: 399. 1913. Type. Peru. Without locality, without collector, hb Meissner (holotype, G), *syn. nov.*

Ceratolejeunea diversiloba Steph., Sp. Hep. 5: 409. 1913. Type. Dominica. Without locality, Elliot 1674 p. p. (holotype, G), *syn. nov.*

Ceratolejeunea furcata Steph., Sp. Hep. 5: 413. 1913. Type. Dominica. Without locality, Elliot 1764 (lectotype (Bonner 1953), G; isolectotype, BM), *syn. nov.*

Ceratolejeunea latiflora Steph., *nom. nud.*, *Icones Hepaticarum*, *Jard. Bot. Genève* 29: 1613. 1985. Type. Martinique. Without locality, Husnot, s. n. (material, G), *syn. nov.*

Ceratolejeunea rionegrensis Steph., *Sp. Hep.* 5: 438. 1913. Type. Brazil. Rio Negro, „in palmarum foliis“, Spruce s. n. (holotype, G), *syn. nov.*

Ceratolejeunea litoralis Herz., *Rev. Bryol. Lich.* 13: 23. 1942. Type. Colombia. Valle: Buenaventura, 0-10 m, E. P. Killip 11710 (holotype, JE; isotype, B), *syn. nov.*

Plants autoicous or dioicous, green or brown to almost black, creeping to hanging, stems with leaves 0.8-2.1 mm wide, sparsely to profusely branched, stems in cross section 70-180 μm in diameter, medullary cells 10-30, ventral cells in surface view quadrate to rectangular, 15-55 x 25-85 μm , dorsal cells quadrate to rectangular, 30-58 x 30-95 μm . Flagelliferous branches occasional; leaflets 150-460 x 240-700 μm , antical leaflet lobe margins entire to roughly toothed, with 5-10 teeth. Stem leaves imbricate; lobe ovate from a wide base, sometimes asymmetrical, 400-600 x 440-750 μm , antical margins entire or toothed at the apical region, teeth 0-4, 1-2 cells long, ca. 10 μm long, postical margin entire or with 0-2 teeth, apex rounded or broadly acute, incurved or plane; median leaf lobe cells isodiametrical to elliptical, 10-40 x 15-50 μm ; marginal cells quadrate to rectangular, 10-15 x 15-30 μm ; oil-bodies smooth, transversely 1-4 septate, spherical to elliptical, 2 x 9 μm , per cell?; ocelli long-hexagonal, 20-40 x 40-65 μm , basal, geminate or rarely seriate, (0-) 3-7 (-8) per leaf; lobules inflated, reduced or spherical, 0.2 (0.1-0.6) the leaf lobe length, free margin involute or plane, with apical tooth short or long and curved; hyaline papilla bulging. Utriculi rare, solitary or in pairs at the base of lateral branches, rounded to reniform. Underleaves orbicular to reniform, 160-730 x 160-560 μm , lobes acute, ending in a one-celled tip, margins entire, plane or rarely incurved, base frequently cordate, lobe auricles rounded.

Androecia lateral on main branches, rarely intercalary on main or lateral branches, in spikes of 4-8 (-14) bract pairs, 480-1000 (-2400) μm long, bracts 2-androus, male bracteole, 120-130 x 120-170 μm , 1-2 per spike, notched or bifid to 1/2.

Gynoecia on lateral branches with 1-2 sterile or repeatedly fertile innovations; female bracts obovate, 450-560 x 750-800 μm , margins dentate throughout or only distally, teeth to 75 μm long, bract lobule ovate lanceolate, 200-300 x 370-650 μm , margins entire, apex acuminate, sometimes with 2 ocelli on the lower central part; bracteoles ovate, 480-520 x 280 μm , bifid to 1/4, lobes short to long acuminate, margins entire, connate at the base with the bracts.

Perianth obconic, 170-800 x 280-900 μm , with four conical horns, slender to inflated, 50-80 x 80-300 μm , edges smooth to crenulate.

Elaters, 12.5 x 190 μm . Spores long rectangular to irregularly shaped, 18-44 x 36-70 μm , verruculose-tuberculate, rosettes simple.

Illustrations. Evans 1905, plate 19 (as *C. valida* Evans), plate 20 (as *C. schwaneckeii* Steph.); Fulford 1945, p. 395 (as *C. megalophysa*, (Spruce) Steph.), p. 380 (as *C. flagelliformis* (Steph.) Fulford), p. 389 (under various names).

Distribution. Neotropical. Ubiquitous species in lowland rainforest and semi-deciduous tropical forest up to montane areas, 0-2500 m, growing usually in well illuminated places, in light-gaps, canopies and old-secondary growth areas. This species forms thin or thick mats or turfs on living bark, but can also grow on rotten logs, rocks, leaves and almost every possible substrate. It grows in pure mats or mixed with other bryophytes, and often appears mixed with other *Ceratolejeunea* species.

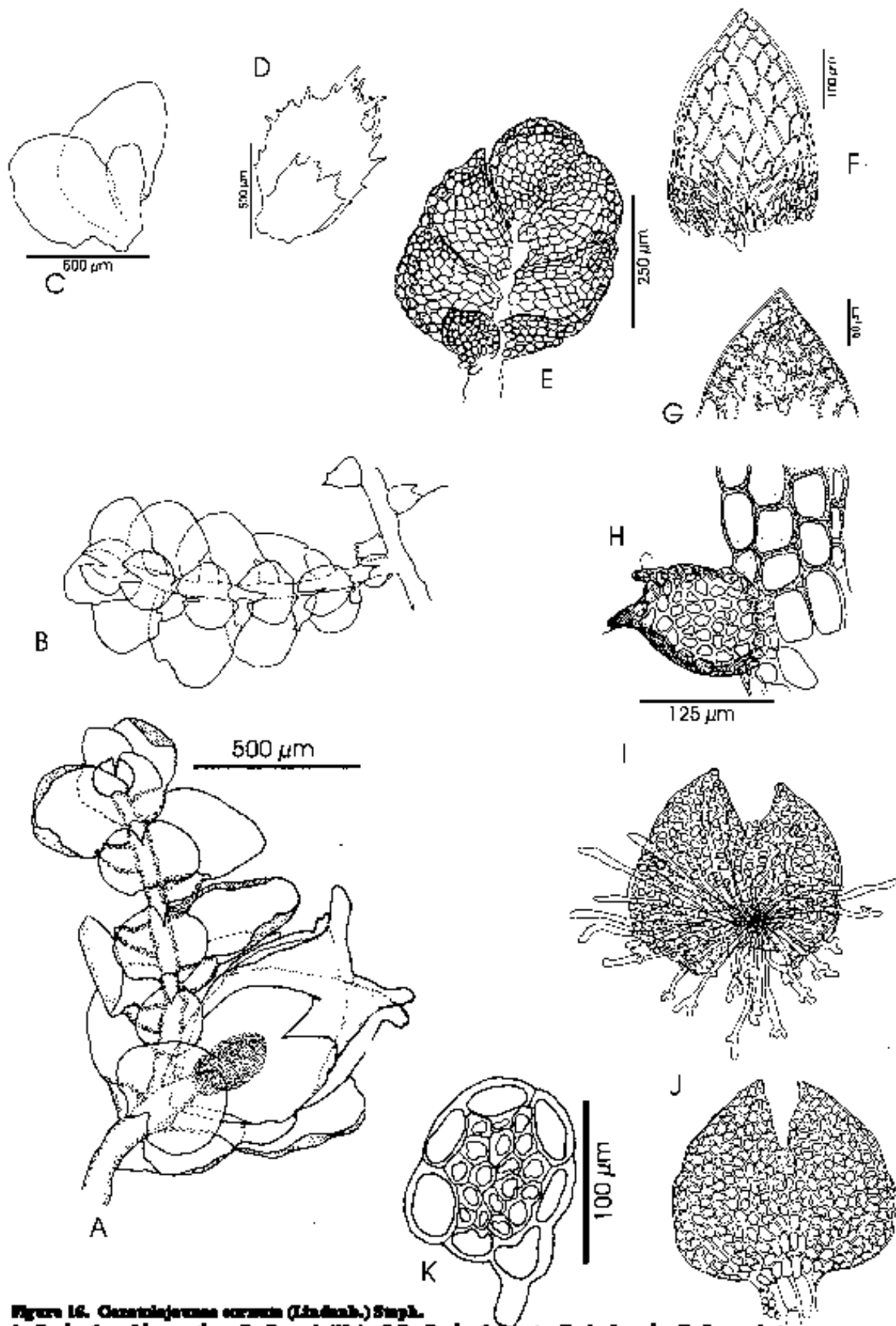


Figure 16. *Cezaniajeviana curvata* (Lindb.) Steph.

A. Farkash and Ivanovsk. B. Rozanik (18a). C-D. Farkash Rozan. E. Andronov. F. Sporephyte valve, inner face. G. Sporephyte valve, outer face. H. Lobule and stem. I, J. Underdeveloped. From Cuba, the type (B, E, J), Walck 17746 (G, H, I, K), from Ecuador Dauphin 2757 (I, G), from Brazil Schiffner s. n. (A).

Specimens examined. MEXICO. **Chiapas:** near Puerto de Vientes, above Pueblo Nuevo, Robinson 9870 (US); Lagos de Monte Bello, near the Guatemala border, ca. 50 km SE of Comitán, Hale Jr. & Soderstrom 20361 (US). **Oaxaca:** Sierra Juarez above Valle Nacional Oaxaca, Sharp s. n. (US), on road km 90, Robinson 10048, 10055 (US); road between Valle Nacional and Ixtlán de Juárez, 42.1 km S of Rio Valle Nacional, Stone s. n. (US). **Veracruz:** 33 km NE of Catemaco, den Held & van Rhijn HH12, HH24, HH25 (GOET, U).

Without department: Mirador, type of *Ceratolejeunea miradorensis* (Steph.) Steph.

GUATEMALA. **Alta Verapaz:** vicinity of Secanquim, Maxon & Hay 3206 (US).

HONDURAS. **Comayagua:** 12km NW of Siguatepeque, Maas & Molina 1049 (GOET, U). **Cortés:** along Rio Lindo, N of Lake Yojoa, Morton 7851a, 7640a (US), mountains on N side of Lake Yojoa, Morto 7636j (US); Peña Blanca, Tag 1983-10 (US).

COSTA RICA. **Alajuela:** Grecia, Laguna Hule, Dauphin & Gonzáles 2138 (GOET, INB); type of *Ceratolejeunea fusilobula* Herz. **Cartago:** Cerro de La Muerte, King c1159b (US); vicinity of Pejiballe. Standley & Valerio 46809 (B, JE, US). **Heredia,** Sarapiquí, Lücking s. n. (GOET), Estación Biológica La Selva, sendero SUR, Bernecker-Lücking s. n. (GOET), 97-10 (hb Bernecker-Lücking), Horquetas cerca del Río Villalobos y Hotel Rara Avis, Dauphin 2204 (GOET, INB). **Limón:** „Chemin de Carrillo, versant atlantique“, Pittier & Biolley 6066 (PC). Pococí, Cuatro Esquinas de San Juan, Dauphin, Morales, Gonzáles & Rojas 1669 (GOET, INB); Tortuguero, up to 5 km inland from Green Turtle station, Steere CR-9, CR-143 (NY). **Puntarenas:** Cocos Island, Chatham bay, Weber 580 (GOET, U); Coto Brus, Parque Internacional La Amistad, Camino Pittier-Altamira, Dauphin 1650 (GOET, INB); Monteverde, James s. n., 31 (US), Monteverde Biological Reserve, Gradstein 9480, 9486, 9506, 9553 (GOET); Osa Peninsula, Centro Boscosa, Gradstein & Dauphin 9336, (GOET), 9346 (GOET, USJ). **San José** Atirro Esperanza?, Maas s. n. (GOET, U); Moravia, Bajo de la Hondura, Standley & Valerio 51842 (US), La Palma, Maas 844h (GOET, U), Standley 37971 (US).

PANAMA. **Canal Zone:** Summit Experimental Garden near Gamboa, Welch 20057, 20153, 20174(NY); Tank Farm area or Gamboa Forest Preserve, N of Gamboa, Welch 20114 (NY). **Chiriquí:** Fortuna, Hornitos, Camino en la Quijada del Diablo hacia el Río Chiriquí Viejo y la quebrada en el camino, Salazar *et al.* 6287 (GOET, U); Santa Marta, Bugaba, Vinda 1517 (NY). **Cocle:** La Mesa, el Valle de Anton, Salazar & Beliz 1379 (NY). **Darién:** Cerro Pirre, Salazar & Gradstein 9246, 9277 (GOET, U); Cerro Sapo, NE slope, approach from Garachiné, Hammel 7249 (GOET, U). **Panama:** Cerro Jefe, Salazar & Gradstein 9405 (GOET, U), behind Intel tower northwards, Salazar & Chung 5205 (GOET, U). **Without locality,** Rottenberg 3 (GOET).

CUBA. **Baracoa:** El Yunque, Underwood & Earle 1275 (NY). **Guantánamo:** Baracoa, Quibijau, Mustelier *et al.* 15000 (HABE). **Moa Holguín:** Reserva Jaguaní, Río Anacleto, Boshidi, Muñiz & Vazquez 5902 (HABE). **Santiago de Cuba:** Gran Piedra, bosque cerca de la cima, Pócs & Reyes 9046/w (HABE); Sierra Cristal, Arroyo Narezano, Mustelier & Vicario 13553 (HABE). **Without locality,** Wright s. n. (BM), s. n. (US).

JAMAICA. **St. Andrew Parish:** Blue Mts., Hardwar Gap. Griffin III 58, s. n. (GOET, U), trail to Mt. Horeb, SE of Hardwar Gap. Gradstein 6325 (GOET, U). **St. Thomas:** N of Bowden Pen, Griffin III s. n. (GOET, U). **Without locality:** the type. Schwarz s. n. (BM). Crownlands, 6.5 km W of Troy Maxon 2909, 2917 (US), Wilas s. n. (NY).

HAITI. Haut Piton ridge, near Bassin Bleu, Leonard & Leonard 15179a, 15180a (GOET, U); Saint Louis du Nord, Summit SW of City, Leonard & Leonard 14499 (GOET, U).

DOMINICAN REPUBLIC. **La Vega:** 10 km W carretera Duarte, camino Janico a el Río y Constanza, cerca del Salto, Zanoní *et al.* 17493 (NY). **Pacificador:** San Francisco de Macorís, Abbott 2104 (US).

PUERTO RICO. **Luquillo:** El Yunque-Luquillo trail, Griffin III s. n. (GOET, U); Caribbean National Forest, along trail from Hwy 186 to top of el Toro, 5,4 mi. south of el Verde Biological Station, Reese 14361 (NY), trail from Hwy 186, 3 km S of entrance to El Verde Biological Station, Reese 14875 (NY); Mt. El Toro, W side, along train from road 168 to summit, Gradstein 6541, 6547 (GOET, U); Catalina-El Yunque trail, Britton *et al.* 7738 (US); East Peak Reserve. D'Arcy s. n. (GOET, U); Luquillo Forest Reserve. Griffin III s. n. (GOET, U); National Forest along road 191, just N of el Yunque Recreation Area, Buck 3492 (NY), type of *Ceratolejeunea valida* Evans. **Maricao:** Without locality, Díaz-Piferrer 168a (US). **Toro Negro:** State Forest, Griffin III s. n. (GOET, U). **Without locality:** type of *Ceratolejeunea schwaneckeii* Steph. Schwanecke s. n. (BM, G). Type of *Ceratolejeunea sintenisii* Steph. Sintenis s. n. (BM). **Without province:** Altuado, River Bank Britton *et al.* 869 (NY); Cerro de Las Pinas, near Las Cruces, Britton *et al.* 6910 (US); Mountain between Guayama and Carey, Britton *et al.* 6608 (US).

GUADELOUPE. **Basse-Terre:** road St. Claude to volcan La Soufrière, Gradstein 6568, 6569, 6571 (GOET, U), Savane des Malets, Gradstein 6590 (GOET, U). **Without locality:** L'Herminier s. n. (US).

DOMINICA. Morne Trois Pitons, N slope, E of Pont Cassé, Schuster 67510 (US). **St. George Parish:** Fresh water Lake, Gradstein 6639, 6675 (GOET, U). **Without locality:** type of *Ceratolejeunea diversiloba* Steph., type of *Ceratolejeunea fuscata* Steph.

MARTINIQUE. Deux Choux, Duss 659 (NY). Gourbeyre (Les Palmistes), Duss 300, 486 (NY). Piton Gelé. Duss 384 (NY). Without locality: Duss s. n. (G); type of *Ceratolejeunea latiflora* Steph.

SAINT KITTS. Type of *Ceratolejeunea variabilis* (Lindenb.) Schiffn. Breutel s. n. (B, BM, G, NY, S, W)

SAINT LUCIA. Morne Fontane King s. n. (NY).

COLOMBIA: **Amazonas:** near Rio Caqueta (Isla Mariñame), Wolf 1497 (GOET); Villazul, E of Araracuara, Isla Mariñame in river Caquetá, Sipman & Duivenvoorden 28155 (GOET, U). **Boyaca:** Camino La Ceiba-La Casirva (Sácama-Llanos Orientales), Hammen & Jaramillo 1724 (GOET, U); road Sogamoso-Pajarito, Valle del Río Cusiana Hammen & Jaramillo 1631 (GOET, U). **Caqueta:** 2.5 km NE of Araracuara. Sipman & Duivenvoorden 28071 (GOET, U), Peneya Satomi 1 (GOET, U). **Casanare:** Sácama, camino a la quebrada Maneque, Aguirre *et al.* 3046, 3122 (GOET, U), camino a la vereda "Africa", Aguirre *et al.* 2491, 2948, 2949, 3012 (GOET, U).. **Chocó:** Isla Gorgona, Gradstein s. n. (GOET); Bahía Tebada, N of Bahía Solano, Wolf 1636 (GOET); Cartegui, road Tabó-Quibdo, ca. 7 km N of Asimas, S of Cergui, Gradstein 8762 (GOET, U); Nuquí, amargal at the Pacific Coast SW of Arusi, Gradstein 8804, 8880, 8881, 8892 (GOET, U); near Quibdo, Bischler 180 (GOET, U), Rio Atrato, Bischler 159 (GOET, U), road Quibdo-Bolívar, 36 km from Quibdo, Bischler 135 (GOET, U), 48 km from Quibdo, Bischler 219 (GOET, U), 54 km from Quibdo, Bischler 217 (GOET, U); road Santa Cecilia-Tadó, 40 km W of St. Cecilia, Gradstein 8759 (GOET, U); Tutunendo, Bischler 127 (GOET, U), Road Tutunendo-El Carmen, shortly W of point 20, Gradstein 8954, 8959a, 8961, 9005 (GOET, U). **Cundinamarca:** road Alban-Sasaima, Finca Cataluna, Hammen & Jaramillo 2149 (GOET, U). **Meta:** Río Guayabero, 10 km S Caño Lozada, Bischler 1586, 1593, 1599, 1636 (GOET, U); Uribe, Fosberg 19460a (US); Villavicencio, forest of S. A. Bavaria, N of town, near Rio Guaitiquia. Linares *et al.* 155 (GOET, U). **Nariño:** Cuyambe, between Altaquer and Junín, Idobro & Kyburz 2337 (GOET, U). **Putumayo:** ca. 15 km NW of Puerto Asís, Merrill-King & Guevara c1075 (US). **Risaralda:** Pueblo Rico, Cerro Montezuma, Wolf 1591 (GOET), W side of Cordillera Occidental, Tatama, camino al lado del Río

Negro, Wolf & Zagt 1512 (GOET); W side of Cordillera Occidental, along trail from Jeguadas to Puerto de Oro, W of Mistrato, Gradstein 8436a, 8492, 8553, 8604, 8606 (GOET, U). **Santander del Norte:** Catatumbo, Campo Oro y alrededores, Bischler 2412 (GOET, U). **Sarare?:** Santa Librada, Bischler 2011 (GOET, U). **Valle:** Buenaventura, Bischler 122 (GOET, U), Pacific coast, type of *Ceratolejeunea litoralis* Herz., Río Caluma, Est. Agroforestal Bajo Calima, Cuatrecasas & Willard 26019b (US), Quebrada López, Cuatrecasas & Willard 26031a (US); Cordillera Occidental, W slope, Hoya del Río Digua, Quebrada del San Juan, Cuatrecasas 23834b (US); road Cali-Buenaventura, 43 km from Buenaventura, Bischler 473 (GOET, U), 49 km from Buenaventura, Bischler 449 (GOET, U), 55 km from Buenaventura, Bischler 306 (GOET, U). **Vaupés:** Río Kananarí (affluent of Río Isibukurí), Evans Schultes & Cabrera 13254 (NY). **Without locality:** Schlim (hb Mitten) s. n. (NY).

VENEZUELA. **Amazonas:** ca. 4 km up Casiquiare from mouth on Río Negro, Liesner 3955 (GOET, U); San Carlos de Río Negro, 20 km from joint Río Negro & Casiquiare, Delascio *et al.* 9453a (GOET, U); Sierra Parima, near Simarawochi, Río Matacuni, Steyermark 107141 (GOET, U). **Apure:** Páez, Selva de Cutufí, between Cutufí on Río Cutufí & Río Samare, Davidse & González 21919 (GOET, U). **Aragua:** Rancho Grande (H. Pittier National Park), Ojasti s. n. (GOET, U). **Bolívar:** Meseta del Jaua, Cerro Sarisariñama, Brewer-Carias s. n. (US), Steyermark *et al.* 109112 (US); Quebrada El Jaspe (Río Cacao), 47 km N of St. Elena Steyermark & Dunsterville 112380 (US); Río Caura, arriba del Salto Para, islas 2-3 km arriba del campamento Las Pavas, Steyermark & Dunsterville 112975 (US). **Carabobo:** sur de Borburrata, Steyermark 95296 (US). **Falcon:** Cerro Santa Ana, Steyermark & Braun 94547 (US); Península de Paraguaná, Cerro Santa Ana, above Santa Ana, top of E ridge, Wingfield 13360a (GOET, U). **Lara:** Cuenca del Río Guyamure, upon Río Clara town, Griffin III *et al.* 238 (GOET, U). **Miranda:** Cerros del Bachiller, Quebrada Corozal, S of Caño Rico & Bachiller, 11 km SSE of el Guapo, Steyermark & Davidse 116609 (GOET, U), S of Santa Cruz Steyermark & Davidse 116715 116816 (GOET, U). **Río Negro:** along mouth of Cañón Grande, vicinity of Neblina Base Camp, along Río Mawarinuma, Halling 4137 (NY). **Sucre:** Paria Peninsula, Cerro de Humo, between Laguna and Roma, NW from Irapa, Steyermark 95117 (GOET, U), NW of Irapa, entre Roma y Santa Isabel, 12 km N of Río Grande Arriba, Steyermark 94943, 95103(US), 14 km N from Río Grande Arriba, Steyermark 94864 (US), Cerro de Río Arriba, Afluentes de Río St. Isabel, Steyermark & Rabe 96280 (US). **Yaracuy:** 7-11 km N of Salom, Nirgua, el Amparo, Steyermark & Caraño 111444 (US)

TRINIDAD. Caroni North Bank Road, Britton *et al.* 852 (NY, US). Trinidad North Range, Welch 21231 (NY) **Without locality:** Crüger s. n. (W).

