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The Genus *Cyclolejeunea* A. EVANS *(Hepaticae, Lejeuneaceae)* in Costa Rica

By

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With 5 Figures

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Summary

BERNECKER-LÜCKING A. 1998. The genus *Cyclolejeunea* A. EVANS (*Hepaticae*, *Lejeuneaceae*) in Costa Rica. – Phyton (Horn, Austria) 38 (1): 175–193, 5 figures. – English with Spanish and German summary.

The genus *Cyclolejeunea* in Costa Rica is treated from the taxonomical point of view. There are five representatives of this genus in Costa Rica. *C. convexistipa* (LEHM. & LINDENB.) A. EVANS is easily recognized by its undivided rounded underleaves. *C. chitonia* (TAYLOR) A. EVANS is the largest species with short emarginate underleaves, whereas in all of the other species the underleaves are deeply bifid. The margin of the lateral leaves is dentate in *C. peruviana* (LEHM. & LINDENB.) A. EVANS and crenulate to serrulate by conical papillose cells in *C. luteola* (SPRUCE) GROLLE and *C. accedens* (GOTTSCHE) A. EVANS. The latter one is additionally characterized by the absence of ocelli. High variability of morphological characters and their dependence on microlimatic conditions, especially water availability is discussed. A key to the species is provided.

Resumen

BERNECKER-LÜCKING A. 1998. El genero *Cyclolejeunea* A. EVANS (*Hepaticae*, *Lejeuneaceae*) en Costa Rica. – Phyton (Horn, Austria) 38 (1): 175–193, 5 figuras. – Ingles con resumenes en español y alemán.

El género *Cyclolejeunea* en Costa Rica es tratado taxonomicamente. Hay cinco especies del género en Costa Rica. *C. convexistipa* (LEHM. & LINDENB.) A. EVANS se

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puede reconocer facilmente por sus anfigastrios redondeados enteros. *C. chitonia* (TAYLOR) A. EVANS es la especie más grande con anfigastrios emarginados. En las demás especies los anfigastrios son pfofundamente bífidos. El margen de las hojas laterales es dentado en *C. peruviana* (LEHM. & LINDENB.) A. EVANS y crenulado a serrulado por células papilosas en *C. luteola* (SPRUCE) GROLLE y *C. accedens* (GOTTSCHE) A. EVANS; la última caracterizada adicionalmente por la falta de ocelos. Se discute la alta variabilidad de carácteres morfológicos y su dependencia a las diferentes condiciones microclimáticas, especialmente la presencia de agua en el sitio en que crecen las plantas. Una clave para determinar las especies tratadas completa el trabajo.

Zusammenfassung

BERNECKER-LÜCKING A. 1998. Die Gattung *Cyclolejeunea* A. EVANS (*Hepaticae, Lejeuneaceae*) in Costa Rica. – Phyton (Horn, Austria) 38 (1): 175-193, 5 Abbildungen. – Englisch mit spanischer und deutscher Zusammenfassung.

Die Gattung *Cyclolejeunea* wird für Costa Rica taxonomisch bearbeitet. Fünf Vertreter sind in Costa Rica zu finden: *C. convexistipa* (LEHM. & LINDENB.) A. EVANS ist leicht an den ungeteilten rundlichen Unterblättern erkennbar. *C. chitonia* (TAYLOR) A. EVANS ist die größte Art mit wenig eingeschnittenen Unterblättern. Bei allen anderen Arten sind die Unterblätter tief zweigeteilt. Der Rand der Flankenblätter ist bei *C. peruviana* (LEHM. & LINDENB.) A. EVANS deutlich gezähnt, während er bei *C. luteola* (SPRUCE) GROLLE und *C. accedens* (GOTTSCHE) A. EVANS durch leicht konisch verdickte Zellwände nur gekerbt, höchstens gesägt ist. *C. accedens* ist weiterhin durch das Fehlen von Ozellen charakterisiert. Die hohe Variabilität der morphologischen Merkmale und ihre Abhängigkeit vom Mikroklima, insbesondere der Verfügbarkeit von Wasser wird diskutiert. Ein Schlüssel zu den Arten ist beigefügt.

Introduction

All species of the genus *Cyclolejeunea* are found solely in the Neotropics where they grow not only as epiphylls, but also on smooth bark or twigs in moist lowland to montane rainforests. Most species were described by STEPHANI 1913. Originally about 35 different species names were known, some of which GROLLE 1984 reduced due to their synonymy to a current number of about 20 species. The high variability of morphological characters led to an unnecessary high number of species descriptions a fact that calls for further revision of the genus (LÜCKING 1995).

The genus is closely related to *Prionolejeunea* (SPRUCE) SCHIFFN. being similar in the dentate or crenulate leaf margins and the form of the perianth. On the other hand *Prionolejeunea* produces no gemmae, ocelli are always absent, and the gynoecial innovations, if present, are of the *Lejeunea*-Type (first leaf is a lateral leaf). In *Cyclolejeunea* the innovations are of the *Pycnolejeunea*-Type (first leaf is an underleaf) (GROLLE 1984).

In Costa Rica five species of *Cyclolejeunea* are known until today, some of them described very well by EVANS 1904. Nevertheless the species are sometimes hard to recognize, due to the variability of morphological characters, depending on microclimatic conditions. Therefore, the species

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are described here in detail and the differences between similar species are discussed.

The acronyms for the herbaria follow HOLMGREN & al. 1990. For the private herbarium of the author the abbreviation Be is used.

Cyclolejeunea A. EVANS

Bull. Torrey Bot. Club 31: 198 (1904). – Type of the genus: *Cyclolejeunea convexistipa* (LEHM. & LINDENB.) A. EVANS (= *Jungermannia convexistipa* LEHM. & LINDENB.).

The distinctive characters of the genus' species are the serrulate to dentate margins of the leaves, the flattened triangular-obovate perianth with an innovation mostly of the *Pycnolejeunea*-type, and the development of gemmae at the antical margin of the lateral leaves. Gemmae are composed of a single layer of cells, but vary within the genus in structure and the mode of germination. They lack adherent cells and stick to the substrate by means of adhesion (EVANS 1904, DEGENKOLBE 1937, HERZOG 1954). In *C. luteola* rhizoids stretch out from the margin of the gemmae in the same plane and help to fix the gemma to the surface of the substrate. In all other species, rhizoids if present project from the margin of the gemmae to its convex side. They may be useful for stabilisation in the air during dispersion, providing an upright orientation that keeps the concave side facing down, to facilitate the fixation on the substrate by means of adhesion. This mechanism is aided by the immediate growth of short rhizoids emerging from the margins of the gemmae which furthermore produce mucous secretions.

All the species of the genus *Cyclolejeunea* are very variable in their morphological characters, particularily in the degree of dentation at the margin of the leaves and underleaves. One cause of this variability seems to be the orientation of the shoots. Young plants are most of the times closely appressed to the substrate but with increasing size and degree of ramification, projecting erect shoots become more frequent. On creeping shoots, the lateral leaves and underleaves are only weakly dentate or rarely entire at the margin. Erect shoots always reveal denticulate to strongly dentate leaf margins. Development of different shoots, with different degree of dentation of leaf margins, is also found in other groups of *Lejeuneaceae*, and can be observed for example in *Ceratolejeunea plumula* (SPRUCE) STEPH. and *Odontolejeunea decemdentata* (SPRUCE) STEPH.

In *Cyclolejeunea*, the gynoecium, the sporophyte, and the gemmae develop on erect shoots, promoting the distribution of diaspores by increasing their exposure to wind and rain. However the morphological modifications on erect shoots seem to be an adaptation to environmental conditions. In wet sites with high daily rainfall and low evaporation rates, appressed shoots tend to be immersed in water for extended periods of

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time which is likely to impede gas exchange. The exposed erect shoots with their distinctly dentate leaf margins are useful to increase transpiration, and as expected those plants are more frequent in wet habitats. The papillae on the dorsal surface of lateral leaf cells in *C. accedens* might also serve as a means to enhance transpiration and to maintain gas exchange in moist habitats as already mentioned by PROCTOR 1979. Likewise a papillose surface has been considered as an adaptation to very wet habitats in vascular plants (CZIHAK & al. 1981; VON DENFFER & al.1983). It should be mentioned that papillae are also known to build up capillary systems serving for water conduction and therefore to work in the opposite way as an adaption to dry conditions (PROCTOR 1979).