GUYANA. **Potaro-Siparuni:** Mabura Hill, 180 km SSE of Georgetown, Cornelissen 45 (GOET, U), Cornelissen & ter Steege 786 (GOET, U); Paramakatoi, Pora Mt., 3km SW of village, Newton *et al.* 3515 (GOET, U); Bassin of Essequibo River, near mouth of Onoro creek. Smith 2747 (NY). **Upper Mazaruni:** ca. 1.6 Km below Kamarang, Robinson 85-0026 (US), 85-0105 (NY, US), Mt. Latipu, ca. 8Km N of Kamarang, Gradstein 5656 (GOET); Makwaima savannah near Mayoripa, Kako river, Gradstein 4979 (GOET, U). **Without locality:** Ekloni s. n.(W), without collector, s. n. (W), (hb Montagne) s. n. (NY).

SURINAM. **Nickerie:** area of Kabaledo Dam project, line E from road km 80, Bekker 1358b, 1476 (GOET, U), near camp road km 212, Bekker 1732c (GOET, U). **Paramaribo:** Kegel s. n. (W). **Without locality:** Lanjouw 831 (NY); type of *Ceratolejeunea splitgerberiana*(Mont.) Steph.

FRENCH GUIANA. **Cayenne:** Montagne de Kaw, 2 km SE of Camp Caiman, Cornelissen & ter Steege 252 (GOET, U), Mt. Serpent, type of *Ceratolejeunea involvens* (Nees & Mont.) Steph. **Kourou:** Mt. des Singes, Sentier

Botanique, Gradstein 6271 (GOET). **Saül:** 2 km SW of town, "Sentier Limonade", Montfoort & Ek 448 (GOET, U); Piste de Carbet Mais, Kruijt, Sipmann & Zimmer 22 (GOET, U).

ECUADOR. **Esmeraldas:** 2-4 km SE of San Lorenzo, along railroad track. Boom 2572 (NY), ca. 5km on the main road, Dauphin 2686, 2687, 2693(GOET, USJ, QCNE), Dauphin 2692, 2696 (GOET, USJ), near the town of El Calderon, Dauphin 2723, 2726, 2728(GOET, USJ), Dauphin 2727 (GOET, USJ, QCNE), Alto Tambo, down hill after Lita, Dauphin 2700 (GOET, USJ, QCNE), 2701, 2703, 2705, 2710, 2711, 2715 2716, 2720 (GOET, USJ). **Galapagos:** San Cristóbal, El Progreso, Gradstein & Lanier H328b (GOET, U), gorge W of El Junco, Gradstein & Lanier H272, H281 (GOET, U), river valley SW of El Junco, Gradstein & Lanier H311 (GOET, U); Santa Cruz, around Media Luna, Gradstein & Weber H86 (GOET, U), H111 (GOET, NY, U), Howell 248 (GOET ex CAS), behind Schiess farm, van der Werff 2227, 2234 (GOET, U), El Junco area, van der Werff 2213 (GOET, U). **Los Ríos:** Bosque Protector Samama, Hacienda Clementina Dauphin, Gradstein, Sipman *et al.* s. n., 2731, 2737, 2741, 2745, 2750 (GOET, USJ); 2751 (GOET, QCNE, USJ); Palenque biological Station, Dauphin, Gradstein, Sipman *et al.* 2759 (GOET, USJ), Gradstein, Frahm & Mues 6960, 6966 (GOET, U). **Napo:** Bosque Selva Viva, road Campo Cocha-Chonta Punta, Dauphin, Núñez & Tapuy 2672 (GOET, USJ, QCNE), 2673, 2675, 2676, 2678(GOET, USJ); Jatun Sacha Biological Station, S margin of Napo River, Dauphin 2665, 2668, 2670, 2671, 2679 (GOET, USJ), Dauphin 2666, 2667, 2681(GOET, USJ, QCNE); near Santa Clara, between Puyo and Puerto Napo, Steere E-81 (NY); Tena, Chambira de Tena, Dauphin 2661 (GOET, USJ, QCNE). **Pichincha:** Minde, Gradstein *et al.* 9902 (GOET); Without locality, Jameson s. n. (NY). **Without department:** type of *Ceratolejeunea andicola* Steph.; Canelos, type of *Ceratolejeunea microrhegma* (Spruce) Steph.; Chimborazo: Spruce s. n. (MANCH). **Without locality:** Hot country near the coast, W base of the Andes, Jameson s. n. (NY).

PERU: **Loreto:** Maynas, Timme 14297 (GOET); Las Amazonas, between Rio Napo and Amazonas, Timme 4894 (NY). **Without department:** Tatanara, type of *Ceratolejeunea peruwiana* Steph.; St. Gavan, type of *Ceratolejeunea brevicornuta* Steph., Lechler s. n. (NY). **Without locality:** Haecker s. n. (G); type of *Ceratolejeunea bullatiloba* Steph.

BRAZIL. **Amazonas:** Cachoeira, Igarapé Foibará, Schuster 79-21-1096 (NY); along Rio Marié, Manauná. Buck 2379 (GOET, U); Manaus, Reserva Campina, Vital *et al.* 3724, 3930 (GOET, U), Tarumã, Vital *et al.* 3926 (GOET, U), Manaus-Caracarai road, km 12, Prance *et al.* 11367 (GOET, NY), 11368 (NY, U), km 45, Prance *et al.* 11375, 11389 (NY), km 60, Griffin III *et al.* 560, 981(GOET, U), km 60, ca. 4 km on W side, Vital *et al.* 4560 (GOET, U), km 61, Vital *et al.*, 3725 (GOET, U), km 115, along Rio Urubu, Vital *et al.* 4525 (GOET, U), km 130, along Rio Lages, Griffin III *et al.* 741 (GOET, U), km 130, near Igarapé, Vital *et al.* 4341 (GOET, U); along road to Balbina hydroelectric dam project from Manaus-Caracarai Road (BR-174), Buck 2736 (GOET, NY, U, US); along the road Manaus-Itacoatiara, km 12, Vital *et al.* 3518 (GOET, U), km 26, Ducke Forest Preserve Vital *et al.* 3869, 3898 3903, (GOET, U), km 30, Estação Agrícola (CEPLAC), Vital *et al.* 3836 (GOET, U); Maurés, Nelson 86 ,88 (NY), between Manaus and São Gabriel, along the shores of the Rio Curicuriari and Igarapé Branco, Buck 2536 (GOET, U, US), 2546 (NY); San Carlos, Spruce s. n. (MANCH); São Gabriel, type of *Ceratolejeunea megalophysa* (Spruce) Steph., Spruce s. n.(MANCH), s. n. (NY), s. n. (NY); NW of São Gabriel, near mouth of Rio Uaupés. Schuster 79-20-1061, 79-20-1064, 79-20-1079, 79-20-1081 (NY), along Rio Curicuriari near mouth of the Rio Cariva, Schuster 79-17-886 (NY), along the Rio Negro, just downstream from junction with the Rio Uaupés, NW of São Gabriel, Buck 2607 (NY), „Flumen Uaupés“, Spruce L328 (MANCH); Rio Negro, type of *Ceratolejeunea rionegrensis* Steph., type of *Ceratolejeunea spruceana*

Zwickel, type of *Lejeunea* (*Ceratolejeunea*) *variabilis* Lindenb. var. *subserrata* Spruce, Spruce s. n. (BM, G), s. n. (BM, G, US), s. n. (MANCH, G), 1568 (MANCH), s. n. (NY), along Rio Cauburi between Rio Negro and Cachoeira do Carangueijo, Schuster 79-10-278, 79-10-280, 79-10-282 (NY), along Rio Negro at high water, ca. 100 km NW of Manaus at Paran Conceio and P. Tauat, Buck 2158a (NY), along Rio Negro, just E of Santa Isabel, Buck 2263 (GOET, U, US), Rio Negro between Ilha da Silva & Tapuruguaa Rocky river Island, Prance *et al.* 11526a (NY), Ilha Acarabo, in the Rio Negro at the mouth of the rio Mari, Buck 2355 (NY), Cataractas Rio Negro, Spruce s. n. (NY), s. n. (US), type of *Ceratolejeunea rionegrensis* Steph., type of *Ceratolejeunea fuliginosa* (Spruce) Steph., Rio Negro et Uaups, Spruce s. n. (NY); Rio Paracuari, tributary of Rio Maus-Acu at Agua Mineral, Hill 13108 (US); Without locality, type of *Ceratolejeunea martiana* (Gottsche) Steph., Spruce s. n. (NY). **Par:** Caripi, Spruce s. n. (NY), type of *Ceratolejeunea maritima* (Spruce) Steph., type of *Lejeunea* (*Ceratolejeunea*) *variabilis* Lindenb. var. *saproxylophila* Spruce, Gurupa, Antonio Lemosipagos. Ltzelberg 150 (GOET, U, US); Serra do Cachimbo, Serra Maze & Vicinity, Km 1223 N of Cuiab, along Cuiab-Santarn highway (BR163), Reese 16818 (NY); type of *Ceratolejeunea hylophila* (Spruce) Steph. **Paran:** Adrianapolis, Vital 2820 (GOET, U). **Rondnia:** 2-4 km above the first rapids of the Rio Pacaas Novos. Reese 13310, 13447 (NY); New Vilhena-Colorado road km 20, 13 km N of Vilhena on BR-364, Nelson 359 (NY). **Sao Paulo:** Canancia, Ilha do Cardoso, ca. 1,5 km S of main house of base, Vital 7051 (GOET, U), N side of Cardoso Island Vital 3149, (GOET, U), Praia don Pontal, Ilha Comprida, Vital 5057 (GOET, U); Itapetinga, Schiffner 4272 (NY, US); Rio Branco near Santos, Schiffner 4380 (BM, G, G, PC, S, US); Santos, Rio Branco. Schiffner s. n. (W); Ubatuba, ca. 2 km NW of town, Vital 4751 (GOET, U). **Without department:** Campana, Spruce s. n. (NY), at base of Mt. Cocui. Spruce s. n. (NY)

BOLIVIA: **Beni:** 10-15 Km NW of Guayamern, along the road to Cachuela Esperanza, Reese 12920, 13108 (NY), NW of town, Reese 13124 (NY); Ballivian, Serrana del Pilon Lajas, Gradstein 7193, 7200, 7208, 7210, 7211, 7257, 7272, 7286, 7169, 7914 (GOET, U), Gradstein *et al.* 9952 (GOET, LPB); NW of Yocumo, Gradstein 9948, 9953 (GOET). **Cochabamba:** Chapare, road Cochabamba-Villa Tunari, km 112, Gradstein 7497, 7597 (GOET, U), Gradstein & Lewis 7564 (GOET, U); El Limbo, old road to El Palmar, Dauphin 2806, 2808, 2809, 2810, 2811 (GOET, USJ), Dauphin, Aranibar & Rojas 2818, 2819, 2821, 2824 (GOET, USJ); Parque N.Carrasco, Cachi Mayu River, Dauphin 2799, 2801, 2802, 2803, 2804, 2805 (GOET, USJ); Villa Tunari, Parque Macha. Dauphin 2771, 2779 (GOET, USJ). **La Paz:** road Caravani-San Borja, 30-40 km beyond Caravani, Gradstein 7082 (GOET, U).

Ceratolejeunea cornuta shows usually one solitary or 2 isolated basal ocelli, a small lobule 0.2 the leaf lobe length, orbicular to reniform underleaves, and a perianth with four developed horns. Branches with series of inflated lobules are also common. This species tends to vary in all mentioned characters. The variation of the underleaf size and shape is very striking: when the plants grow in thick mats or even turfs they may be small, ovate, the base without lobes, about the width of the stem; when the plants grow more robust, the underleaves become larger, reniform, the base cordate with rounded lobes and up to 6 times the stem width. Lucking (1995) described this variation on a single stem growing first on bark and then accidentally on a leaf.

Forms with small underleaves are likely to be confused with *C. cubensis* (Mont.) Schiffn. Both can be separated by the ocelli in *C. cubensis*, which are usually in contiguous, basal pairs, in contrast with the single or two, usually isolated ocelli in *C. cornuta*. The presence of series of spherical lobules in some branches definitely separate *C. cornuta* from *C. cubensis* which lacks them. In presence of fresh material, the smooth, septate oil-bodies allow to separate material from *C. cornuta* from that of *C. cubensis* which has botryoidal oil-bodies.

Some specimens of very wet regions develop some leaves with more basal and almost suprabaasal ocelli as seen in the type of *C. multiocellata* Herz. Even in that specimen, most of the leaves have one single or two isolated ocelli.

Middle and high elevation corticolous or epiphyllous, robust forms, producing flagelliferous branches with dentate leaves, lacinate gynoecial bracts and long, slender perianth horns, have been described as *Ceratolejeunea filaria* (Taylor) Steph., *C. spinosa* var. *flagelliformis* Steph., *C. furcata* Steph., *C. sacculosa* Herz. and more recently as *C. flagelliformis* Steph. ex Fulford. The above cited characters besides a „long, slender, curved apical tooth of the lobule“ as well as the absence of inflated lobuli, have been used to separate those forms into different taxa (Fulford 1945). Flagelliferous branches lack in some specimens cited by Fulford under *C. flagelliformis*, and the length of the apical lobule tooth is variable even in the type material of the species. The length of the horns is always variable from colony to colony, and even in the same plant. A combination of flagelliferous branches and secondary branches bearing utriculi and a series of spherical lobuli is found in the type of *C. sacculosa* Herz. Stephani (1913, p. 413) describes the occurrence of laminar ocelli on flagelliferous branches of this growth form. Some cells of the lamina show irregular patterns of thickening on the cell walls, and may appear darker than other cells. I have not been able to identify them as ocelli, fresh material is needed to determine the cell contents.

A transition form between robust and weaker specimens of *Ceratolejeunea cornuta* is represented by the type material of *C. valida* Evans. As in many leaves of robust specimens, ocelli are lacking there. The branching pattern is also intermediary between the long, robust main stems with smaller lateral branches and the plumose form of epiphyllous specimens.

Ceratolejeunea cornuta is probably a pantropical taxon. Miller *et al.* (1983) reported it as *C. maritima* (Spruce) Steph. from Polynesia. Grolle (1995) reported *C. cornuta* (Lindenb.) Steph. from Madagascar and Reunion without certainty of its identity at species level. He also reported *C. variabilis* (Lindenb.) Schiffn. from this region.

6. *Ceratolejeunea cubensis* (Mont.) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 125. 1893; *Lejeunea cubensis* Mont., in Ramón de la Sagra, Hist. Phys. Pol. et Nat. Cuba: 481. 1842; *Colura cubensis* (Mont.) Trevis., Mem. Ist. Lomb. Sci. Mat. Nat., Ser. 3: 402. 1877. Type. Cuba. Without locality, „Ad cortices repentem Lejeuniae serpyllifoliae Radulaeque pallenti immixtam“, Auber s. n. (holotype, PC). Figure 16.

Ceratolejeunea commixta (Spruce) Steph., Sp. Hep. 5: 404. 1913; *Lejeunea* (*Cerato-Lejeunea*) *commixta* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 204. 1884. Type. Peru. Tarapoto, „in *Bryo-lejeunea fruticosa* Tayl. Repens, cum *L. plumula* Spruce mixta“, Spruce s. n. (holotype, MANCH; isotype, G), *syn. nov.*

Ceratolejeunea pyriformis (Steph.) Steph., Sp. Hep. 5: 435. 1913; *Lejeunea pyriformis* Steph., Hedwigia 29: 93. 1890. Type. Mexico. Zapacuam, Liebmann s. n. (hb Lindenb. 6781) (holotype, W), *syn. nov.*

Ceratolejeunea amazonica Steph., Sp. Hep. 5: 395. 1913; *Lejeunea amazonica* Steph., Hedwigia 29: 134. 1890, *nom. illeg.; non* Spruce 1884. Type. Surinam. Paramaribo, Kegel 530 (holotype, G; isotype, G), *syn. nov.*

Ceratolejeunea granatensis Steph., Sp. Hep. 5: 414. 1913. Type. Ecuador. Morona-Santiago: Gualaquiza, „ad truncum semiputridum“, Allioni s. n. (holotype, G), *syn. nov.*

Ceratolejeunea guadelupensis Steph., Sp. Hep. 5: 415. 1913. Type. Guadeloupe. Without locality, Duss. 511 (lectotype (Bonner 1953), G), *syn. nov.*

Ceratolejeunea mosenii Steph., Sp. Hep. 5: 428. 1913. Type. Brazil. Sao Paulo: Santos Sorrocaba, „ad arborem silvae primaevae“, Mosén s. n. (holotype, G; isotypes, G, S). (Fulford 1945, Schuster 1980).

Ceratolejeunea parisii Steph., Sp. Hep. 5: 429. 1913. Type. French Guiana. Maroni: Camp à la forestière, Michel s. n. (holotype, G), *syn. nov.*

Ceratolejeunea tenuicornuta Steph., Sp. Hep. 5: 444. 1913. Type. Brazil. Without locality. Ule 214 (holotype, G), *syn. nov.*

Plants autoicous or dioicous, light-green to dull-brown, stem with leaves 0.6-1.6 mm wide; sparsely to profusely branched. Stems in cross section 60-95 μm in diameter, medullary cells 9-17, ventral cells in surface rectangular, 25-45 x 25-65 μm , dorsal cells rectangular, 25-40 x 25-60 μm . Flagelliferous branches not seen. Leaves imbricate, lobe ovate, 280-440 x 400-590 μm , apex rounded to broadly acute, plane or incurved, margins entire, irregularly crenulate or with 1-6 teeth in the apical region, teeth 10-20 μm long; median leaf lobe cells isodiametrical to elliptical, 10-25 x 10-35 μm , marginal cells quadrate to rectangular, 10-20 x 15-25 μm , cell walls regularly thickened, intermediate thickenings frequent; oil-bodies botryoidal, elliptical, 2-3 (-6) per cell; ocelli, 25-35 x 20-60 μm , basal or geminate; lobules inflated or reduced, 0.2-0.4 the leaf lobe length, free margin plane or slightly involute, apical tooth unicellular, short, hyaline papilla bulging. Utriculi absent, single or in pairs at the base of lateral branches. Underleaves ovate, usually slightly longer than broad, 130-350 x 140-350 μm , bifid to $\frac{1}{2}$, lobes acute, ending in a 1-2 celled tip, margins entire or crenulate, rarely with one or two unicellular teeth, plane or rarely recurved. Vegetative regeneration from leaf lobe cells reported by Fulford (1944b).

Androecia lateral on main branches, terminal or intercalary on secondary branches, in spikes of 3-5 (-8) bracts pairs, 530-680 (-1500) μm long; bracteole ovate, 90-175 x 105-175 μm , bifid to $\frac{1}{2}$, 1-2 per spike.

Gynoecia on lateral branches with one, rarely two sterile or repeatedly fertile innovations; bracts obovate, 470-500 x 830-900 μm , margins entire to serrate distally, with up to 7 geminate ocelli on the central lower part; bracteole ovate to orbicular, 275-580 x 400-770, bifid to $\frac{1}{2}$, entire to dentate distally, teeth to 50 μm long, rarely with up to 3 basal ocelli.

Perianth, obconic, 360-600 x 480-930 μm , with four horns (rarely five (Schuster 79-2-34 (NY)), 60-140 x 70-180 μm , slender or inflated.

Spores irregularly shaped, mostly rectangular, 20-25 x 50-60 μm , brown, papillose-tuberculate, with 10-12 rosettes.

Illustrations. Schuster 1980, p. 920, 923.

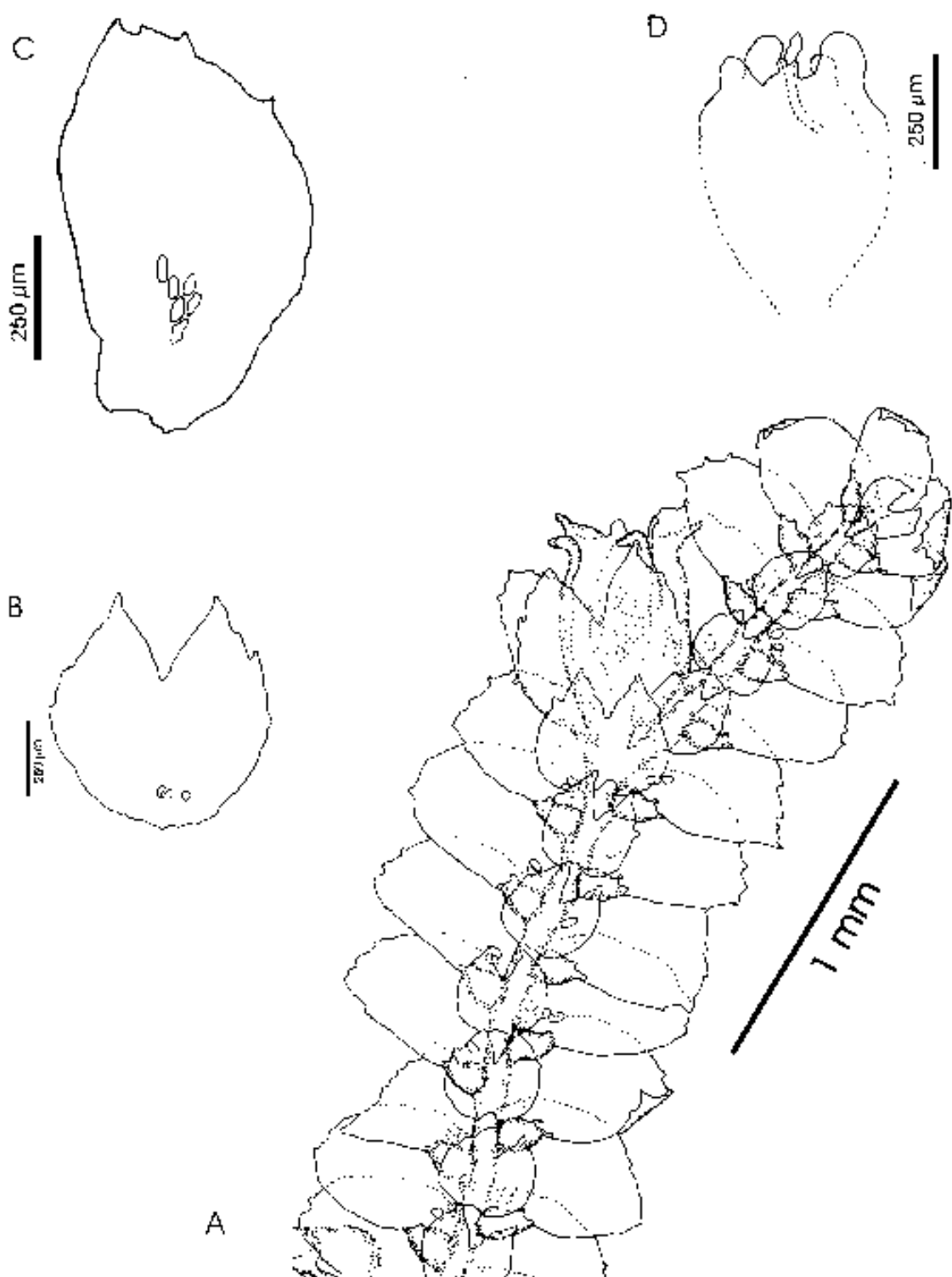


Figure 16. *Ceratolycium cubensis* (Spruce) Schiffn. A. Habit and perianth. B. Bracteole. C. Perianth bract lobe. D. Perianth. From Brazil, Ule 214 (A-C), Mosén s. n. (D).

Distribution. Widespread in tropical America. Apparently common only in Central America, the Caribbean, Chocó and the Amazonian basin, its spreading from Southeastern North America to Southeastern Brazil. *Ceratolejeunea cubensis* grows in canopies or open places of primary and old secondary growth vegetation in wet forest and seasonal forest areas, up to lower montane areas from 0-1200 (-1900) m altitude. Corticolous, frequently mixed with *Ceratolejeunea cornuta*, tending to be more frequent than the latter in dryer habitats.

Specimens examined. UNITED STATES. **Florida:** Camp Longview, Homestead trail, Small & Wilson 1527 (NY), about Silver Palm School, Small 2349 (NY); Highland Hammock State Park, Griffin III 991 (GOET, U); Miami, Small s. n. (GOET, U); Sanford, Rapp 362 (GOET, U).

MEXICO. **Without department:** type of *Ceratolejeunea pyriformis* Steph..

COSTA RICA. **Heredia:** San Isidro, Yerba Buena, Standley & Valerio 50010 (JE); Sarapiquí, La Selva Biological Station, Bernecker-Lücking 97-11 (hb Bernecker-Lücking). **Limón:** Braulio Carrillo National Park, Quebrada Gónzales, Bernecker-Lücking 92-578 (hb Bernecker-Lücking). **Puntarenas:** Isla de Cocos, Serranías NE, Dauphin 1106 (GOET, USJ).

PANAMA. Canal Zone: Barro Colorado Island, Salazar & Gradstein 15142 (GOET); Summit Experimental Garden near Gamboa, Welch 20160, 20166 (NY), Tank Farm area or Gamboa Forest Preserve, N of Gamboa, Welch 20066 (NY). **Darién:** base of Cerro Pirre, Estación de INRENARE, Salazar & Gradstein 9212 (GOET, U). **Panamá:** Sabanas near Chepo, Hunter & Allen s. n. (US).

BAHAMAS. **Oppice:** Northern Section, near Nicholl's Town, Small & Carter 8925a (NY).

CUBA. **Baracoa:** El Yunque, Underwood & Earle 915 (NY). **Isla de Pinos:** Britton *et al.* 14780 (NY); Cerros de San Juan, Britton *et al.* 14984 (NY). **Without locality:** the type; Wright s. n. (US).

JAMAICA. Bath, Evans 346 (NY, US). **Portland Parish:** John Crow Mts., SW of Ecclesdown, Welch, 17546, 17639a (NY). **St. Thomas:** N of Bowden Pen, Griffin III s. n. (GOET, U).

PUERTO RICO. Luquillo Mts.: N slope, Heller 5 (US). Mt. between Guayma and Carey, Britton *et al.* 6598 (US).

GUADELOUPE. **Basse-Terre:** road St. Claude to volcan La Soufrière, Gradstein 6579 (GOET, U).

Without locality: type of *Ceratolejeunea guadelupensis* Steph.

COLOMBIA. **Chocó:** Cartegui, road Tadó-Quibdo, ca. 7 km N of Asimas, S of Cartequi, Gradstein 8767 (GOET, U); Nuqui, amargal at the Pacific Coast SW of Arusi, Gradstein 8801, 8832, 8850, 8857, 8860, 8871, 8872, 8878 (GOET, U); road Santa Cecilia-Tadó, 40 km W of St. Cecilia, Gradstein, 8714, 8756 (GOET, U).

Risaralda: W side of Cordillera Occidental, above Jeguadas, W of Mistrato, Gradstein 8606, 8613 (GOET, U). Valle: Pacific coast, Rio Calima, Quebrada de López, Cuatrecasas & Willard 26031b (US).

VENEZUELA. **Sucre:** Península de Paria, Cerrto Patao, N of Puerto de Hierro, Steyermark & Agostini 910005 (US).

TRINIDAD. Mt. Tocuche, Britton *et al.* 1463 (US). **Without locality:** Fendler s. n. (NY).

SURINAM. **Nickerie:** area of Kabaledo Dam project, line opposite cam road km 212, Bekker 1651, 1681d (GOET, U). **Wanica:** Paramaribo, Kegel 530 (G).

FRENCH GUIANA. **Maroni:** type of *Ceratolejeunea parisii* Steph.

ECUADOR. **Esmeraldas:** San Lorenzo, Alto Tambo, Dauphin 2708-a (GOET, USJ); ca. 5km on the main road from San Lorenzo, Dauphin 2690, 2694(GOET, USJ), near the town of El Calderon, Dauphin 2725 (GOET, USJ). **Los Ríos:** Bosque Protector Samama, Hacienda Clementina, Dauphin, Gradstein, Sipman *et al.* 2729, 2733 2735, 2739, 2744, (GOET, USJ), 2752, 2753, 2754 (GOET, USJ, QCNE). **Morona-Santiago:** Gualaquiza, Allioni s. n. (G). **Napo:** Bosque Selva Viva, road Campo Cocha-Chonta Punta, Dauphin, Núñez & Tapuy 2677 (GOET, USJ); Jatun Sacha Biological Station, S margin of Napo River, Dauphin 2669, 2680, 2689, (GOET, USJ).

PERU. **Loreto:** Maynas, Explorama lodge on the quebrada Yanomono east of Indiana, Timme & Castner 14273 (GOET), Las Amazonas, between Rio Napo and Amazonas, Timme 4855(NY). **San Martín:** Lamas, road Yurimaguas-Tarapoto, km 107, Frahm *et al.* 1400 (GOET, U), km 112, Frahm *et al.* 1788 (GOET, U); Tarapoto, type of *Ceratolejeunea commixta* (Spruce) Steph.

BRAZIL. **Acre:** sena Madureira, Nelson 557 (NY). **Amazonas:** Acãnga, across from Ilha do Japó, Schuster 79-3-57a (NY); along the road Manaus-Itacoatiara, km 26, Ducke Forest Preserve, Vital *et al.* 3905 (GOET, U), km 30, Estação Agrícola (CEPLAC), Vital *et al.* 3843 (GOET, U), km 65, Egler Reserve, Griffin III *et al.* 503 (GOET, U); Manaus-Caracarai road, km 60, Griffin III *et al.* 11, 572 (GOET, U), Vital *et al.* 3705 (GOET, U), Prance *et al.* 18729 (NY); Morro dos seis Lagos, ca. 80 km N of São Gabriel, Schuster 79-19-993 (NY); Manaus, Spruce s. n., (US); Rio Negro & Uaupés, Spruce s. n. (US). **Pará:** Belem, Reserva Mocambo, Lisboa 661b (GOET, U). **Paraíba:** Areal, Vital 5426 (GOET, U). **Rio de Janeiro:** Silva Jardim, Poço das Antas Biological Reserve, Costa *et al.* 2067 (GOET); **Sao Paulo:** Rio Branco near Santos, Schiffner 4380pp (US); Santos Sorrocaba, type of *Ceratolejeunea mosenii* Steph. **Without locality:** type of *Ceratolejeunea tenuicornuta* Steph.

BOLIVIA. **Beni:** Ballivian, Serranía del Pilon Lajas, Gradstein 7126 (GOET, U). **Cochabamba:** Chapare, road Cochabamba-Villa Tunari km 135, Gradstein 7528 (GOET, U); Villa Tunari, Parque Machía Dauphin 2778, 2781 (GOET, USJ). **La Paz:** Hills on W side of the town of Mapiri, Dauphin 2862 (GOET, USJ). **Santa Cruz:** Ichilo, 15 km SSE of Buenavista, Estancia San Rafael de Amboró, Gradstein 7732 (GOET, U).

Ceratolejeunea cubensis varies especially in the degree of dentation of the leaf apices, the development and form of the perianth, the number and disposition of the basal or geminate ocelli and the size of the underleaves. For the distinction from *Ceratolejeunea cornuta*, see under the latter.

The variation of the perianth horns in this species deserves special attention, for it has erroneously lead to the description of various taxa, *e. g.* *C. mosenii*, on the basis of the more or less bulbous horns, sometimes becoming almost flaps (*e. g.* Dauphin *et al.* 96-36 (USJ)), and *C. pyriformis* (Steph.) Steph., based on the weak developed horns. The variation of the horn development must be checked carefully in each sample.

7. *Ceratolejeunea dentistipula* Gottsche ex Steph., Sp. Hep. 5: 407. 1913. Type. Cuba. Without locality, Wright s. n. (holotype, G). Figure 17.

Plants autoicous, brown, creeping, stems to 4.5 cm long, with leaves 0.8-1.8 mm wide; with frequent short lateral branches from a main stem. Stems in cross section 80-145 μm in diameter, medullary cells 20-25, cells thick walls, walls ca. 10 μm thick, ventral cells in surface quadrate to rectangular, 30-60 x 30-80 μm , dorsal cells quadrate to rectangular, 40-50 x 30-65 μm . Flagelliferous branches not seen. Stem leaves imbricate, lobe ovate to ovate-ligulate, 450-640 x 510-820 μm , antical margin crenulate or toothed throughout, teeth mostly unicellular, 8-22 per leaf, 5-20 μm long, leaf apex rounded; median leaf lobe cells isodiametrical to elliptical, 15-30 x 20-45 μm ; marginal cells 5-25 x 20-30 μm ; walls regularly thickened, with frequent intermediary thickenings; oil-bodies not seen; ocelli 30-40 x 40-60 μm , moniliate, (2-) 4-6 per leaf, row 115-305 μm long; lobules inflated, 0.2-0.3 the leaf lobe length, free margin involute, apical tooth short, spherical and reduced lobules not seen. Utriculi in pairs at the base of lateral branches. Underleaves ovate to ovate-lanceolate, 250-430 x 290-450 μm , bifid to $\frac{1}{2}$, lobes acute to short-acuminate, ending in a one or two-celled tip, margins crenulate or with 1-2 teeth on both sides. Androecia lateral on main branches, in spikes of 1-3 bract pairs; spikes 250-400 μm long; bract bifid, 85 x 115 μm . Gynoecia on lateral branches with one sterile innovation; bracts obovate, 300 x 475 μm , apex dentate; bracteoles ovate, 325-340 x 430-550 μm , bifid $\frac{1}{4}$ to $\frac{1}{2}$, lobes long acuminate, ending in a 2-3 celled tip, margins toothed, connate at the base with the bracts. Perianth obconic, 360-500 x 580-750 μm , with four conical horns, 150-260 μm long. Sporophyte not seen.

Illustrations. Bonner 1953, p. 184.

Distribution. Known only from Cuba and Guadeloupe. Epiphyll in lowland forests, 300-650 m altitude, mixed with other bryophytes.

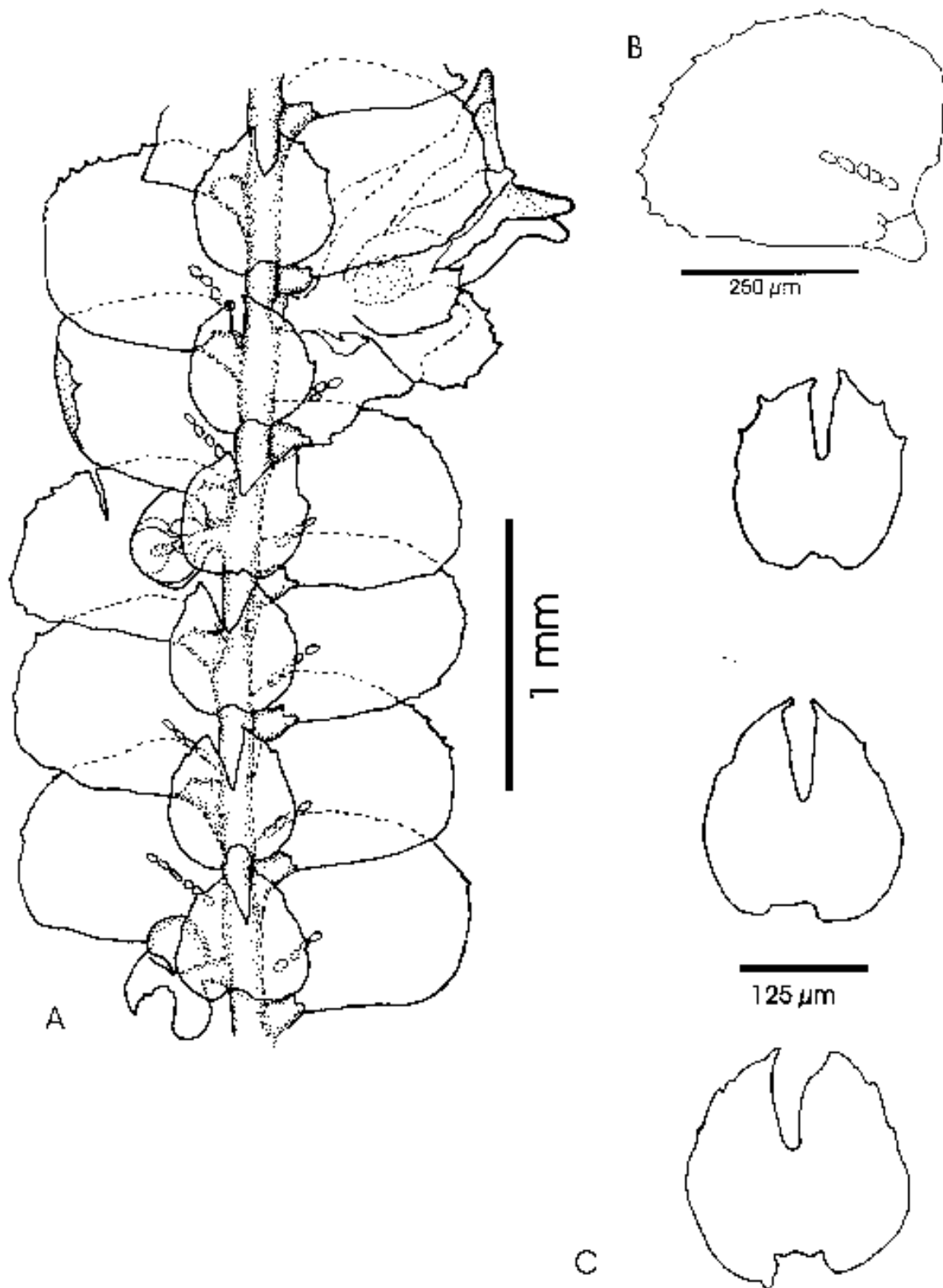


Figure 17. *Ceratolejeunea dentistipula* Steph. A. Habit. B. Leaf. C. Underleaves. From Cuba, the type.

Specimens examined. CUBA. **Oriente:** Baracoa, Mina Iberia, Bisse & Köhler 6531a (JE). **Santiago de Cuba:** Sierra Cristal, Albergue la Chica, Mustelier & Motito 13355 (HABE, USJ). **Without locality:** the type.

GUADELOUPE. **Without locality:** L'Herminier, s. n. (G).

Ceratolejeunea dentistipula resembles a robust *Ceratolejeunea cornuta*. It differs from the latter by having constantly 4-6 moniliate (not seriate) ocelli per leaf, underleaves longer than broad, never reniform, and the leaf lobe margin on main stem leaves is crenulate, denticulate throughout or sometimes entire. Another Caribbean species, *C. brevinervis* (Spruce) Evans has also moniliate ocelli in the leaf lobe, but the teeth are restricted to the leaf lobe apex, the leaves are strongly incurved and the plants are much darker and robust. In addition, *C. dentistipula* has been collected as epiphyllous from low elevation areas in Cuba and Dominica, whereas *C. brevinervis* grows on bark at higher elevations in the Caribbean mountains. This species could also be confused with *C. fallax* (Lehm. & Lindenb.) Bonner, which has seriate ocelli in the leaf lobe, but has teeth restricted to the leaf apex.

8. *Ceratolejeunea dussiana* (Steph.) G. Dauphin, *comb. nov.*; *Pycnolejeunea dussiana* Steph., in Urban, *Symb. Antill.* 3: 278. 1902. Type. Guadeloupe. Rivière Rouge, Matouba, „in cortice arboris“, XI.1901, Duss 699 (holotype, G). Figure 18.

Ceratolejeunea dentato-cornuta Steph., *Sp. Hep.* 5: 407. 1913. Type. Ecuador. Morona-Santiago: Gualaquiza, „in silva ad rivum Sapotilla, Allioni s. n. (lectotype (*fide* Grolle *in sched.* 1990), G; isolectotype, JE), *syn. nov.*

Hygrolejeunea ocellata Steph., *Sp. Hep.* 5: 565. 1914; *Pycnolejeunea cocosana* Mizut., *Journ. Hattori Bot. Lab.* 33: 253. 1970. Type. Costa Rica. Puntarenas: Cocos Island, Pittier s. n. (holotype, G), *syn. nov.*

Plants dioicous or monoicous, pale-brown, stem with leaves 0.5-1.5 mm wide; sparsely branched. Stems in cross section 70-110 μm in diameter, medullary cells 6-15, ventral cells in surface rectangular to quadrate, 25-45 x 25-85 μm , dorsal cells rectangular to quadrate, 20-40 x 25-55 μm . Flagelliferous branches not seen. Leaves imbricate, lobe ovate to slightly asymmetric-ovate, 320-780 x 400-950 μm , apex rounded or broadly acute, plane or slightly incurved, margins entire or crenulate by projecting cells; median leaf lobe cells isodiametrical

to short-elliptical, 15-30 x 25-45 μm , marginal leaf lobe cells quadrate to rectangular, 10-25 x 15-30 μm , intermediate thickenings rare, middle lamellae with hardly noticeable pale-brown color, cuticle smooth or papillose; oil-bodies not seen; ocelli scarcely differentiated from normal leaf cells, 25-40 x 40-70 μm , 2 (0-5) per leaf, suprabasal or basal, contiguous or isolated, when basal, frequently distant from the lobule free margin; lobules inflated or completely reduced, 0.2-0.4 the leaf lobe length, free margin involute. Utriculi absent. Underleaves distant to imbricate, wide-ovate to reniform, 110-300 x 140-300 μm , bifid to 1/3, sinus broad, lobes acuminate, ending in a 1-2 cells tip, margins crenulate by bulging cells or with blunt projections, plane. Vegetative reproduction by gemmae rare, gemmae marginal on old stem leaves, irregularly shaped, papillose.

Androecia lateral on main branches, rarely intecalary on lateral branches, in spikes of 3-6 bracts pairs, spikes 600-900 μm long, bracteole?

Gynoecia on lateral branches with one sterile innovation; bracts elliptical to obovate, 400-430 x 700-800 μm , margins entire, bract lobule lanceolate, 230 x 300 μm ; bracteole ovate, 340 x 550 μm , bifid to 1/3, lobes acuminate, margins entire, connate at the base with the bracts.

Perianth obconic, 300-410 x 450-600 μm , with four flat, short ramified, horns, ca. 130 μm long, margins erose-dentate.

Sporophyte not seen.

Illustrations. Bonner 1953, p. 183; Onraedt 1989, p. 123 (as *C. dentato-cornuta* Steph.).

Distribution: a rare species known from Costa Rica, Panama, Chocó and the Amazon, found in wet submontane forests, as epiphyte mixed with other hepaticae.

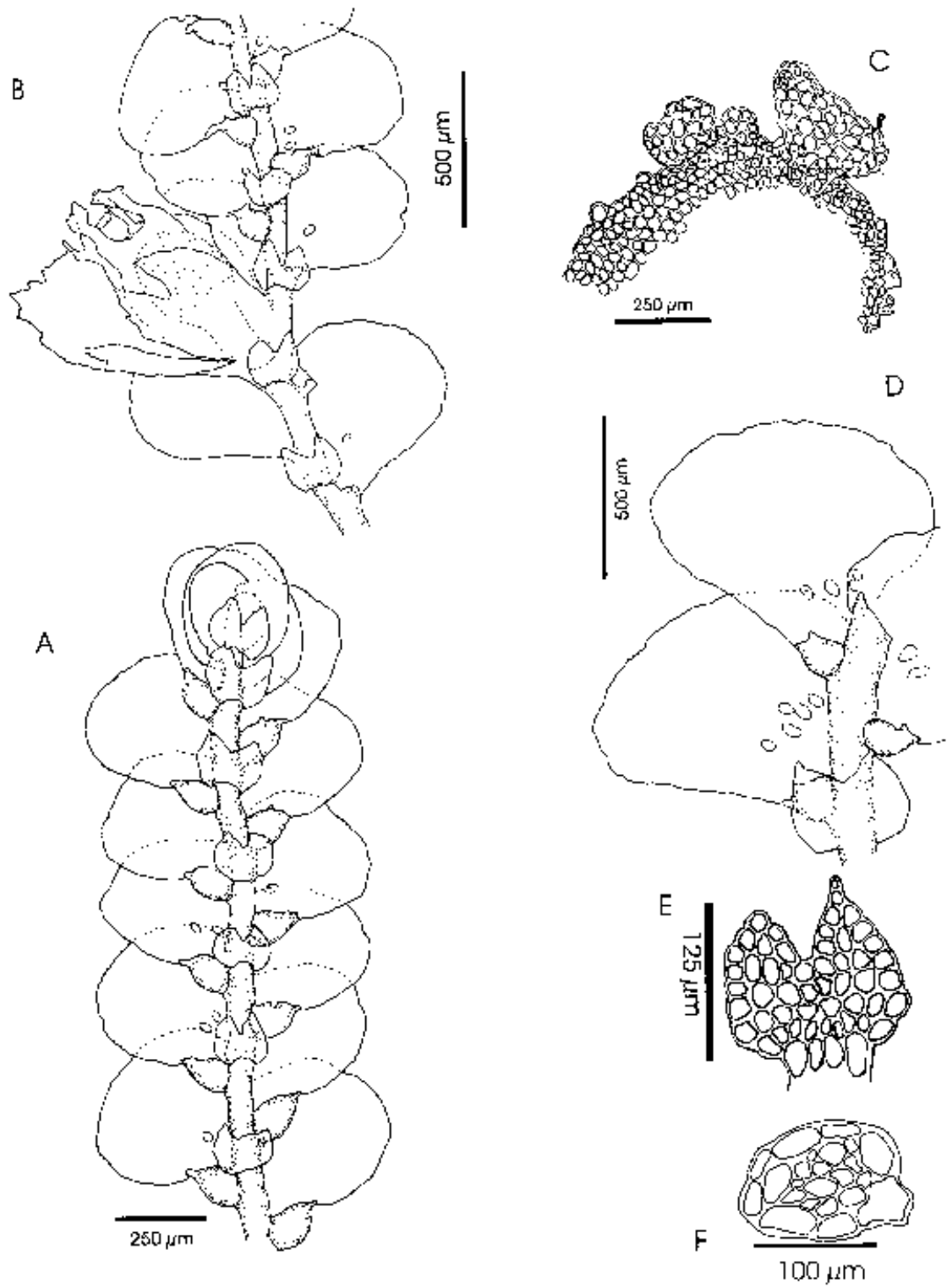


Figure 18. *Canthalegnum davisii* (Steph.) Dauph. A. Habit. B. Perianth and innovation. C. Gemmae on leaf margin. D. Leaves, underleaf and lobules. E. Underleaf. F. Stem cross section. From Cocos Island, Pitier s. n. (A, D, F) and from Guadeloupe, the type (B, C, E).