Besides the stronger dentation of leaf margins on erect shoots, large rounded lobules with a strongly involute free margin serve to collect water. The lateral leaves are reduced in *C. convexistipa*, *C. accedens* and *C. luteola* but larger with strongly involute postical margin in *C. peruviana* and *C. chitonia*. The underleaves are also frequently enlarged, thus forming a gap together with the lateral leaves as a water reservoir. The storage of water was considered to be an important role of the water sacs by GOEBEL 1905, but some experiments of BLOMQUIST 1929 raise doubts on the efficiency of these structures since the water sacs themselves do not obstruct the transpriation to a considerable degree. Nevertheless, the water sacs serve to prevent the water from dropping down immediately which increases the availablility of this resource for the plant, likewise as already shown for the gaps formed by the underleaves together with the lateral leaves (PROCTOR 1979). The co-occurence of adaptations to store water on one hand and enhance transpiration on the other seems to be a paradox. However, this combination enables the plants to loose water under wet conditions as well as to resist loss of water under drier conditions. This ambiguity broadens the ecological range of the species. As a matter of fact all these species are generalists which can be found on different substrates like bark or living leaves and from lowland to montane forest, in the canopy as well as in the understorey (BIEBL 1964; CORNELISSEN & TER STEEGE 1989; MONTFOORT & EK 1990; GRADSTEIN 1992, 1994).

Key to the species of *Cyclolejeunea*

1a Underleaves on creeping shoots emarginate, with broad, rounded or apiculate lobes and entire margins (Fig. 2A); (on erect shoots with slightly to strongly dentate margins); lobules oblong to tubular with a distinct, short, generally curved tooth (Fig. 2F); gemmae reniform, usually plane, rarely slightly vault, usually without, rarely with 1–2 marginal rhizoids (Fig. 2G). . . . . *Cyclolejeunea chitonia*

1b Underleaves on creeping shoots rounded, slightly reniform (Fig. 3A), or deeply bifid with triangular erect lobes (Fig. 1A, 4B, 5A) and entire, crenulate or denticulate margins; (on erect shoots with crenulate or slightly to strongly denticulate

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margins); lobules short ovoid to trapezoidal, inflated with a distinct tooth, or oblong with a reduced blunt tooth; gemmae various in form but usually with two or more marginal rhizoids 2

2a Lateral leaves without ocelli; cells at the dorsal side of the lobe conical with papillae, but someimes smooth and papillae developed only at the border of the leaves (Fig. 1A, 1B); underleaves on creeping shoots bifid with triangular erect lobes; gemmae orbicular and 0.1–0.15 mm in diameter, usually with two marginal rhizoids (Fig. 1F) . . . . . *Cyclolejeunea accedens*

2b Lateral leaves with ocelli present at the base; cells at the dorsal side of the lobe smooth (rarely slightly crenulate); underleaves on creeping shoots bifid with triangular erect lobes (Fig. 4B, 5A) or rounded to slighly reniform (Fig. 3A); gemmae orbicular and more than 0.18 mm in diameter or ligulate, usually with three or more marginal rhizoids 3

3a Margin of the lateral leaves entire, crenulate or regularly serrulate by projecting cells; underleaves on creeping shoots bifid with triangular erect lobes with the margin entire to irregular crenulate, often angular-dentate at the sides (Fig. 4B); gemmae oval to elongate in shape with a median constriction and marginal spreading rhizoids (Fig. 4D) . . . . . *Cyclolejeunea luteola*

3b Margin of lateral leaves weakly to strongly dentate; underleaves on creeping shoots bifid with triangular erect lobes with the margin dentate, or rounded to slighly reniform with the margin entire; Gemmae rounded and domed like a watch-glass, usually with three or more rhizoids projecting from the margin to the convex side of the gemma (Fig. 3F, 5E) 4

4a Underleaves on creeping shoots rounded to slightly reniform with the margin entire (Fig. 3A); lobules with the apical tooth pointed, consisting of one short cell; gemmae with a marginal incision opposite the apical region (Fig. 3F) . . . . . *Cyclolejeunea convexistipa*

4b Underleaves on creeping shoots bifid with triangular erect lobes with the margin slightly to strongly dentate (Fig. 5A); lobules with a reduced and blunt apical tooth, built by an elongated, straight cell lying side by side with the adjacent cells (Fig. 5D); gemmae evenly rounded, with a mucus-papilla at the apical region (Fig. 5E) . . . . . *Cyclolejeunea peruviana*

Cyclolejeunea accedens (Gottsche) A. Evans (Fig. 1)

Bull. Torrey Bot. Club 31: 201 (1904). – *Lejeunea accedens* Gottsche, in Gottsche, Lindenberg & Nees, Syn. Hep.: 339 (1845). – Type: Lesser Antilles, St. Christopher. S. loc., 1841, Breutel s. n. (G).