Specimens examined. COSTA RICA. **Heredia:** Sarapiquí, el Plástico, Sendero Tigre, Dauphin 2174pp (GOET). **Puntarenas:** Cocos Island, type of *Hygrolejeunea ocellata* Steph., Dauphin 999, A-4/17 (USJ).
ECUADOR. **Morona-Santiago:** type of *Ceratolejeunea dentato-cornuta* Steph.
FRENCH GUIANA. Route de Payenne a St. Laurent pk185, 10 km after Maná branching, Cremers 5984a (JE).
GUADELOUPE. **Without locality:** the type.
PANAMA. **Darién:** Cerro Pirre, Salazar & Gradstein 9268, 9279 (GOET, U).

This very particular species can be recognized by its very pale brown color almost unnoticeable in the middle lamellae, but more obvious in the stem transversal section, the usually suprabasal or distant basal ocelli, its fragility, the rare presence of brood bodies (gemmae) on some of the leaves on older branches and the „ripened“ perianth horns.

Even though Stephani (1913) described the species as having no ocelli and Zwickel (1932) could not decide on his observations, the presence of ocelli is evident in the samples examined. Grolle (in shed., JE) signals the presence of utriculi in both samples, but I could not confirm his observations.

A robust, sterile specimen from Cocos Island was first described by Stephani under *Hygrolejeunea*, latter by Mizutani under *Pycnolejeunea*. More recently, He (1999) suggested that the specimen may be a *Ceratolejeunea*. Even though sterile, the pale coloration of the plant and the distant basal and suprabasal position of the ocelli as well as the underleaf shape, indicate that the sample belongs to this distinctive species.

9. *Ceratolejeunea fallax* (Lehm. & Lindenb.) Bonner, Candollea 14: 189. 1953;
Jungermannia fallax Lehm. & Lindenb., in Lehmann, Pugillus 5: 17. 1833; *Lejeunea fallax*
(Lehm. & Lindenb.) Lehm. & Lindenb., in Gottsche, Lindenb. & Nees, Syn. Hep.: 407.
1845. Type. Brazil. Rio de Janeiro. Serra d' Estrella, Beyrich s. n. (holotype, S; isotype, W).
Figure 19.

Ceratolejeunea brasiliensis (Gottsche) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 1, 3: 125.
1893; *Lejeunea brasiliensis* Gottsche, in Gottsche, Lindenberg & Nees, Syn. Hep.: 398. 1845.
Type. Brazil. Without locality, „Ad flumen Amazonum inter muscos“, Martius s. n.
(lectotype (*fide* Bonner 1953), G; isotypes, S). (Bonner 1953).

Ceratolejeunea corniculata Spruce ex Steph., Sp. Hep. 5: 404. 1913. Type. Brazil. Amazonas: „Rio Negro et Casiquiari, in truncis inundatis“, Spruce s. n. (*lectotypus nov.*, G; isolectotype, G), *syn. nov.*

Spruce (1884) mentioned 2 type localities in the protologue. The selected lectotype was included there and also distributed in the Hepaticae Spruceanae.

Ceratolejeunea fusilobula Herz., Rev. Bryol. Lich. 20: 149. 1951. Type. Costa Rica. Alajuela: Viento Fresco, 1600-1900m, Standley 47806 p. p. (holotype, JE), *syn. nov.*

Plants autoicous or dioicous, brown to almost black, stems with leaves 0.9-1.4 mm wide, sparsely to profusely branched, stems in cross section 90-160 μm in diameter, medullary cells 12-22, ventral cells in surface view quadrate to rectangular, 35-60 x 40-90 μm , dorsal cells quadrate to rectangular, 35-60 x 40-90 μm , cell walls thick, ca. 12 μm thick.

Flagelliferous branches with toothed leaflets rare. Stem leaves imbricate, lobe ovate to ligulate from a wide base, 380-600 x 560-760 μm , margins entire or toothed at the apex, teeth 2-6 per leaf, 1-2 cells long, ca. 20 μm long, postical margin entire or with 0-2 teeth, apex rounded or broadly acute, weakly incurved or plane; median leaf lobe cells isodiametrical to elliptical, 15-30 x 20-35 μm ; marginal cells quadrate to rectangular, 10-20 x 15-25 μm ; oil-bodies not seen; ocelli 20-40 x 40-65 μm , mostly seriate, basal or geminate, isolate or contiguous, 1-5 per leaf; lobules inflated or spherical, 0.2-0.3 the leaf lobe length, free margin involute or plane, apical tooth short or elongate and curved. Utriculi absent or in pairs at the base of lateral branches. Underleaves imbricate or shortly distant on main branches, ovate-lanceolate to reniform, 320-795 x 280-700 μm , lobes acute, ending in a one-celled tip, margins entire, base usually cordate, lobes rounded.

Androecia lateral on main branches, in spikes of 3-7 bract pairs; spikes 550-950 μm long; bracteole, 65-170 x 80-200 μm , bifid, 2 per spike.

Gynoecia on lateral branches with 1-2 sterile or repeatedly fertile innovations; bracts obovate, 330-470 x 520-850 μm , margins toothed distally, apex rounded to acute; bracteole ovate, 460-580 x 650-750 μm , bifid to 1/3, lobes acuminate, margins entire, connate at the base with the bracts. Perianth obconic, 480-530 x 720-900 μm , with four horns, slender triangular to inflated, 50-80 x 80-300 μm .

Spores irregularly shaped, mostly rectangular, 20-30 x 45-60 μm , strongly papillose, with well defined rosettes.

Illustration. Bonner 1953, p. 190, 191.

Distribution. Widespread from Mexico to Southern Brazil, this species grows from lowland rainforests to lower montane forests, from 200-1600 m, but reaching almost 3000 m in the Venezuelan Andes. It usually grows as epiphyte on bark in very wet habitats.

Specimens examined. MEXICO: **Without department:** Mirador, Liebmann s. n. (W).

COSTA RICA. **Puntarenas:** Cocos Island, Stewart 1354 (GOET); Monteverde Biological Reserve, Gradstein 9610 (GOET); Osa, P. N. Corcovado, trail from Sirena to Los Patos, Kunz s. n. (USJ).

PANAMA. **Panama:** Rottenberg 2 (GOET).

CUBA. **Santiago de Cuba:** Gran Piedra, Finca Isabelia, Pócs 9202/r (HABE).

COLOMBIA. **Chocó:** road Santa Cecilia-Tadó, 40 km W of St. Cecilia, Gradstein 8750 (GOET, U).

Risaralda: W side of Cordillera Occidental, along trail from Jeguadas to Puerto de Oro, W of Mistrato, Gradstein 8396 8436 8514, 8520 (GOET, U).

VENEZUELA. **Falcon:** Cerro Madre de Agua, Serranía de Avaria, 117 km SW of Coro, Wingfield 11262 (GOET, U). **Yaracuy:** fila cumbre el Amparo towards Candelaria, 7-10 km N from Salom, Steyermark *et al.* 106746 (GOET, U). **Zulia:** above Río Socuy, near the Gran Savana, Griffin III 317 (GOET, U); Sierra de Perija, along trail leading to Topochalito, Griffin III 123 (GOET, U).

ECUADOR. Without locality: Spruce L558 (MANCH).

BRAZIL. **Amazonas:** highway between Humanitá & Porto Velho, 60km S, highway crossing of Sao Joao Stream, Fife *et al.* 3989 (NY); Rio Negro, Spruce s. n. (NY); road Manaus-Caracarai, km 130, near Igarapé, Vital *et al.* 4362 (GOET, U). Without locality: type of *Ceratolejeunea brasiliensis* (Gottsche) Steph. **Rio de**

Janeiro: the type. **Rondônia:** 2-4 km above the first rapids of the Rio Pacaas Novos, Reese 13318, 13447 (NY). **São Paulo:** Cananeia, ca. 3,5 km W of Porto Cubatão, Vital 5354 (GOET, U); Praia don Pontal, Ilha Comprida, Vital 5061 (GOET, U).

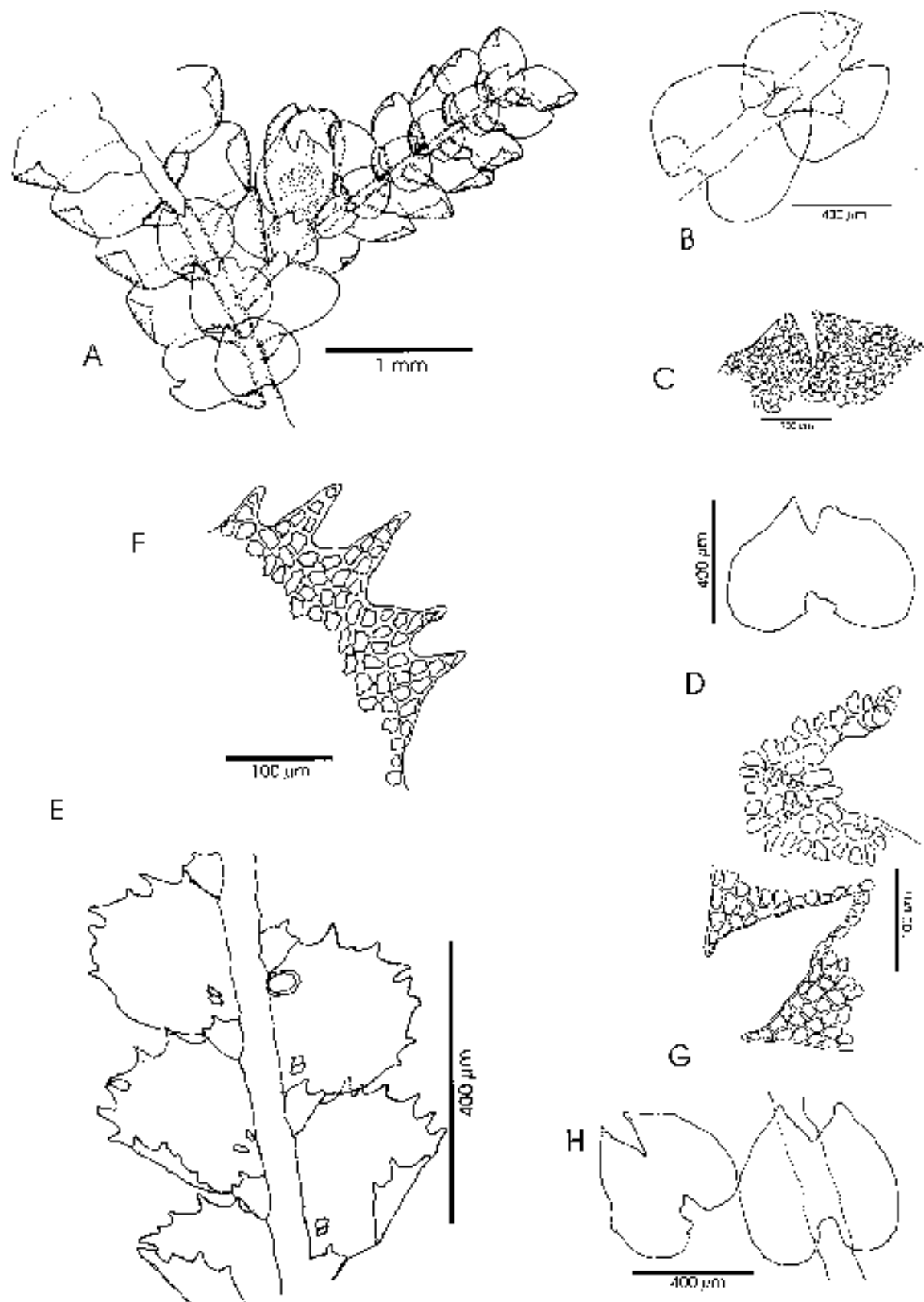


Figure 19. *Ceratoljeunea fallax* (Lindb.) Bonner (A-D). A. Habit and perianth with innovation. B-D. Underleaves. From Brazil, Beyrich s. n., and Martius s. n. *Ceratoljeunea filaria* (Taylor) Steph. E. Portion of flagelliferous branch. F. Leaf margin. G. Underleaf apex and insertion. H. Underleaves.

Ceratolejeunea fallax is defined by the combination seriate ocelli, the robust size and the imbricate, reniform underleaves with cordate bases. The seriate ocelli in some leaves is the only character that allows to separate this taxon from robust forms of *Ceratolejeunea filaria* (Taylor ex Lehm.) Steph. This species bears also resemblance to the Caribbean *C. brevinervis* (Spruce) Evans, which has moniliate ocelli, but has very strongly recurved leaf apices and a more robust, darker appearance.

10. *Ceratolejeunea filaria* (Taylor ex Lehm.) Steph., Sp. Hep. 5: 412. 1913; *Lejeunea filaria* Taylor ex Lehm., Pugillus 8: 28. 1844, Syn. Hep.: 402. 1845. Type. Venezuela: La Esmeralda, Jameson s. n. (isotypes, BM, G, MANCH, W), *syn. nov.* Figure 19.

A specimen in S is marked as holotype but does not correspond to this species but to *C. spinosa* (Gottsche) Steph.

Ceratolejeunea longicornis (Gottsche) Steph., Sp. Hep. 5: 421. 1913; *Lejeunea longicornis* Gottsche, in Gottsche, Lindenbergh & Nees, Syn. Hep.: 401. 1845. Type. Saint Kitts. Without locality, Breutel s. n. (isotypes, BM, G, W), *syn. nov.*

Ceratolejeunea fastigiata (Spruce) Steph., Sp. Hep. 5: 411. 1913; *Lejeunea (Cerato-Lejeunea) fastigiata* Spruce, Mem. Torrey Bot. Club 1: 123. 1890. Type. Bolivia. La Paz: Yungas, 6000 ft., Rusby 3035a (holotype, MANCH; isotype, NY?), *syn. nov.*

Ceratolejeunea spinosa var. *flagelliformis* Steph., Hedwigia 34: 238. 1895, *nom. inval.* (Art.43.1.). Material. Martinique. Without locality, Duss 408 (holotype, G), *syn. nov.*

Ceratolejeunea sacculosa Herz., Rev. Bryol. Lich. 13: 20. 1942. Type. Colombia. El Cauca: Micay Valley, La Gallera, 1400-1600m, forest epiphyll, Killip 7780 (holotype, JE; isotype, B, US), *syn. nov.*

Ceratolejeunea flagelliformis Steph. ex Fulford, Bull. Torrey Bot. Club. 71: 637. 1944, *nom. inval.* (Art. 3.6.1). Type. Guadeloupe. Without locality, Duss s. n. (holotype, G-024481), *syn. nov.*

Ceratolejeunea multiocellata Herz., Rev. Bryol. Lich. 20: 150. 1951. Type. Costa Rica. Cartago: Pejivalle, 900 m, Standley 46809 (holotype, JE; isotypes, B, US), *syn. nov.*

Plants dioicous?, green or brown to almost black, creeping to hanging, stems with leaves 0.75-2.0 mm wide, with profuse, short lateral branches (subsimpler), stems in cross section 125-145 μm in diameter, medullary cells 18-29, ventral cells in surface view quadrate to rectangular, 25-70 x 25-110 μm , dorsal cells quadrate to rectangular, 45-60 x 55-70 μm . Lateral branches becoming flagelliferous, leaflets 150-460 x 240-700 μm , antical leaflet lobe margins entire in younger branches to roughly toothed in older ones, 5-10 teeth?. Stem leaves imbricate; lobe ovate from a wide base, sometimes asymmetrical, 620-720 x 830-900 μm , antical margins entire or sometimes toothed at the apical region, teeth 0-4, 1-2 cells long, ca. 10 μm long, postical margin entire, apex rounded or broadly acute, incurved or plane; median leaf lobe cells isodiametrical to elliptical, 20-30 x 20-60 μm ; marginal cells quadrate to rectangular, 10-20 x 15-20 μm ; oil-bodies granular, elliptical, 2-5 per cell; ocelli long-hexagonal, 30-40 x 50-60 μm , basal, 0-1 per leaf; lobules inflated, reduced? or spherical?, 0.2 the leaf lobe length, free margin involute or plane, with apical tooth short or long and curved; hyaline papilla bulging. Utriculi frequent, solitary? or in pairs at the base of lateral branches, rounded? to reniform. Underleaves imbricate, long ovate to reniform, 370-950 x 310-880 μm , lobes acute, ending in a one-celled tip, margins entire, plane or rarely incurved, base frequently cordate, lobe auricles rounded asymmetrical (one bigger than the other). Vegetative regeneration from laminar leaf lobe cells reported by Fulford (1944b).

Androecia in lateral spikes of 3-6? bract pairs, spikes 500-1125 μm long;

Gynoecia with one or two innovations, fertile or sterile?. Bracts toothed to lacinate; bracteole ovate, 300-500 x 400-550 μm . Perianth obconical, 400-450 x 530-920 μm , horns long, slender.

Sporophyte seta 145 μm in diameter, ca. 1200 μm long. Elaters 290 μm long. Spores 32.5 x 77.5 μm , rosettes simple.

Distribution. A mountain species, found in high elevation forest areas over 2000 m and descending to middle elevations in very wet areas from Costa Rica to Bolivia. Usually growing in well illuminated places, such as light-gaps, canopies and old-secondary growth areas, this species forms hanging mats on branches or twigs, but can also grow on leaves. It grows in pure mats or mixed with other bryophytes.

Specimens examined. COSTA RICA: **San José:** Moravia, La Palma, Maas 844 (GOET, U); Bajo de la Hondura, Standley 36412 (US, S); Cerro de La Muerte, Reserva 3 de junio and surroundings, Gradstein & Mues 9689 (GOET).

PANAMA: **Darién:** Cerro Pirre, Salazar & Gradstein 9246 (GOET, U).

GUADELOUPE. **Without locality,** Duss s. n. (G-024481).

MARTINIQUE. **Without locality,** Duss s. n. (G).

ST. KITTS. **Without locality:** Breutel s. n. (BM, G, W).

COLOMBIA. **Cauca:** Cordillera Occidental, Micay Valley, La Gallera, Killip 7780 (B, JE). **Valle:** Cordillera Occidental, La Cumbre, Killip 11389 (JE).

VENEZUELA. La Esmeralda., Jameson s. n. (BM, G, MANCH, S, W). **Falcon:** Península de Paraguan, Cerro Santa Ana, above Santa Ana, top of E ridge, Wingfield 13360 (GOET, U).

ECUADOR. **Esmeraldas:** San Lorenzo, Alto Tambo, down hill after Lita, Dauphin 2701, (GOET, USJ, QCNE), 2703, 2710 (GOET, USJ).

PERU. **San Martín:** Lamas, road Yurimaguas-Tarapoto, km 107, Frahm *et al.* 1387 (GOET, U); Rioja, road Moyobamba-Chachapoyas, km 403, Frahm *et al.* 54 (GOET, U).

BOLIVIA. **La Paz:** Yungas, type of *C. fastigiata*, Rusby 3044 (MANCH). **Cochabamba:** Chapare, road Cochabamba-Villa Tunari, km 112, Gradstein & Lewis 7564 (GOET, U).

Distinguished by the morphology of the underleaves on main stems: strongly reniform with „deep insertion“ and rounded, unequal lobes (one bigger than the other). In high elevation specimens, *e. g.* Gradstein & Mues 9689 (GOET), the underleaves appear incurved. Diagnostic for this species are the long perianth horns enclosed by the bracts with lacinate margins, the presence of flagelliferous branches in very developed specimens and lateral pinnate branching. The main stem leaves can be toothed or entire, a greater development of teeth is seen on flagelliferous branches.

11. *Ceratolejeunea guianensis* (Nees & Mont.) Steph., Sp. Hep. 5: 416. 1913; *Lejeunea guianensis* Nees & Mont., Ann. Sci. Nat., Bot. ser. 2, 14: 335. 1840; *Colura guianensis* (Nees & Mont.) Trevis., Mem. Ist. Lomb. Sci. Mat. Nat., Ser. 3, 4: 402. 1877. Type. French Guiana. Without province: „*ad cortices arborum in sylvis humidis montis vulgo Serpent dicti*“, Leprieur 291 (*lectotypus nov.*, PC; isolectotype G). Figure 20.

In the protologue, Leprieur 281 & 291 were cited (Montagne 1840). Number 281 was not found in PC, and the chosen lectotype has abundant material.

Plants monoicous or dioicous, dull-green to light-brown, stem with leaves 0.4-1.2 mm wide; sparsely branched. Stems in cross section 80-100 µm in diameter, medullary cells 14-19,

ventral cells in surface view rectangular, 15-45 x 15-60 μm , dorsal quadrate to rectangular, 40-55 x 40-50 μm . Microphyllous lateral branches frequent, leaflets with lobules ca. 0.5 the leaflet lobe length. Leaves imbricate, lobe ovate, 200-450 x 340-600 μm , apex rounded, rarely broadly acute, incurved, margins entire; median leaf lobe cells isodiametrical, 15-25 x 20-40 μm , intermediate thickenings frequent, marginal cells 12.5-20 x 12.5-20 μm ; oil-bodies not seen; ocelli 30-35 x 45-55 μm , basal, 1-2 per leaf, contiguous or isolate; lobules inflated or reduced, 0.3-0.4 the leaf lobe length, free margin plane or slightly involute, apical tooth slightly curved. Utriculi single or in pairs at the base of lateral branches. Underleaves orbicular to ovate, 160-250 x 160-240 μm , bifid to $\frac{1}{2}$, lobes acute, ending in a 1-2 cells tip, sometimes connivent, margins entire, plane or rarely recurved.

Androecia lateral on main branches or intercalary on secondary branches; spikes of 4-9 bracts pairs, 730-1175 μm long; bracteole obovate, 105-140 x 125-175 μm , bifid to $\frac{1}{4}$.

Gynoecia on lateral branches with one sterile innovation, bracts ligulate to obovate, 500-520 x 780-860 μm , margins entire; bracteole orbicular to ovate, 375 x 590 μm , bifid to $\frac{1}{4}$, lobes acuminate, margins entire, to crenulate distally or with a single distal tooth on both sides.

Perianth not seen.

Sporophyte not seen.

Distribution. Known from Southern United states and the Amazonian Basin. A corticolous species, usually grows mixed with other Lejeuneaceae.

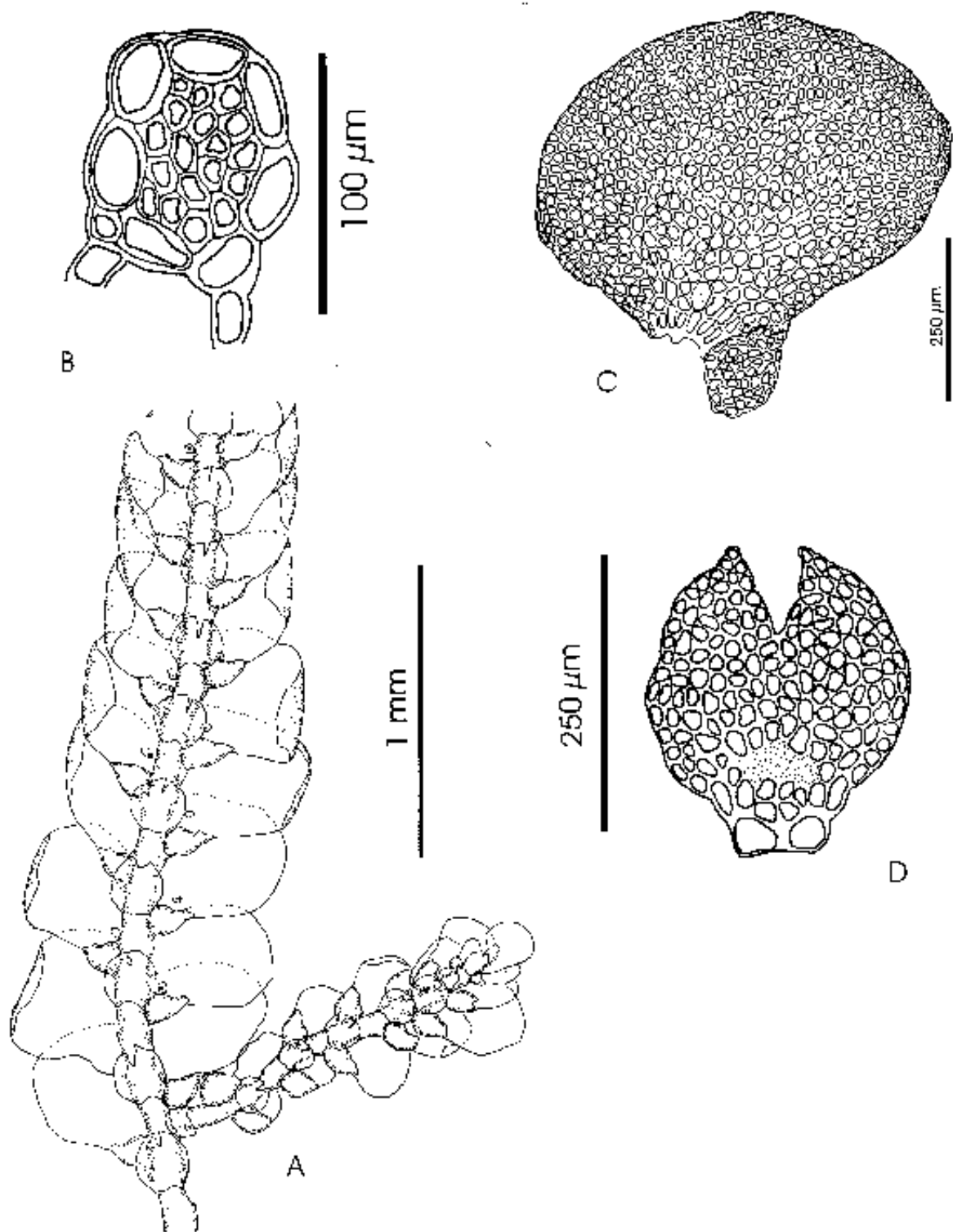


Figure 20. *Carulobryopsis guianensis* (Nees & Mont.) Steph. A. Habit. B. Stem cross section. C. Leaf. D. Underleaf. From French Guiana, the type.

Specimens examined. UNITED STATES. **Florida:** N of Gulf Hammock, along a Canal, Levy Co., Schuster F-118 (G).
COLOMBIA. San José del Guaviare, Evans Schultes 11121 (NY).
VENEZUELA. Carabobo: sur de Borburrata, Steyermark 95326 (US).
GUYANA. Mahury, Bac de Stupan, Herbar du Centre Orstom 3894 (GOET, U).
FRENCH GUIANA. **Without locality:** Leprieur 271 (STR), the type.

Ceratolejeunea guianensis is very closely related to *Ceratolejeunea cubensis*, from which it can be distinguished by its constantly entire leaf lobes with incurved leaves, the frequent microphyllous lateral branches which bear leaflets with very developed lobules, and the smaller number of ocelli. The underleaves are usually scarcely broader than the stem, exceptionally up to twice the stem width. The perianth of the species has not been seen by the author. Fulford (1945) described the perianth in this species as having a low four keeled perianth. The latter author and Schuster (1956) discuss the affinities of the species with *C. laetefusca* (Aust.) Schust., and even though they affirm to have seen the type, the specimen citations are not clear. But other vegetative characters, such as the more robust stems with incurved leaves and the presence of lateral microphyllous branches serve to separate both taxa. *C. laetefusca* is a more common species found throughout the continent, from *C. guianensis* we know not many collections. Fulford (1944b) reported vegetative regeneration for this taxon, based on specimens of *C. laetefusca* (Small *et al.* 6158 (NY)).

I consider the extant morphological data unsatisfactory to clearly separate both taxa. Further analysis of collections and molecular sequence data might help solve this dilemma.

12. *Ceratolejeunea laetefusca* (Aust.) Schust., Journ. Elisha Mitchell Soc. 72: 306. 1956; *Lejeunea laete-fusca* Aust., Bot. Gaz. 1: 36. 1876. Type. United States. Florida, Donnell Smith s. n. (lectotype (Schuster 1956), NY). Figure 21.

Ceratolejeunea caducifolia (Spruce) Steph., Sp. Hep. 5: 400. 1913; *Lejeunea* (*Cerato-Lejeunea*) *caducifolia* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 205. 1884. Type. Brazil. Amazonas: Manaus, Rio Negro, on bark, Spruce L276 (holotype, MANCH), *syn. nov.*

Ceratolejeunea patulistipa Steph., Hedwigia 34: 235. 1895. Type. Surinam. Without locality, Kegel 755 (holotype, G), *syn. nov.*

Ceratolejeunea integrifolia Evans, Bull. Torrey Bot. Club 38: 213. 1911. Type. Bahamas Archipelago. Coppice, Waterloo, Britton 721 (holotype, YU), *syn. nov.*

Ceratolejeunea deficiens Herz., Rev. Bryol. Lich. 20: 148. 1951. Type. Costa Rica.

Guanacaste: vicinity of Tilarán, 500-650 m, Standley & Valerio 44392 p.p. (*lectotypus nov.*, JE; isolectotype US); Standley 44309 p.p. (syntype, JE); Heredia: Yerba Buena, 2000 m, Standley 50010 p.p. (syntype, JE; isosyntype, JE); Standley 50049 (syntype, JE; isosyntype, JE), *syn. nov.*

Herzog (1951) cited several specimens in the protologue, without indicating a type. The two specimens from Tilarán (Standley 44309 p.p. & 44392 p.p.) belong in this taxon, but the ones from Heredia (Standley 50010 p.p. & 50049) belong to *Ceratolejeunea cubensis* (Mont.) Schiffn.

Plants dioicous or rarely autoicous, light brown, stem with leaves 0.3-1.2 mm wide, sparsely branched. Stems fragile, in cross section 35-115 μm in diameter; medullary cells 3-15, ventral cells quadrate to rectangular, 10-25 (-40) x 20-45 (-60) μm , dorsal cells mostly rectangular, 15-40 x 15-40 (-55) μm . Branches fragile, often appearing bare because of caducous leaf fall. Leaves slightly imbricate, lobe ovate, 190-260 (-390) x 240-360 (-500) μm , apex rounded, curved when dry, plane when moist, margins entire or irregularly crenulate, rarely toothed at the apical region, teeth 0-3, to 25 μm long; median leaf lobe cells mostly hexagonal or elliptical, 10-20 (-25) x 10-25 (-40) μm , walls thin, regularly thickened, intermediate thickenings rare to frequent, weak, marginal cells quadrate to rectangular, 7.5 x 10-30 μm ; oil-bodies not seen; ocelli elliptical, 15-25 x 25-50 (-60) μm , basal, contiguous or isolate, 2 (1-3) per leaf; lobules inflated or reduced, 0.2-0.4 the leaf lobe length, free margin involute or plane, with a single apical tooth, hyaline papilla proximal. Utriculi absent. Underleaves orbicular to ovate, 80-180 (-360) x 75-180 (-370) μm , bifid to 1/2 with acuminate lobes, lobes ending in a 1-2 cells tip, margins entire and plane. Vegetative reproduction by caducous leaf lobes frequent to rare.

Androecia lateral on main branches, or intercalary on lateral or main branches, in spikes of 2-8 bract pairs, spikes 350-1225 μm long; bracteole ovate to orbicular, 95-170 x 100-170 μm , bifid to 1/3, lobes acute.

Gynoecia on lateral branches with one or two sterile or repeatedly fertile innovation; bracts obovate, 270-460 x 415-680, margins entire or toothed distally, teeth to 25 μm long, bract lobule ligulate, 165 x 425 μm ; bracteole ovate, 220-380 x 385-610 μm , bifid to 1/2, lobes acuminate. Perianths more or less globose, 260 x 370 μm , with four low, rounded keels, sometimes with a fifth smaller antical keel.

Sporophyte not seen.

Illustrations. Fulford 1945, p. 383; Schuster 1980, p. 923.

Distribution: Widely distributed in the Neotropics, from southeastern United States to Southern Brazil, not excluded from the Brazilian Planalto. This species grows in dry or moist primary and secondary lowland forests up to open submontane habitats, from 500 to 1300 m, in open places on living bark, rotting bark and rocks, frequently mixed with other bryophytes.

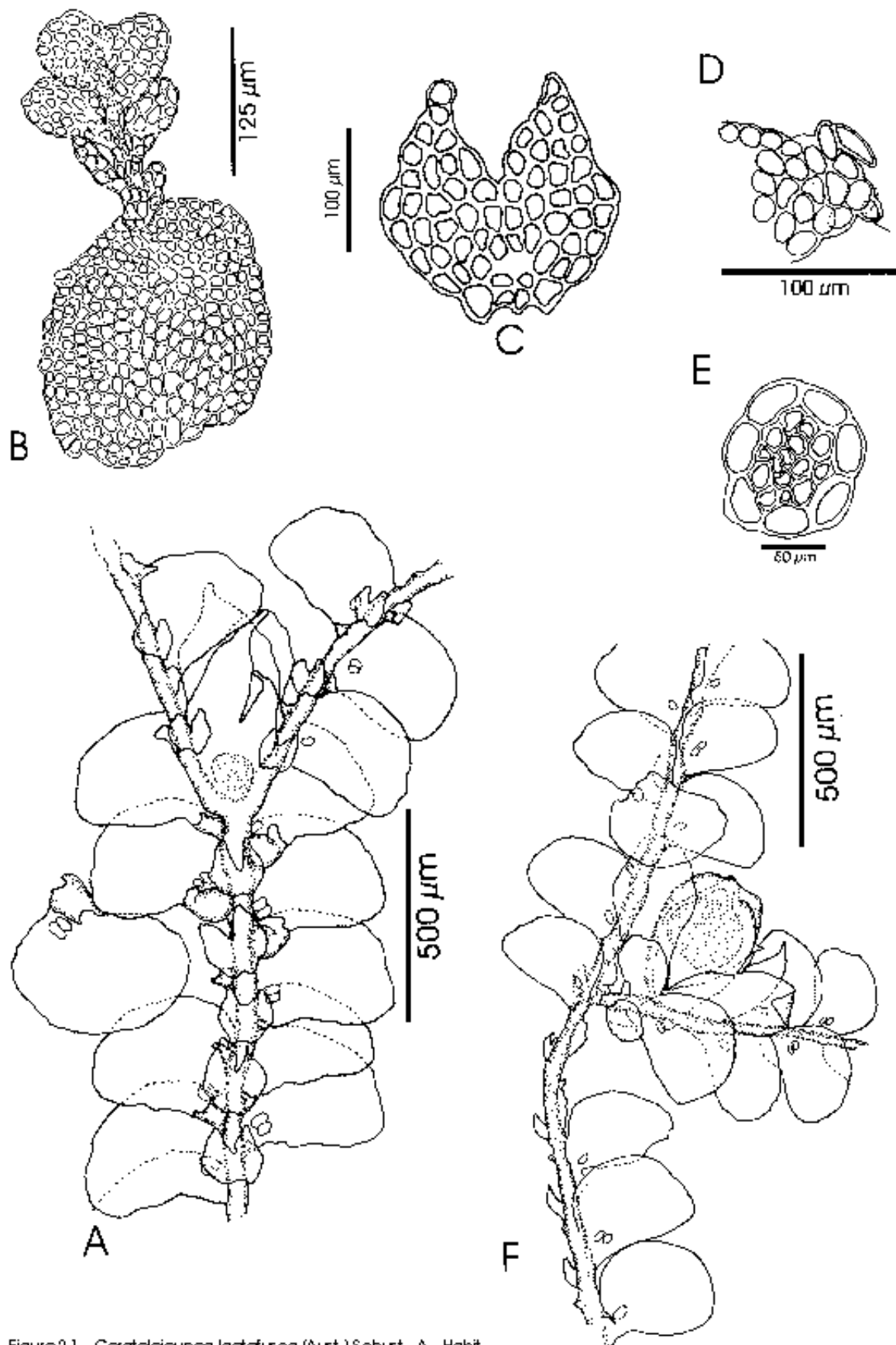


Figure 21. *Ceratolejeunea laetefusca* (Aust.) Schust. A. Habit. B. Caducous leaf lobe with juvenile plant. C. Underleaf. D. Lobule apical tooth. E. Stem cross section. F. Habit dorsal view and perianth. From Brazil, Spruce 1276.

Specimens examined. UNITED STATES. **Florida:** Alachua Co., Devils Millhopper, N of Gainesville, Breil 2481 (US); Dade Co., Shields Hammock Small *et al.* 6153 (US); Timms Hammock, Small *et al.* 6187, 6148 (US); Gulf Hammock, Levy County (sec. 10), Griffin III 60 (GOET, U); Sanford, Rap 362 (US); Washington Co., Moss Hill, behind Methodist Church, Breil 2535 (US); without locality, the type. **Louisiana:** Baton Rouge, Langlois 201 (US); Chinchuba, St. Tammany Co., Langlois 619a, 742 (US); vicinity of Corington, Arsène 14748 (US), Sulphur Springs, Arsène 14394 (US).

COSTA RICA. **Guanacaste:** type of *Ceratolejeunea deficiens* Herz.

BAHAMA ARCHIPELAGO. Coppice, Waterloo, type of *Ceratolejeunea integrifolia* Evans; Maidenhead, Britton 3320 (YU). Soldiers Road, Britton 822 (YU).

CUBA. **Guantánamo:** Baracoa, camino hacia Aguacate, Potroney 14373 (HABE); Luisa Plateau, San Roque. Vicario 16570 (HABE).

GUADELOUPE. **Basse-Terre:** road to Chute des Carbet, Gradstein & Sastre de Jesús 6592 (GOET, U).

TRINIDAD. Without locality, Fendler s. n. (NY), Black s. n. (NY).

SURINAM. **Nickerie:** area of Kabaledo Dam project, road km 117, Bekker 1553 (GOET, U), road km 92, Bekker 1430b (GOET, U). **Without locality:** type of *Ceratolejeunea patulistipa* Steph.

ECUADOR. **Los Ríos:** Palenque biological Station, Dauphin, Gradstein, Sipman *et al.* 2764 (GOET, USJ, QCNE).

PERU. **San Martín:** Lamas, Straße Yurimaguas-Tarapoto km 112, Frahm *et al.* 1788 (JE). **BRAZIL.** Acre: Estrada rio Branco-Porto Ave km 39, Nelson 696 (NY). **Amazonas:** Manaus, the type, „in trunco putrescente“, Spruce s. n. (MANCH, US, W); San Gabriel, „ad rupes cum *Lophocolea*“, Spruce s. n. (MANCH). **Minas Gerais:** Santa Barbara, Serra de Caraça, Schäfer-Verwimp & Verwimp 7869 (JE).

BOLIVIA. **Beni:** Ballivian, Serranía del Pilon Lajas. Gradstein 7110 (GOET, U); **Beni** Forest Reserve, Gradstein 9937, 9939, 9945, 9946 (GOET). **Cochabamba:** Villa Tunari, Parque Machía, Dauphin 2765, 2780 (GOET, USJ).

BRAZIL: type of *Ceratolejeunea caducifolia* (Spruce) Steph.

Specimens of *C. laetefusca* from dryer environments often appear with bare stems due to caducous leaves, which had led Fulford (1945) to keep them as a separate species, *C. caducifolia* (Spruce) Steph. These caducous-leaved plants are small in size, may have only three or four medullary cells in transversal stem section, and the leaf lobule is frequently reduced. In some specimens some branches appear to be caducous and may serve as the caducous leaves in the vegetative reproduction. The number of medullary stems cells vary until they overlap with those of plants which have fewer or lacking caducous leaves. More robust specimens of *C. laetefusca* have about 10 medullary cells in stem cross section, and may have or lack caducous leaves.

Fulford (1945) treated *C. integrifolia* as a synonym of *C. guianensis*, but based on the type of the latter (see under *C. guianensis*) I cannot agree with that placement.

This species is closely related to *Ceratolejeunea cubensis* (Mont.) Schiffn. from which it differs in the lack of utriculi and perianth horns. Plants of *C. cubensis* are frequently autoicous, the leaf lobe margin can be entire or weakly to strongly toothed at the apex, and in robust specimens the ocelli tend to be also geminate. In contrast, *C. laetefusca* appears most of the time sterile (or at least with female bracts), with entire leaf lobe margins, and two basal, contiguous or isolate ocelli.

Both species have been attempted to separate by means of general plant and cell size (cf. Schuster 1980), but the plant size and number of medullary cells in *C. laetefusca* vary so strongly that robust specimens overlap in size with *C. cubensis*.

Even though dioecy has been strongly emphasized in this species, Evans (190X) assigned monoicous specimens the name *C. integrifolia* Evans. Most populations are sterile, or dioicous but monoicous plants have been collected too (e. g. Langlois 201 (US), Gradstein 9937, Dauphin 2780 (GOET)).

13. *Ceratolejeunea malleigera* (Spruce) Steph., Sp. Hep. 5: 422. 1913; *Lejeunea* (*Ceratolejeunea*) *malleigera* Spruce, Mem. Torrey Bot. Club 1: 123. 1890. Type. Bolivia. „Andibus Boliviae orientilibus, in fronde *Acrostichi*“, Rusby 3025p.p. (holotype, MANCH; isotypes, BM, G, NY). Figure 22.

Plants autoicous, brown, stem with leaves 0.3-1.6 mm wide, profusely branched. Stems in cross section 55-70 μm in diameter, medullary cells 6, ventral cells in surface view mostly rectangular, 20-35 x 30-70 μm , dorsal cells rectangular, 25 x 45-60 μm . Leaves imbricate, lobe ovate, slightly asymmetrical, 280-460 x 330-550 μm , apex rounded to acute, margins entire and plane; median leaf lobe cells isodiametrical or variously shaped, 15-30 x 15-35 μm , intermediate thickenings rare, walls mostly uniformly thickened, marginal cells quadrate to rectangular, 10 x 10-20 μm ; oil-bodies not seen; ocelli isodiametrical, 20-25 x 25 μm , scattered in the leaf lamina; lobules inflated, 0.4 the leaf lobe length, free margin plane, with no apical tooth, hyaline papilla proximal. Utriculi absent. Underleaves ovate, slightly longer than wide, 140-190 x 160-200 μm , bifid to about 1/2 with acute or rounded lobes, lobes ending in a 1-2 celled tip, margins entire and plane.

Androecia lateral on main branches, in spikes of 3-4 bract pairs, 300-600 μm long, bracteole single, 90-95 x 140-150 μm , bifid to 1/3.

Gynoecea on lateral branches with one sterile innovation; bracts ligulate, margins entire; bracteole more or less rectangular in shape, 135-150 x 340-400 μm , bifid to 1/4, lobes acute, margins entire. Perianth ovoid, 220-240 x 380-500 μm , with 2 (-3) bulbous horns, 230-250 μm long. Sporophyte not seen.

Illustrations. Fulford 1945, p. 378.

Distribution: Known only from the type collection, the species grows as an epiphyll on fern leaves in a montane forest.

Specimens examined. BOLIVIA. The type.

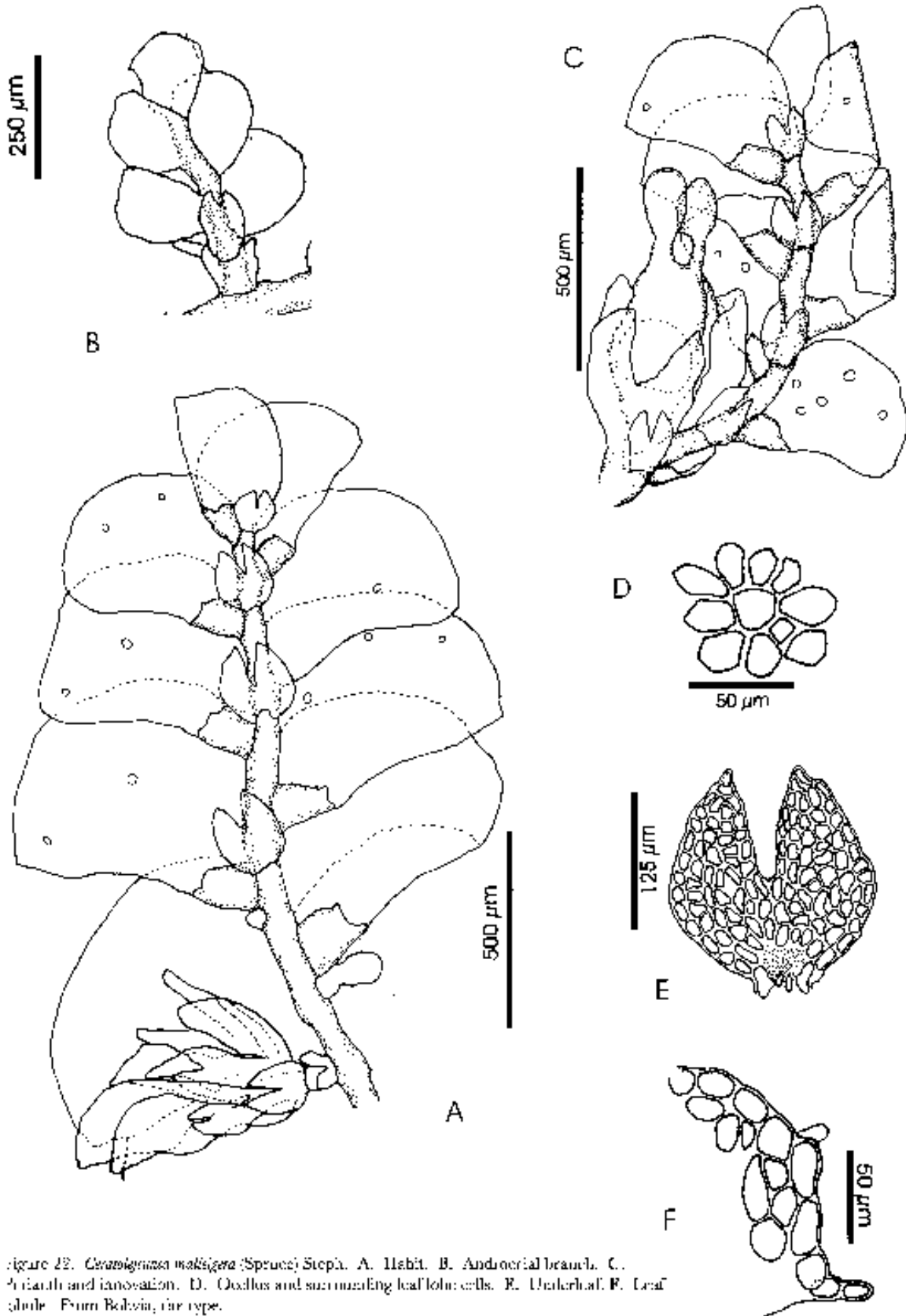


Figure 22. *Ceratopteris walkera* (Spruce) Steud. A. Habit. B. Androecial branch. C. Archegonium and innovation. D. Ocellus and surrounding leaf lobe cells. E. Underleaf. F. Leaf abaxial. From Bolivia, the type.

This rare species can be easily distinguished from all other *Ceratolejeuneas* with bifid underleaves by the ocelli scattered in the leaf lamina, and the two-horned perianth. In addition to those characters, the sporeling has an aberrant development, with the secondary thallus being 6 cells broad instead of the usual 4 cells (Fulford 1944b, 1945). Due to those differences the latter author suggested the possibility that this taxon may not belong in the genus *Ceratolejeunea* (Fulford 1944, p 642).

This species seems related only to the African *C. stictophylla* Herz. which also shows the combination of bifid underleaves and disperse ocelli, but differs in its perianth type, which bears (as usual in the genus) four inflated, not bulbous horns (Jones 1957).

14. *Ceratolejeunea minuta* G. Dauphin, *sp. nov.*

Planta minor, brunnea. Caulis irregulariter multiramulus, 3-4 ordines medullosos cellularum habens. Folia imbricata, ovata, apice rotundata. Amphigastria minora, ad 1/2 inciso-biloba, sinu lato, marginibus dentatis. Gynoecea uno latere innovata; folia floralia obovata, integerrima; amphigastrium florale oblongum, ad 1/2 inciso-bilobum. Perianthia pyriformia, apice cuadriplicata, plicis latis, cornis nullis. Type. French Guiana. Road 2: Cayenne to Cacao, near bridge over river Comté, on tree trunk, Gradstein 6659 (holotype, GOET). Figure 23.

Plants dioicous?, light-brown, stem with leaves 0.4-0.6 mm wide; sparsely branched. Stems in cross section 30-45 µm in diameter, medullary cells 3-4, ventral cells in surface view mostly rectangular, 25-35 x 35-55 µm, thin-walled, dorsal cells mostly rectangular, 25-40 x 30-45 µm, thin-walled. Flagelliferous branches not seen. Leaves imbricate, lobes ovate, 160-260 x 250-350 µm, apex rounded, plane, margins entire or slightly crenulate; median leaf cells isodiametrical to elliptical, 10-25 x 20-30 µm, walls thick, irregularly thickened, intermediate thickenings frequent, trigones conspicuous, sometimes confluent, marginal cells quadrate to short rectangular, 10-15 x 10-20 µm; oil-bodies not seen; ocelli 15-30 x 35-55 µm, basal, 2 per leaf, contiguous; lobules inflated or reduced, 0.3-0.6 the leaf lobe length, free margin involute, apical tooth unicellular, curved, hyaline papilla proximal. Utriculi absent. Underleaves, 50-100 x 95-145 µm, bifid to 1/2, sinus U-shaped, lobes lanceolate-acuminate, ending in a 1-3 cells tip, margins constantly bearing a tooth, tooth unicellular, rarely a second tooth is present.

Androecia intercalary on main branches, in groups of 1-3 bract pairs, 250-560 µm long.

Gynoecia on lateral branches with one sterile innovation; bracts obovate, 270 x 500 μm , margins entire or slightly crenulate, apex rounded or broadly acute, bract lobules obovate, 140-170 x 400-450 μm , apex acute; bracteole long rectangular, 175 x 375-400 μm , bifid to ca. $\frac{1}{2}$, lobes long acuminate, ending in a 2-3 celled apex, with 1-2 teeth on the sinus margin. Perianth obconic, 430-470 x 630-650 μm , with four inflated carinae, not protruding from the perianth body.

Sporophyte with short seta; capsule with four colorless valves, 60 x 115 μm . Elaters 7.5 x 160 μm , single spiraled, 5? per valve. Spores not seen.

Distribution. Known from two areas in the Amazon basin. A lowland rainforest species, growing on bark.

Specimens examined. FRENCH GUIANA. The type.

BRAZIL. **Pará:** Melgaço, Floresta Nacional de Caxiuanã, Est. Científica Ferreira Penna, Ilkiu-Borges *et al.* A-946p.p, A-982 (GOET); Reserva Mocambo, Lisboa & Lisboa 2326a (GOET, U).

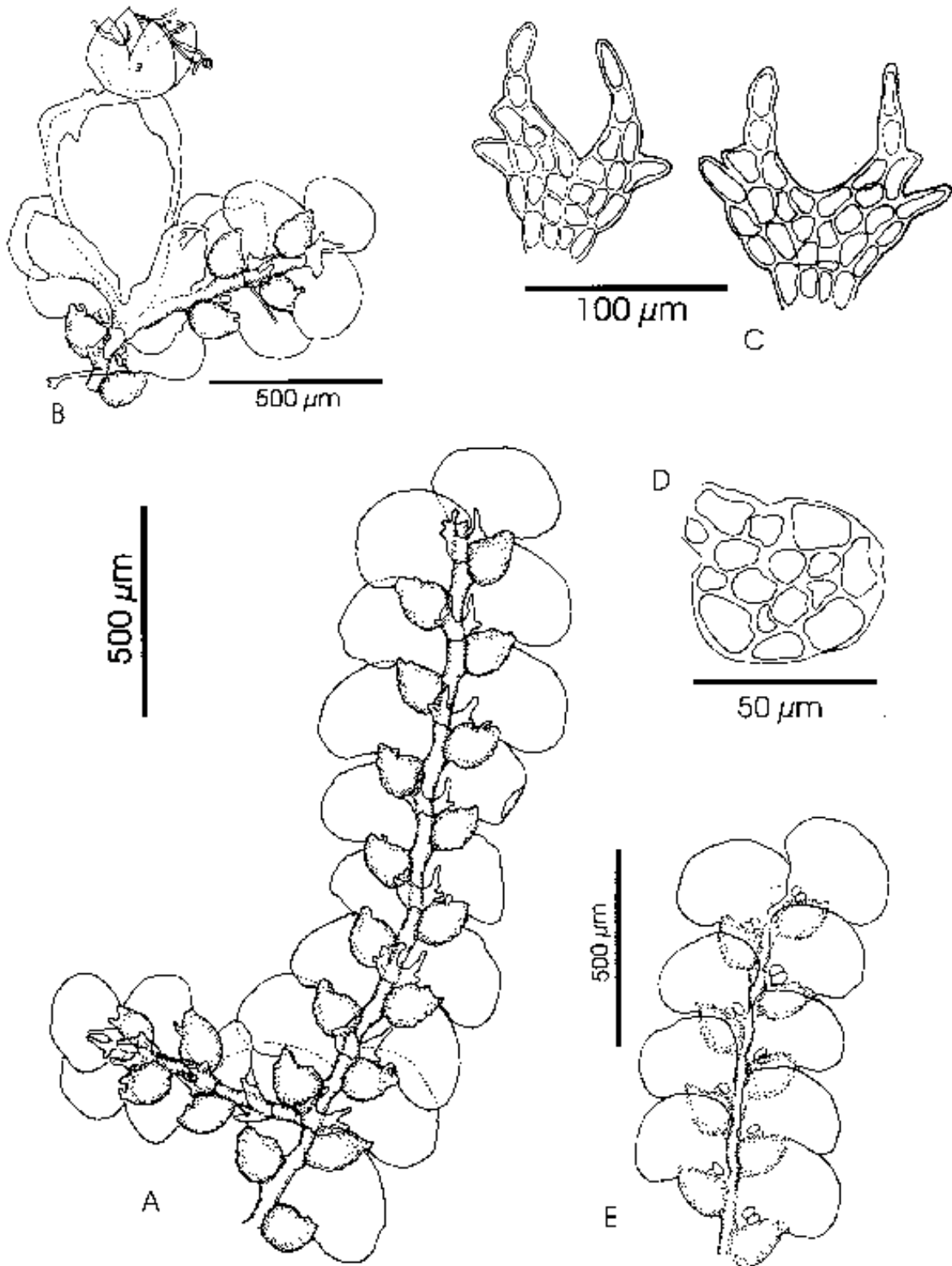


Figure 23. *Coratolejeunea nimta* Dauphin. A. Habit. B. Perianth and innovation. C. Uceriferous. D. Stem cross section. E. Stem dorsal view. From Brazil, the type.

This tiny, beautiful species can be distinguished from all members in the genus by its particular underleaf structure, having constantly a U-shaped sinus. In the other *Ceratolejeuneas* with bifid underleaves the underleaf sinus is V-shaped (with exception of a few underleaves in *C. oxygonia* Gottsche ex Steph.). The underleaf margins on both sides bear constantly a unicellular tooth, and the underleaf lobes are lanceolate, ending in an uniseriate tip of 1-3 elongated cells. The small, thin-celled stem with only 3-4 medullary cells also separates this species from others in the genus. Judging from the abundance of the type material, one would expect the species to be widespread, event though only very few collections are available. Maybe due to its small size, *C. minuta* has been overlooked by bryophyte collectors in the Amazon basin.

15. *Ceratolejeunea oxygonia* Gottsche ex Steph., Sp. Hep. 5: 429. 1913. Type. Cuba. Mt. Verde, Wright s. n. (holotype, G). Figure 24.

Plants dioicous, reddish-brown, stems with leaves 1.0-1.5 mm wide; sparsely branched. Stems 75-90 μm in diameter, medullary cells 13, ventral cells in surface view rectangular to quadrate, 25-45 x 35-70 μm , dorsal cells rectangular to quadrate, 30-40 x 40-75 μm . Flagelliferous branches not seen. Stem leaves slightly imbricate, lobe ovate from a wide base, 250-450 x 390-700 μm , apex usually acute, margins crenulate by projecting cells; median leaf cells isodiametrical to elliptical, rectangular to quadrate, 15-30 x 20-45 μm , walls regularly thickened, intermediate thickenings frequent, cuticle papillose; marginal cells, quadrate to rectangular, 10-20 x 15-25 μm ; oil-bodies not seen; ocelli absent or single, basal, 25-30 x 45-55 μm ; lobules 0.1-0.3 the leaf lobe length, inflated, not reduced?, free margin plane. Utriculi solitary at the base of lateral branches. Underleaves wide ovate to reniform, 250-500 x 200-450 μm , bifid to ca. $\frac{1}{2}$, sinus frequently U-shaped, lobes usually acuminate, ending in a one or 2 to 4-celled tip, frequently connivent, margins undulate or with 1 tooth on both sides, base frequently cordate, with rounded lobes.

Androecia not seen.

Gynoecia on lateral branches with one sterile innovation; bracts elliptical to obovate, 270-345 x 650-780 μm , margins distally dentate, bract lobule lanceolate, margins entire; bracteoles ovate, 275-520 x 280-500 μm , bifid to ca. $\frac{1}{2}$, sinus U-shaped, lobes acuminate, connivent, margins sparsely toothed, connate at the base with the bracts. Perianth not seen.

Sporophyte not seen.

Illustrations. Bonner 1953, p. 219.

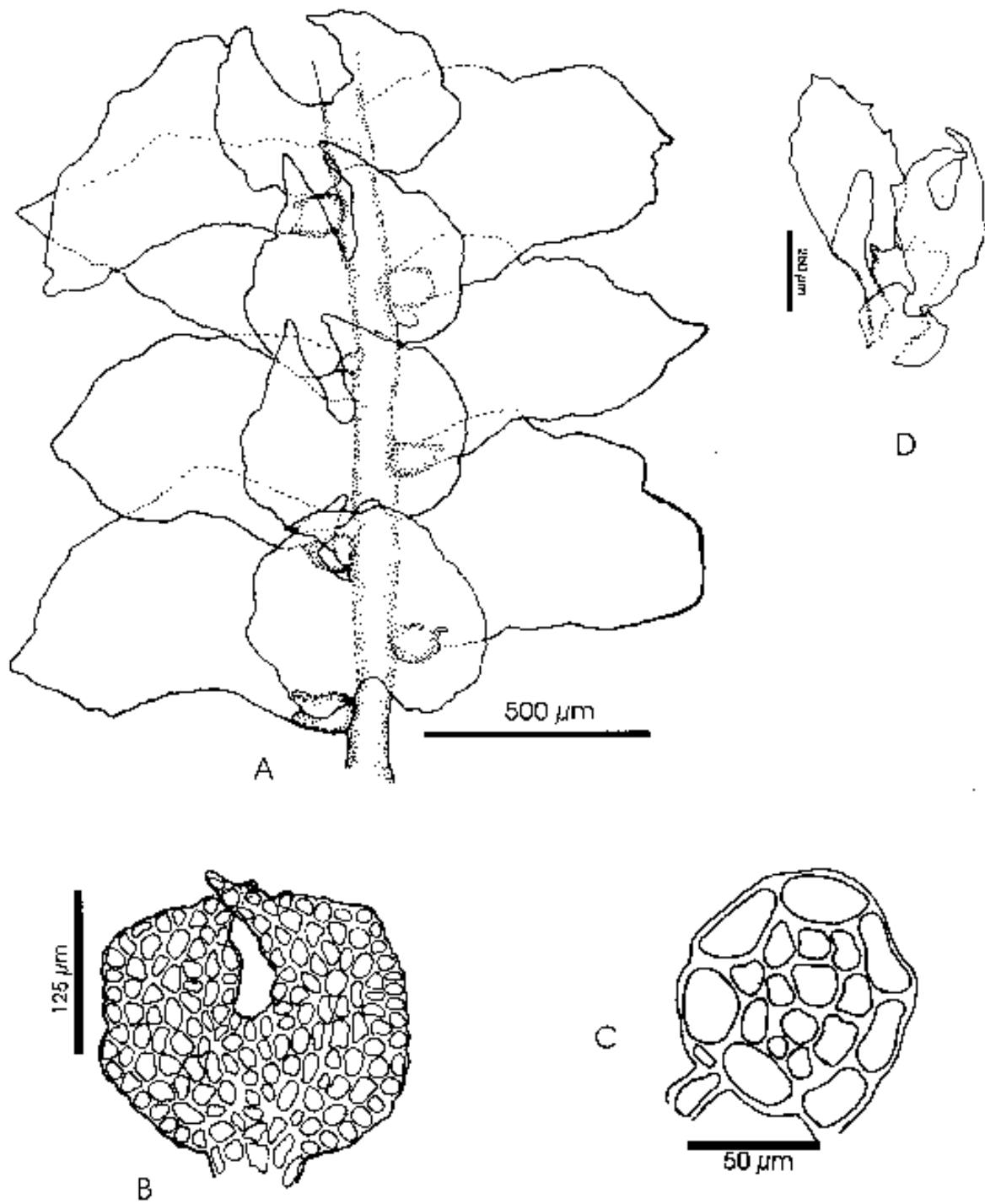


Figure 24. *Ceratolejeunea oregonia* Gottsche ex Steph. A. Habit. B. Underleaf. C. Stem cross section. D. Young perianth. From Cuba, the type.

Distribution. Known only from two collections. A submontane forest species, from middle elevations (ca. 1200 m) in Colombia and Cuba, growing mixed with other hepatics (Stephani 1913).

Specimens examined. CUBA. **Without locality:** the type.

COLOMBIA. **Boyaca:** Camino de Sácama a la Ceiba, quebrada Maneque, Hammen & Jaramillo 1716 (GOET, U).

This rare species differs from all other *Ceratolejeuneas* in the long, ovate leaves that taper to an acute apex, and the underleaves with long, acuminate lobes that are frequently connivent. The marginal cells are bulging, making the margin outline look irregular. The underleaf sinus is V-shaped or U-shaped in some underleaves.

16. *Ceratolejeunea patentissima* (Hampe & Gottsche) Evans, Bull. Torrey Bot. Club 32: 286. 1905; *Lejeunea patentissima* Hampe & Gottsche, Linnaea 25: 355. 1852. Type. Puerto Rico. Without locality, Schwanecke s. n. (holotype BM; isotypes, G). Figure 25.

Ceratolejeunea wallisii Steph., Hedwigia 34: 239. 1895. Type. Ecuador. Manabi, Wallis s. n. (holotype, G), *syn. nov.*

Ceratolejeunea stenostoma Herz., Mem. Soc. Flora & Fauna Fennica 25: 67. 1950. Type. Bolivia. La Paz: Mapiri, San Carlos, 850m Buchtien 283 (holotype, JE), *syn. nov.*

Ceratolejeunea patentissima (Hampe & Gottsche) Evans var. *acutifolia* Fulford, in Steyermark *et al.*, Mem. New York Bot. Gard. 23: 843. 1972, *nom. nud.*

Ceratolejeunea andicola Schust., Phytologia 39: 430. 1978, *nom. illeg.* (Art. 53.1); *non* Steph. 1895. Type. Venezuela. Tachira: S Villa Paez, Páramo de Tamá, pico Banderas, Schuster & Ruiz-Terán 76-1955a (isotype, MERC), *syn. nov.*

Plants dioicous, dull reddish-brown, stem with leaves (0.35-) 0.40-0.80 (-1.22) mm wide; sparsely branched. Stems in cross section (60-) 75-115 (-125) μm in diameter, medullary cells 9-23, ventral cells in surface view mostly rectangular, 15-50 x 15-50 μm , dorsal cells frequently transversely oriented, quadrate or irregularly shaped, 40-65 x 35-65 μm . Branches

tapering to the tips. Leaves imbricate to spreading, lobe ovate, 65-300 (-400) x 205-450 (-650) μm , leaf apex rounded to acute, margins entire or toothed at the apex; median leaf lobe cells isodiametrical, 10-30 x 15-40 μm , smooth, marginal cells 10-15 x 15-25 μm ; intermediate thickenings frequent; oil-bodies granular, solitary, small, 2.8-3 x 5-8 μm (Schuster 1992); ocelli basal, solitary or in pairs, 15-35 x 30-55 μm , with a large ellipsoidal, homogeneous oil-body (Schuster 1992); lobules flask shaped or like in the genus, 0.3-0.8 the leaf lobe length, frequently constricted at the mouth, free margin involute or plane, lobule tooth elongated, curved, frequently hidden. Utriculi rare, single or in pairs at the base of lateral branches. Underleaves ovate, 60-250 (-420) x 65-230 (-370) μm , distant to imbricate on male plants, frequently erect, notched at apex or bifid to 1/3, lobes acuminate or rounded, margins entire. Androecia terminal or intercalary in secondary branches, in spikes of 2-8 bract pairs, 100-1275 μm long, bracteole ovate, 30-50 x 40-50 μm , emarginate, notched (1-3 cells) or shortly bifid. Gynoecia on lateral branches with one, rarely two sterile innovations, bracts obovate, 370 x 650 μm , toothed distally; bracteole ovate, 320-400 x 500-640 μm , bifid to 1/3, margins entire, with blunt projections or an occasional tooth, connate at the base with the bracts. Perianth obconic, 380-390 x 550-660 μm , with 4-5 inflated keels or low horns (*e. g.* Halling 5549). Sporophyte not seen.

Illustrations. Schuster 1992, p. 224.

Distribution: A mountain species, collected at middle and higher elevations in Costa Rica, Panama, Caribbean, the northern Andes and the Guyana Highlands. It grows on bark of upper tree trunks, rotten logs and rarely on soil, usually mixed with other Lejeuneaceae and with *Ceratolejeunea cornuta*, from 450 to 2300 m in montane rain forest areas to the base of the páramo in Venezuela.

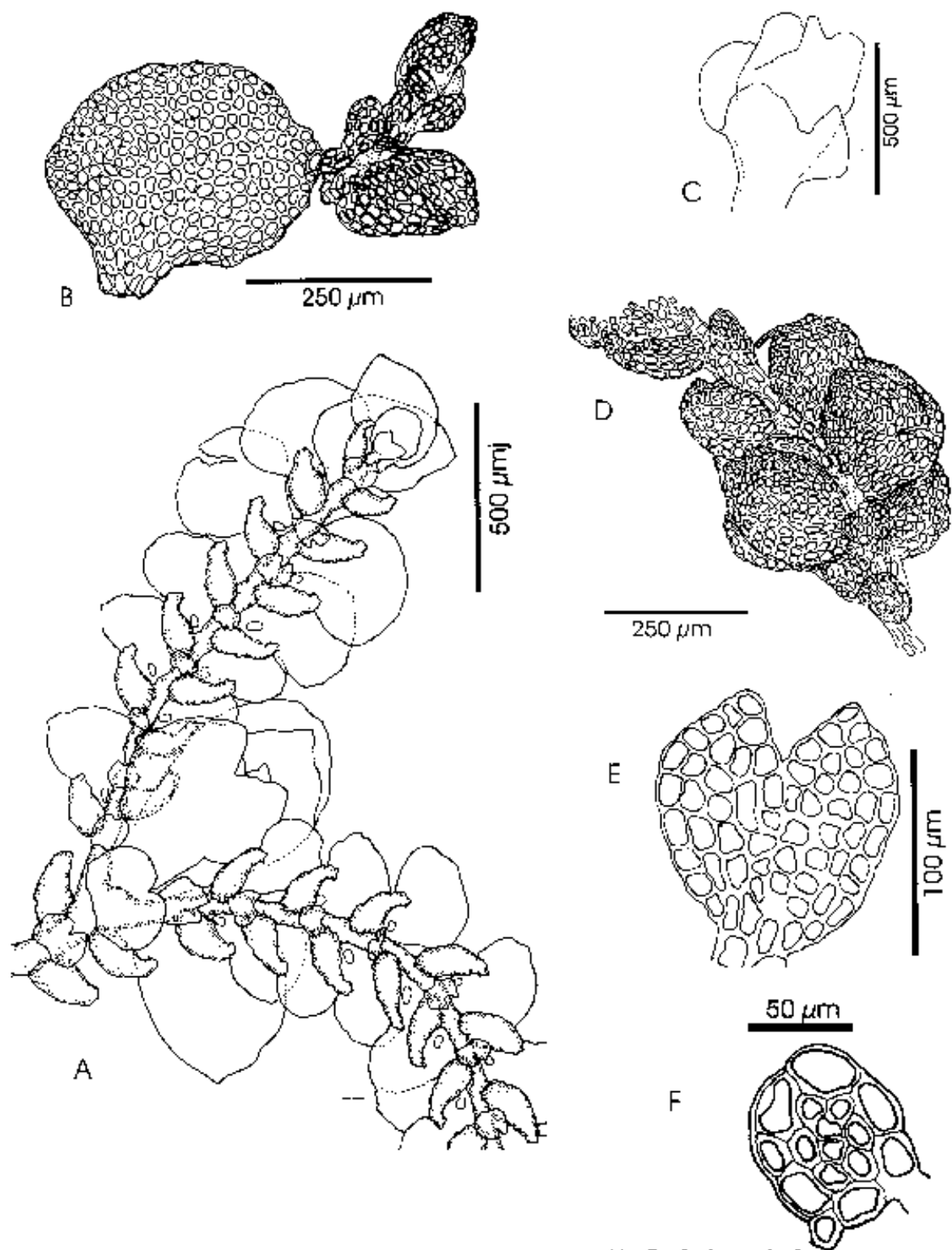


Figure 25. *Ceratolejeunea falsidissima* (Hampe & Gottsche) Evans. A. Habit. B. Caducous leaf lobe with juvenile plant. C. Perianth outline. D. Androecial branch. E. Underleaf. F. Stem cross section. From Puerto Rico, the type (B), from Cuba, Pócs 9084/AG (A, E-F), Pócs 9076 (C-D).

Specimens examined. COSTA RICA. **Puntarenas:** Rincón de Osa, Trail Boscosa-Cerro Chocuaco, Gradstein & Dauphin 9333b (GOET, USJ).
PANAMA. Without locality, Gradstein & Salazar Allen 9249d (JE).
CUBA. **Oriente:** Sierra Maestra, región de Pico Turquino, T. Pócs 9086au (JE); Holguín, Cuchillas de Moa, T. Pócs 9176m (JE). **Santiago de Cuba:** Falda N y cima del Pico Turquino, Vicario 10180 (HABE). **Without locality,** Wright s. n. (G, MANCH, NY)
PUERTO RICO. The type.
GUADELOUPE. **Without locality,** L'Herminier s. n. (G).
VENEZUELA. **Bolívar:** Ayuan Tepui, Steyemark 94054 (NY). **Tachira:** Type of *Ceratolejeunea andicola* Schust.
GUYANA. **Upper Mazaruni:** N slopes of Mount Roraima, Gradstein 5400d (GOET, JE, U).
ECUADOR. Type of *Ceratolejeunea wallisii* Steph.
BOLIVIA. **La Paz:** type of *Ceratolejeunea stenostoma* Herz.

An unmistakable species, *Ceratolejeunea patentissima* can be easily distinguished from other species by its caducous leaf lobes, leaving only the flask-shaped lobules on the stem. The plant gives superficially the impression of a *Frullania* species, also because of its dark color. In some specimens (*e. g.* type of *C. wallisii* Steph., type of *C. stenostoma* Herz.), the degree of constriction at the lobule mouth varies, the long, curved apical tooth becomes visible. This may influence the lack of caducous leaves in the specimen with free lobule margins. The perianth lacks horns but has 4 or 5 inflated carinae instead and the leaves usually have a single basal ocellus.

Schuster (1978) described *C. andicola* based on a small specimen from a páramo area. In his plants, the underleaves are notched about 1-3 cells, and the author reports that the medullary cells are in number of 4-6 in the stem cross section. The examination of a fragment of the type did not confirm his observations, for 9 medullary cells were found in one of the stems. This overlaps with the number of medullary cells given by Schuster for *C. patentissima* (ca. 10). The notched underleaves in *C. patentissima* are here regarded as a juvenile character based on the observation that underleaves of young stem tips tend to be less bifid at earlier stages. The number of oil-bodies per cell and the number of ocelli per leaf lobe as given by Schuster (1992) also overlap in the cited specimens. Therefore *C. andicola* Schust. is here reduced to synonymy.

17. *Ceratolejeunea pungens* Spruce ex Steph., Sp. Hep. 5: 434. 1913. Type. Ecuador. Canelos: Andes Quitenses, Canelos, "in arborum ramis", Spruce s. n. (holotype, G; isotypes, B, G, JE, MANCH, NY, US). Figure 26.

Plants dioicous, light to dark reddish-brown, creeping to almost hanging, sparsely branched. Stem with leaves 1.9-3.0 mm wide; profusely branched, in cross section 125-190 μm in diameter, medullary cells 21-24, ventral cells in surface view rectangular, 30-65 x 60-125 μm , dorsal cells rectangular, 45-65 x 85-90 μm . Flagelliferous branches not seen. Leaves imbricate, lobe ovate-lanceolate from a wide base, 525-850 x 975-1250 μm , apex rounded to acuminate into an awn, awn 250-360 μm , antical margin strongly toothed, with 5-8 teeth, teeth 1-7 cells long from a 2-4-celled base, 20-225 μm long, postical margin with 0-4 teeth, some teeth unicellular; median leaf cells mostly hexagonal with variable stellate to short-elliptic lumina, marginal cells 10-20 x 15-40 μm ; ocelli, 25-40 x 35-70 μm , single or moniliate, 2-6 per leaf, row 125-320 μm long; oil-bodies finely granular, rounded to elliptic, 2 per cell in all cells; lobules inflated or spherical forming series on branches, 0.1 the leaf lobe length, free margin plane; series of spherical inflated lobules present. Utriculi frequent, in pairs at the base of lateral branches. Underleaves ovate-lanceolate, 270-520 x 400-700 μm , the margins entire bearing a tooth at one or both sides, lobes acute, ending in a one-celled tip, attachment to the stem forming a shallow curved line.

Androecia lateral on main branches, in spikes of 4-7 bract pairs, spikes 780-950 μm long; bracteoles single?, 150 x 175 μm , bifid to 1/3.

Gynoecia and sporophyte not seen.

Illustrations. Fulford 1945, p. 374.

Distribution. Known only from a few collection from the Chocó and the northern Andes. Epiphytic (almost hanging) on tree trunks in wet lower submontane forest, 200-650 m.

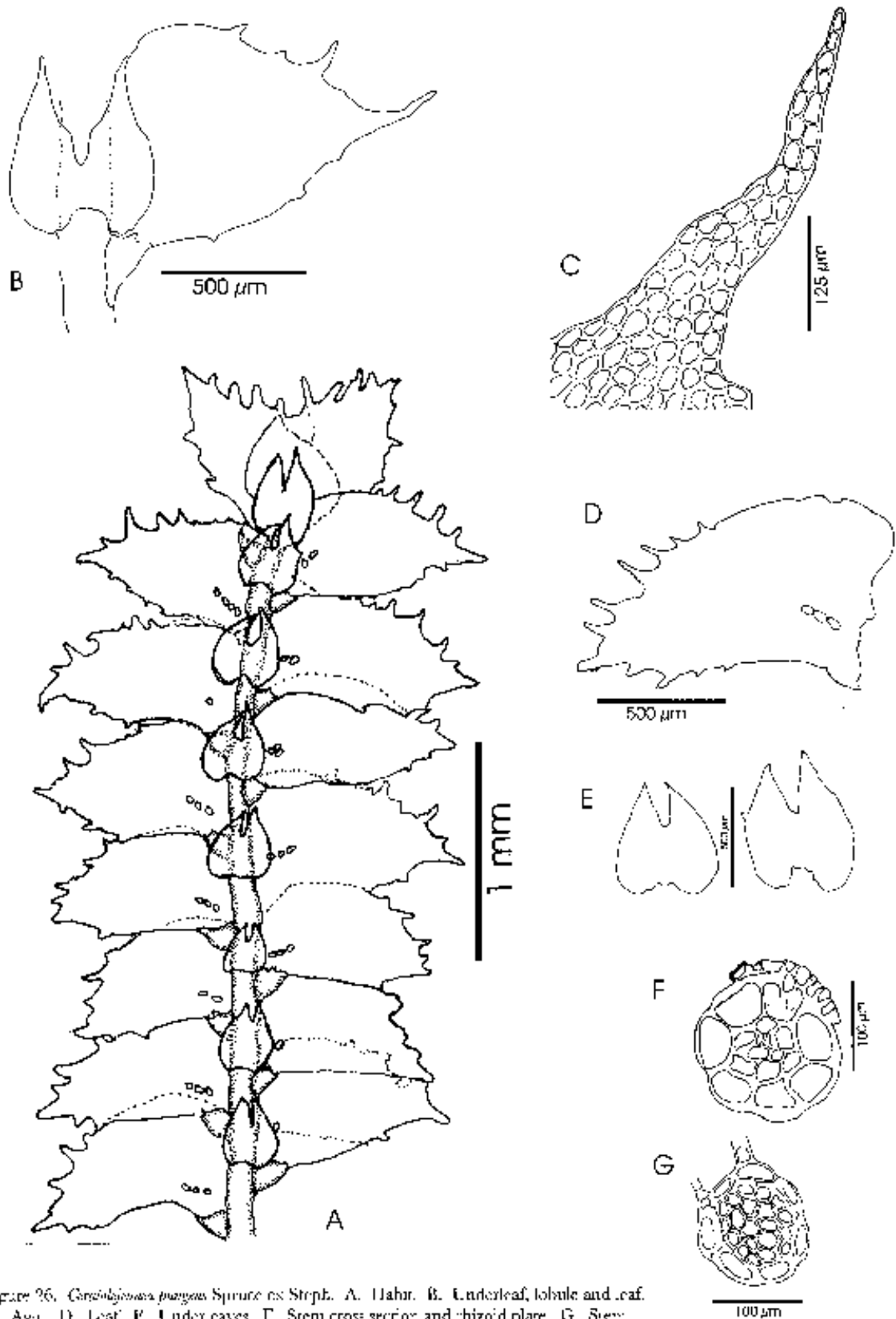


Figure 26. *Carex blymiana* Spruce ex Steud. A. Habit. B. Underleaf, lobule and leaf. C. Awn. D. Leaf. E. Underleaves. F. Stem cross section and rhizoid plate. G. Stem cross section. From Ecuador, the type (B-C), Dauphin 2704 (A, D-G).

Specimens examined. COLOMBIA. **Chocó:** road Santa Cecilia-Tadó, 40 km W of St. Cecilia, Gradstein 8755 (GOET, U).

ECUADOR. **Chimborazo:** Spruce L 142 (MANCH). **Esmeraldas:** San Lorenzo, Alto Tambo, Dauphin 2704 (GOET, USJ); **Pastaza:** the type.

Ceratolejeunea pungens is an unmistakable species. It can be distinguished by its relatively large size and almost hanging habit, coarsely dentate leaves with multicellular teeth and the ocelli forming a nerve oriented towards the rounded to long acuminate leaf apex.

18. *Ceratolejeunea rubiginosa* Steph., Hedwigia 34: 237. 1895. Type. Cuba. Without locality, Wright s. n. (holotype, G). Figure 27.

Ceratolejeunea pseudoneura Zwickel, Annal. Bryol. 6: 110. 1933. Type. Cuba. Without locality, Wright s. n. (holotype, M). (Fulford 1945).

Plants autoicous, reddish-brown, stem with leaves 0.3-1.0 mm wide; sparsely branched. Stems in cross section 60-90 μm in diameter, medullary cells 9-21, ventral cells in surface view quadrate to short rectangular, 15-30 x 20-50 μm , dorsal cells rectangular, 20-35 x 25-40 μm . Flagelliferous branches not seen. Leaves imbricate, lobe ovate, slightly asymmetrical, 200-390 x 240-1000 μm , apex rounded to acute, margins entire, irregularly crenate to toothed with 3-20 teeth on the antical margin, teeth to 15 μm long, sometimes appearing as cuticular projections between marginal cells; median leaf lobe cells isodiametrical to short elliptical, 10-30 x 15-35 μm , intermediate thickenings frequent; marginal leaf lobe cells 5-15 x 10-20 μm ; oil-bodies not seen; ocelli rectangular, 25-35 x 15-55 μm , 2-7 per leaf, moniliate, rows 1-2, 95-185 μm long; lobules inflated, 0.3 the leaf lobe length, free margin slightly involute, reduced lobules absent?. Utriculi single at the base of lateral branches. Underleaves ovate, 110-190 x 90-210 μm , margins plane, entire or with one or two blunt cellular projections, bifid to $\frac{1}{2}$, lobes acute.

Androecia lateral on main branches, in spikes of 2-7 pairs of bracts, 475-1100 μm long; bracteole obovate, 90-110 x 105-125 μm , bifid to $\frac{1}{3}$, lobes acute.

Gynoecia on lateral branches with one sterile innovation; bracts obovate, margins dentate at the apex; bracteoles ovate, 285-350 x 400-500 μm , dentate at the apex, teeth to 20 μm (1-2 cells) long, bifid to $\frac{1}{2}$, lobes acuminate. Perianth, obconic, 290-320 x 550 μm ; horns inflated, 110-120 μm long.

Seta 195 μm (4+12 cells) in cross section, hyaline or rarely tinged with brown. Capsule valves 162,5 x 305-315 μm . Elaters 10-12.5 x 170-225 μm , 4-5 per valve, base rarely tinged with brown. Valves lanceolate-elliptic, ca. 150 x 250 μm . Spores 20 x 45-52.5, with few, well defined rosettes.

Distribution: Distributed in the Caribbean, Costa Rica and Cocos Island. Fulford (1945) and Schuster (1980) reported it also from Florida. This species can be epiphyllous, corticolous or may grow on rotting bark in humid areas from lowlands up to the lower montane forest (0-ca. 1000).

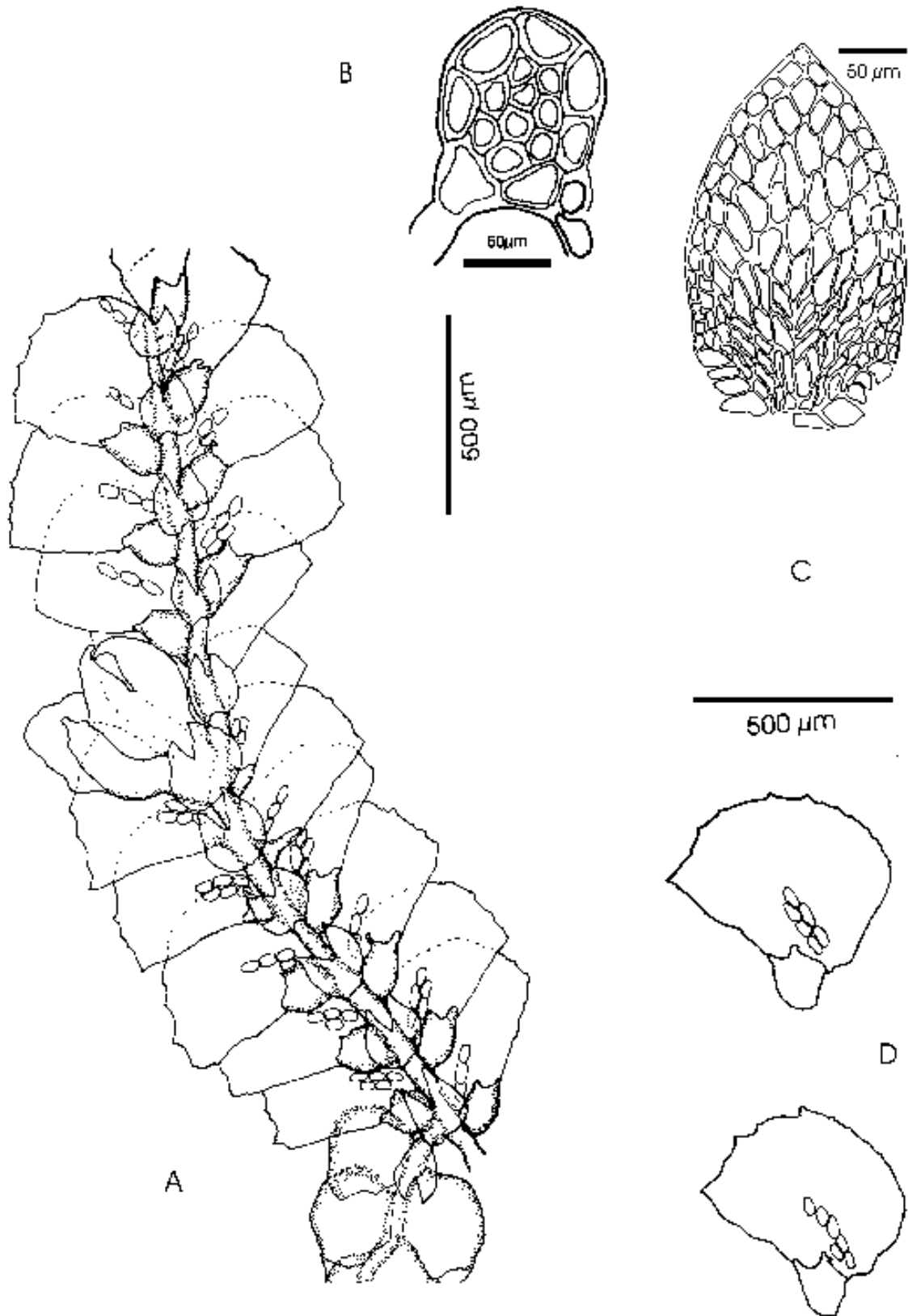


Figure 27. *Ceratolepisosa rubiginosa* Steph. A. Habit. B. Stem cross section. C. Sporophyte capsule valve. D. Leaves. From Cuba, the type.

Specimens examined. COSTA RICA. **Heredia:** La Selva Biological Station, Bernecker-Lücking 97-9 (hb Bernecker-Lücking). **Puntarenas:** Cocos Island, Stewart 1354pp (GOET), Dauphin 1055, 1076, 1121 (USJ). BAHAMA ARCHIPELAGO. **Oppice:** Northern Section, near Nicholl's Town., Small & Carter 8925app (NY).

CUBA. **Oriente:** Yateras, Finca las Gracias, Maxon 4331, 4491 (US). **Without locality:** the type, type of *Ceratolejeunea pseudoneura* Zwickel.

PUERTO RICO. Cordillera Central above Vilalba, Doña Juana recreation area., Thiers 5298 (NY).

This species can be separated from *C. cubensis*, *C. guianensis* and *C. laetefusca* by the moniliate ocelli and its reddish-brown color. It can be separated from *Ceratolejeunea ceratantha* which has up to 3 seriate ocelli, by the occurrence of tiny teeth throughout the antical leaf margin. Robust specimens of *C. rubiginosa* may also be recognized by the occurrence of a second row of ocelli.

19. *Ceratolejeunea spinosa* (Gottsche) Schiffn., Bot. Jahrb. 23: 595. 1897; *Lejeunea spinosa* Gottsche, in Gottsche, Lindenberg & Nees, Syn. Hep.: 402. 1845, Trans. & Proc. Soc. Bot. Edinburgh 15: 211. 1884; *Colura spinosa* (Gottsche) Trevis., Mem. Ist. Lomb. Sci. Mat. Nat., Ser. 3 (4): 402. 1877. Type. Saint Kitts. Without locality, Breutel s. n. (*lectotypus nov.*, G; isolectotypes, B, S, W). St. Vincent. Without locality, without collector (isosytype, S). Figure 28.

In the original description (Gottsche *et al.* 1845), samples from three localities were mentioned, the one chosen as lectotype is the first one referred in the protologue and from which are more duplicates available.

Ceratolejeunea platyceras (Spruce) Steph., Sp. Hep. 5: 432. 1913; *Lejeunea (Cerato-Lejeunea) platyceras* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 210. 1884. Type. Ecuador. Tungurahua: „In valle Fl. Pastasa infra Baños, alt. 1500m“, Spruce s. n. (*lectotypus nov.*, MANCH; isolectotype, G). Pastaza: Canelos, „in cortice“, Spruce L172 (syntype, MANCH), *syn. nov.*

Spruce (1884) mentioned several type localities. The chosen lectotype comes from the first mentioned type locality and represents the robust habit of the taxon.

Ceratolejeunea dominicensis Steph., Sp. Hep. 5: 410. 1913. Type. Dominica. Without locality, Armitage s. n. (holotype, G), *syn. nov.*

Ceratolejeunea heteroloba Steph., Sp. Hep. 5: 417. 1913. Type. Bolivia. Without locality, Rusby, s. n. (holotype, G), *syn. nov.*

Plants dioicous, yellowish green to reddish-brown, stems to 6 cm long, with leaves 0.8-1.6 mm wide, profusely and irregularly branched. Stems in cross section 70-160 μm in diameter, medullary cells 15-24, with two ventral in surface view quadrate to short rectangular, 15-75 x 25-80 μm , dorsal cells subquadrate to rectangular, 25-40 x 30-70 μm . Flagelliferous branches not seen. Branch leaves imbricate, lobe asymmetric-ovate, 290-690 x 400-760 μm , antical margin usually strongly toothed, with 5-20 teeth, 10-50 μm (1-4 cells) long, postical margin entire or with 0-3 teeth, apex rounded or broadly acute; median leaf lobe cells with rounded, short-elliptic or irregular shaped lumina, 15-30 x 20-45 μm , marginal cells 10-20 x 12-35 μm , margins plane or incurved; walls thin, intermediate thickenings rare, oil-bodies elliptical, 6-11 μm long (*vide* Thiers 4669 (NY)), botryoidal, 1-6 per cell, in all cells; ocelli 20-40 x 45-85 μm , basal, sometimes geminate, contiguous or isolate, 1-4 per leaf; lobules inflated or spherical forming series on lateral or main stems, reduced lobules rare, 0.2-0.4 the leaf lobe length, free margin involute or plane, apical tooth curved. Utriculi frequent, in pairs or solitary at the base of lateral branches. Underleaves distant to subimbricate, ovate, 140-390 x 150-400 μm , bifid to 2/3, lobes acute to short acuminate, ending in a one or two-celled tip, margins entire, crenulate or with blunt projections, plane or recurved. Vegetative regeneration from leaves observed in a single case by Fulford (1944b).

Androecia on lateral branches, in spikes of 4-7 bract pairs, spikes 750-1300 μm long, male bracteole ovate, 160 x 200 μm , bifid to 1/4, lobes rounded.

Gynoecia lateral on main branches, with one sterile innovation; bracts obovate, 500 x 800 μm , with 3-4 geminate ocelli on the lower central lobe portion, proximal margin half entire, distal margin half toothed, teeth uniseriate, to 65 μm long; bracteoles ovate to rectangular, 300-360 x 500-600 μm , bifid to 1/2, lower margins entire, apical region with 2-3 teeth (also on sinus!). Perianth, 330-620 x 550-950 μm , surface mammillose, horns four, compressed laterally, inflated when young, the tips collapsing after development, 110-200 μm long.

Sporophyte valves elliptical-lanceolate, 185 x 345 μm . Elaters ca. 300 μm long. Spores not seen.

Illustrations. Evans 1905, plate 19; Fulford 1945, p. 375.

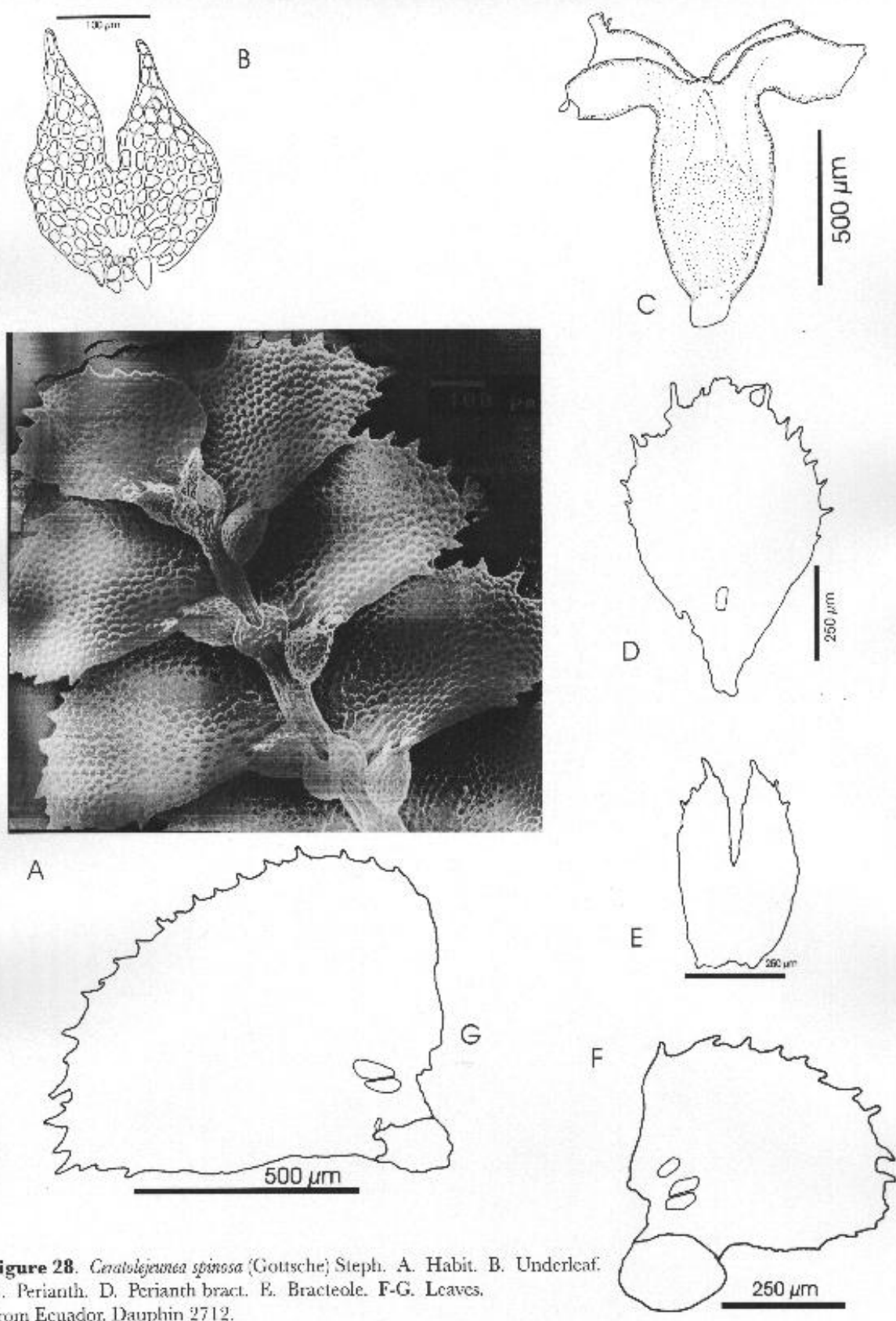


Figure 28. *Ceratolejeunea spinosa* (Gottsche) Steph. A. Habit. B. Underleaf. C. Perianth. D. Perianth bract. E. Bracteole. F-G. Leaves. From Ecuador, Dauphin 2712.

Distribution: Occurring in very wet regions of Costa Rica, Panama, the higher peaks of the Caribbean, Chocó, northern Andes and the Amazonian foothills of the northern Andes. A corticolous species, collected in open places in wet submontane forest areas at middle elevations, 500-1500 (-2080) m.

Specimens examined. COSTA RICA. **Heredia:** Sarapiquí, el Plástico, Sendero Tigre, Dauphin 2172, 2174 (GOET, INB). **Limón:** Braulio Carrillo National Park, Quebrada Gonzales, Bernecker-Lücking 92-594 (hb Bernecker-Lücking). **Puntarenas:** Monteverde, James 1971-34 (US).

PANAMA. **Darién:** Cerro Pirre, Salazar & Gradstein 9232, 9300, 9728 (GOET, U). **Veraguas:** Santa Fe, near Escuela de Agricultura Alto Piedra, Antonio 3945b (GOET, U).

CUBA. **Santiago de Cuba:** Sierra Cristal, Arroyo Narezano, Mustelier & Vicario 13475 (HABE).

JAMAICA. John Crow Peak, Maxon & Killip 1066 (US).

PUERTO RICO. **Luquillo:** El Yunque, Evans 61, 97(US).

DOMINICA. Morne Trois Pitons, E of Pont Cassé, Schuster 67513e (US). **Without locality:** type of *C. dominicensis* Steph.

ST. KITTS: the type.

COLOMBIA. **Cauca:** Isla Gorgona, Gradstein s. n. (GOET). **Chocó:** Nuquí, amargal at the Pacific Coast SW of Arusi, Gradstein 8822 (GOET, U); road Santa Cecilia-Tadó, 40 km W of St. Cecilia, Gradstein 8724 (GOET, U); Road Tutunendo-El Carmen, shortly W of point 20, Gradstein 8906, 8928, 8943 (GOET, U); San José del Palmar, vereda El Talmar”, Aguirre & van Reenen 3772 (GOET, U). **Risaralda:** Pueblo Rico, W slope Western Cordillera, Cerro Montezuma, Wolf 1596 (GOET); W side of Cordillera Occidental, along trail from Jeguadas to Puerto de Oro, W of Mistrato, Gradstein 8296a, 8447, 8459, 8488 (GOET, U)

ECUADOR. Canelos, Spruce L172 (MANCH). **Esmeraldas:** San Lorenzo, Alto Tambo, down hill after Lita, Dauphin 2708, 2709, 2712 (GOET, USJ). **Tungurahua:** type of *Ceratolejeunea platyceras* (Spruce) Steph.

BOLIVIA. **Beni:** Ballivian, Serranía del Pilon Lajas, Gradstein 7159 (GOET, U). **Cochabamba:** Villa Tunari, Parque Nacional Carrasco, Old road to Cochabamba, Dauphin 2812 (GOET, USJ). **Without locality:** Rusby s. n. (G).

Ceratolejeunea spinosa can be easily distinguished by its dioicous, corticolous habit and its strongly serrate, asymmetrical leaves on main branches. Because of its laterally compressed horns, Spruce named it *C. platyceras*. *Ceratolejeunea spinosa* may be compared with *C. coarina* (Gottsche) Schiffn., which has similarly shaped leaves and ocelli, but the latter species is usually much smaller, usually epiphyllous, monoicous and the leaf margin has numerous small, unicellular teeth or is entire.

Doubtful names and excluded taxa

Ceratolejeunea anomala (Lindenb. & Gottsche) Steph., Sp. Hep. 5: 396. 1913; *Lejeunea anomala* Lindenb. & Gottsche, Lineal 24: 636. „1851“ 1892; *Euosmolejeunea anomala* (Lindenb. & Gottsche) Zwickel, Annal. Bryol. 6: 112. 1933. Type. Surinam. Paramaribo, Kegel 993 (holotype, W; isotype, G, GOET).

Plants dioicous (?), light brown, stem with leaves 1-1.5 mm wide; sparsely branched. Stems in cross section 105-115 μm in diameter, with 7 epidermal enlarged cells and 17-21 medullary cells, with 2 ventral rows of cells in surface view, these cells rectangular to quadrate, 30-65 x 40-75 μm , and 3 rows of dorsal stem cells, mostly rectangular, 25-50 x 35-75 μm . Branches *Lejeunea*-type; flagelliferous branches not seen. Leaves slightly imbricate, leaf lobe ovate-ligulate, symmetrical, 390-410 x 550-750 μm , apex rounded, plane, margins entire; median leaf lobe cells isodiametrical to elliptical, 30-35 x 30-65 μm , walls regularly thickened, intermediate thickenings frequent, 1 or rarely 2 per wall, trigones small, cuticle densely papillose, marginal cells rounded or quadrate to rectangular, 15-30 x 25-30 μm ; oil-bodies allanthoid, 17-20 μm long, brownish, surface asperulate (*vide* Thiers 4697 (NY)); ocelli absent; lobules mostly reduced, 0.1 (-0.2) the leaf lobe length, free margin plane, apical tooth unicellular, hyaline papilla proximal. Utriculi absent. Underleaves reniform, 300-650 x 300-530 μm , bifid to 1/4, lobes acute, margins entire, base cordate.

Androecia on short spikes on main stems, in spikes of 2 bract pairs.

Gynoecia on lateral branches with one fertile innovation; bracts obovate, 270 x 780 μm , margins entire, apex rounded or broadly acute, bract lobules ligulate, 116 x 500 μm , apex rounded; bracteole obovate, 250-340 μm x 620-800 μm , bifid 1/3-2/3, lobes long acuminate, ending in a 2-3 celled apex, margins entire, connate at the base with the bracts. Perianth dorsiventrally compressed, with 5 keels, not protruding from the perianth body smooth or slightly toothed.

Sporophyte not seen.

Distribution. Known from Surinam, growing on wet rocks (Stephani 1913).

Specimens examined. SURINAM. The type, Kegel 169 (G). ECUADOR. Pastaza: Baños-Puyo road, along Río Alpayacu, 15 km W of Puyo, Thiers 4697 (NY).

With a brownish color and superficially resembling a *Ceratolejeunea*, closer examination of specimens of this taxon reveals the lack of brown coloration of the middle lamellae and

absence of ocelli, which excludes it from *Ceratolejeunea*. The densely papillose cuticle and the regularly thickened cell walls sometimes showing two intermediate thickenings are also untypical for *Ceratolejeunea*. The description of the oil-bodies given by Thiers 46197 (NY) wholly differs from typical *Ceratolejeunea*.

Zwickel (1933) placed *C. anomala* in the genus *Euosmolejeunea* (Spruce) Schiffn., which is generally considered a synonym of *Cheilolejeunea* (Spruce) Schiffn (*e. g.* Schuster 1980). The present plant material does not fit in *Cheilolejeunea*, however, because the position of the hyaline papilla is proximal.

The fertile gynoeical innovations in rows of 2 on branches with smaller leaves, the proximal papilla and the absence of ocelli, suggest that this plant belong in the genus *Taxilejeunea* (Spruce) Schiffn. or *Lejeunea* Libert.

Ceratolejeunea devexa (Lindenb. & Gottsche) Steph., Sp. Hep. 5: 408. 1913; *Lejeunea devexa* Lindenb. & Gottsche, in Gottsche, Lindenberg & Nees, Syn. Hep.: 750. 1845.
=***Neurolejeunea breutelii*** (Gottsche) Evans, *vide* Zwickel (1933), Herzog (1933), Fulford (1945), Gradstein (1994).

Ceratolejeunea graminicolor (Spruce) Steph., Sp. Hep. 5: 414. 1913;
Lejeunea graminicolor Spruce, Journ. Linn. Soc. 30: 343. 1895; *Taxilejeunea graminicolor* (Spruce) Steph, Sp. Hep. 5: 489. 1914. Type. St. Vincent. „ In monte Bonhomme, super *Plagiochilas repens*“, Elliot 80, 92 (not seen).

Type not available in MANCH (L. Stables pers. com.). According to the original description, „flores fem. in ramo innovando quasi-seriati“ this species may well belong in the genus *Taxilejeunea*.

Ceratolejeunea lobata Clark, Proc. Cal. Acad. Sci 27: 597. 1953. Type. Costa Rica. Puntarenas: Cocos Island, Clark 221 (not seen). The type of the species is not available in the herbarium of the California Academy of Sciences (M. Bourrell, pers. com.). Judging from the description and drawings (p. 617), and as suggested by Schuster (1956, 1980), this taxon may be a synonym of *Ceratolejeunea cubensis* (Mont.) Schiffn.

Ceratolejeunea luteola (Spruce) Steph., Sp. Hep. 5: 422. 1913; *Lejeunea* (*Cerato-Lejeunea*) *luteola* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 205. 1884.

= ***Cyclolejeunea luteola*** (Spruce) Grolle, Wiss. Zeitschr. Friedrich-Schiller-Univ. Jena, Math.-Nat. Reihe 33: 761. 1984.

Ceratolejeunea mollis Pearson, Annales Bryol. 4: 99. 1931. Type. Jamaica. Without locality, Bower s. n. (holotype, MANCH; isotype, MANCH), *syn. nov.*

= ***Lepidolejeunea involuta*** (Gottsche) Grolle, Journ. Hattori Bot. Lab. 55: 504. 1984.

Ceratolejeunea portoricensis (Hampe & Gottsche) Evans, Bull. Torrey Bot. Club. 34: 15. 1907; *Lejeunea portoricensis* Hampe & Gottsche, Lineal 25: 352. „1852“ 1853; *Lejeunea* (subgen. *Neurolejeunea*) *portoricensis* Hampe & Gottsche, in Stephani, Hedwigia 27: 288. 1888; *Neurolejeunea portoricensis* (Hampe & Gottsche) Schiffn., in Engler & Prantl, Nat. Pflanzenfam. 13: 131. 1893.

= ***Physantholejeunea portoricensis*** (Hampe & Gottsche) Schust., Phytologia 39: 429. 1978.

Ceratolejeunea radicata (Nees ex Mont.) Steph., Sp. Hep. 5: 435. 1913; *Lejeunea radicata* Nees ex Mont., in Ramón de la Sagra, Hist. Phys. ...Ile de Cuba, Bot. Pl. Cell.: 475. 1842; *Colura radicata* (Nees ex Mont.) Trevis., Mem. Real Instit. Lombard. Sci. Nat. ser. 3, 4: 402. 1877.

= ***Leptolejeunea radicata*** (Nees ex Mont.) Grolle, Journ. Hattori Bot. Lab. 45: 178. 1979.

Ceratolejeunea rigidula (Nees ex Mont.) Steph., Sp. Hep. 5: 437. 1913; *Lejeunea rigidula* Nees ex Mont., Ann. Sci. Nat. Bot., ser. 2, 14: 336. 1840.

= ***Cheilolejeunea rigidula*** (Nees & Mont.) Schust. (Schuster 1980).

Ceratolejeunea scaberula (Spruce) Steph., Sp. Hep. 5: 439. 1913; *Lejeunea* (*Priono-*
Lejeunea) *scaberula* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 159. 1884;
=***Prionolejeunea scaberula*** (Spruce) Steph., Sp. Hep. 5: 214. 1913. See also Zwickel
(1933).

Ceratolejeunea uleana Steph., Sp. Hep. 5: 445. 1913.
=***Neurolejeunea breutelii*** (Hampe & Gottsche) Evans, *vide* Zwickel (1933), Gradstein
(1994).

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CHRONOLOGY

of publications on the genus *Ceratolejeunea*.

Year	Author/Work	Comments
1884	Spruce, Hepaticae Amazonica et Andinae	Describes the subgen. <i>Cerato-Lejeunea</i> with 12 new spp. 17 in total (based on the Sectio <i>Ceratantha</i> (Gottsche <i>et al.</i> 1844; with 17 spp. worldwide).
1892	Jack & Stephani. Hepaticae Wallisiana. Hedwigia 31: 16-	Lists <i>Ceratolejeunea</i> among other genera and describe the first sp. validly in the genus: <i>C. grandiloba</i> .
1893	Schiffner <u>in</u> : Engler & Prantl (eds.), Nat. Pflanzfam. 1 (3): 61-134.	Describes <i>Ceratolejeunea</i> among other genera, mentions the existence of 54 tropical spp., lists 7 names.
1905	Evans. Hepaticae of Puerto Rico. V. Ceratolejeunea. Bull. Torrey Bot. Club 32: 273-290.	<i>Ceratolejeunea</i> of Puerto Rico: with 7 spp., including <i>C. valida</i> sp. nov. Incorporates new cytological Characters in the taxonomy of the genus...
1913	Stephani. Species Hepaticarum. Vol. V: 391-450.	Lists 100 world spp., includes 20 new taxa for the Neotropics and 9 for the Paleotropics and 38 new combinations of taxa previously described by Spruce or himself under the subgen. <i>Cerato-Lejeunea</i> .
1932	Zwickel. Studien über die Ocellen der Lebermoose. Beih. Bot. Centralbl. 49: 569-648.	Describes and classifies ocelli of 32 Neotropical and 7 Paleotropical taxa and adds from Literature (Spruce 1884, Stephani 1913), in total 90 (75 + 15) names. Classification for ocelli type and distribution on the leaf, discusses taxonomical value.
1933	Herzog. Beiträge zur Kenntnis von <i>Neurolejeunea</i> . Ann. Bryol. 6: 46-58.	Discusses on the relationship of holostipe <i>Ceratolejeuneas</i> and <i>Neurolejeunea</i> . Combines species previously in <i>Cerato</i> into <i>Neuro-</i> and suggests placing <i>N. portoricensis</i> in subgen. With relationship to <i>Ceratolejeunea</i> .
	Zwickel. Zwei neue Gattungen, einige neue Arten un Umstellungen bei den Lejeuneaceen. Ann. Bryol. 6: 105-121.	Describes two new species (both synonyms now) and transfers <i>C. scaberula</i> (Spruce) Steph. to <i>Prionolejeunea</i> (without looking at the type), <i>C. anomala</i> to <i>Euosmolejeunea</i> , <i>C. devexa</i> to <i>Neurolejeunea</i> and <i>C. aberrans</i> to <i>Cladolejeunea</i> gen. Nov. from Africa.
	Fulford. 1944b. Sporelings and vegetative reproduction in the genus <i>Ceratolejeunea</i> . Bull. Torrey Bot. Club 71: 638-654.	Sporeling studies. First to identify and define a <i>Ceratolejeunea</i> -Type of sporeling, description of development and variation in some taxa (12 names). Describes vegetative reproduction for 8 taxa in the genus.
1945	Fulford. Studies on American Hepaticae VI. Ceratolejeunea. Brittonia 5: 368-403.	Treatment of 41 neotropical names, accepts 19 (but did not see the types). Sporophyte descriptions for the 1rst time? Gives special attention to perianth and lobe characters in the key and classification.
	Vanden Berghen, C. Contribution a l'étude des espèces africaines du genre <i>Ceratolejeunea</i> (Spruce) Schiffner Bull. Jard	Treats 10 african taxa, accepting 9 spp. <i>C. beninensis</i> Jones & Van den Bergen and <i>C. stictophylla</i> Herz. are described. A key to the african species is provided.

- Ceratolejeunea* (Spruce) Schiffner. Bull. Jard. Bot. Brux. 21: 61-81. The species are separated in four groups based on the orientation of the ocelli and perianth shape.
- Bonner. De Hepaticis III. A contribution to the study of the genus *Ceratolejeunea* (Spruce) Schiffner. Candollea 14: 163-252. Lists 120 taxa worldwide, provides some drawings from Stephani (Icones Hepaticarum) for most of the names, references to specimens (G) and literature for the spp., provides some lectotypifications and a new combination: *C. fallax* (Lehm. & Lindenb.).
- 1954 Schuster & Hattori. The oil-bodies of the Hepaticae. II. The Lejeuneaceae. Journ. Hattori. Bot. Lab. 11: 11-86. Provide oil body classification and description of oil bodies in 3 *Ceratolejeunea* spp.
- 1956 Schuster. North American Lejeuneaceae V. Schizostipae: *Ceratolejeunea*. Journ. Elisha Mitchell Soc. 72: 292-316. Treats 3 regional species and description of *C. confusa* from Trinidad. Drawings of oil bodies of *C. cubensis*. Introduces the anatomy of the stem as a criterium to separate holostipe species from *Neurolejeunea*. Describes a new subgenus: *Ceratophora* including *C. desciscens* and *C. portoricensis*.
- 1963 Bonner. Index Hepaticarum, pars IV; *Ceratolejeunea* to *Cystolejeunea*. J. Cramer, New York. Lists 127 World spp. and varieties, with 33 paleotropical and 94 neotropical taxa.
- 1969 Crandall. Morphology and development of branches in the leafy hepaticae. Beih. Nova Hedwigia 30: 1-261. Description of stem morphology, utriculi and development of branches. Includes 4 taxa in the studies (at least in the drawings).
- 1978 Schuster. Studies on Venezuelan Hepaticae, II. Phytologia 39: 425-432. Describes *Physantholejeunea gen. Nov.* based on *C. portoricensis* (Hampe & Gottsche) Evans, *Ceratolejeunea Caduciloba subgen. Nov.* (type: *C. patentissima* (Hampe & Gottsche) Evans and *C. andicola sp. nov.* (= *C. patentissima*).
- 1980 Schuster. The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian Vol. IV. Columbia University Press, New York. 1334p. Provides a key to the subgenera. Provides a key and descriptions of 3 regional species.
- 1981 Mizutani. Notes on the Lejeuneaceae. 5. Some Asiatic species of the genus *Ceratolejeunea*. Journ. Hattori Bot. Lab 49: 311-313. Treats 7 Asiatic spp. Describes *C. minor* and *C. inflata* (= *C. grandiloba* ?) from Borneo and Java. Puts 4 taxa under synonymy of *C. oceanica* (Mitt.) Steph (= *C. cornuta* ?)
- 1986 Thiers, B. M. Branching in the Lejeuneaceae (Hepaticae). IV. Lejeuneoideae. Nova Hedwigia 42: 237-275. Describes the branching type in *Ceratolejeunea*. Finds no difference in branching patterns between the subgenera recognized by Schuster.
- 1987 Grolle. Taxonomische Anmerkungen zu einigen Lejeuneaceae aus Peru, in W. Schultze-Motel & M. Menzel, Die Lebermoosflora im Bryotrop-Transsect von Peru. Beih. Nova Hedwigia 88: 61-104. Treats holostipous species, accepts 5 spp. in the subgenus *Ceratophora* Schust., puts 2 under synonymy. Provides key to the species. Comments on cell and perianth bract variability in *C. grandiloba* Jack & Steph.
- 1989 Gradstein. A key to the Hepaticae and Anthocerotae of Puerto Rico and the Virgin Islands. Bryologist 92: 329-348. Provides a key for 8 regional taxa, suggests that *C. cubensis* might be a synonym of *C. cornuta*.

- Onraedt. Contribution a la flore bryologique de Guyane Française. IV. Cryptogamie, Bryol. Lichenol.(10)2: 119-129.
- 1992 Schuster. The oil-bodies of the Hepaticae. II. Lejeuneace. Journ. Hattori Botanical Lab. 72: 223-227.
- 1999-2000 Dauphin. The Genus *Ceratolejeunea* Jack & Steph. in tropical America.
- Treats 9 regional spp., provides a key and illustrations for every taxon.
- Provides description and drawings of oil-bodies of 5 taxa and a „phenotype“ including also description of cytological features (cell shape, size, walls, lamellae, intermediate thickenings, trigones, ocelli). Suggests a primary division of the schizostipous species based on the orientation of the ocelli.
- Treats 110 Neotropical names, accepts 23 spp., including *C. minuta* sp. nov. and *C. dussiana* (Steph.) Dauphin *comb. Nov.*