Plants mostly epiphyllous, pale green to yellowish when dry. Shoots with leaves 0.8–1.7 mm wide. Stems 65–140 μm in diameter. Lateral leaves imbricated, 0.5–0.8 mm long, 0.4–0.7 mm broad, the margin weakly to sharply crenulate or denticulate from projecting cells. Lobule inflated, ovoid to trapezoidal, 120–190 μm long, 85–120 μm wide, keel smooth to crenulate, free margin involute. Apical tooth 1-celled, short, straight or slightly curved. Mouth straight to obliquely lunulate, consisting of 4 cells. Cells of the lobe at the margin 17–24 μm and in the middle 20–35 μm, isodiametric-polygonal, at the base slightly elongate 20–35 × 34–51 μm; cells

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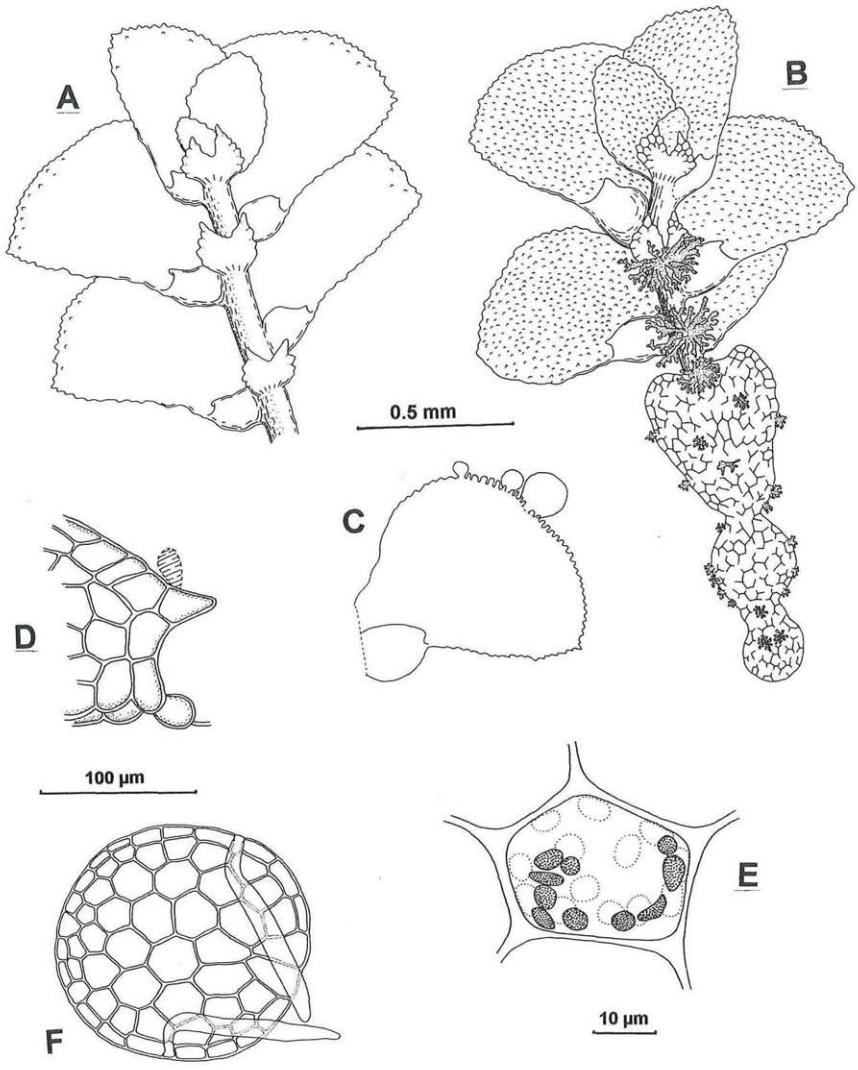

Fig. 1: *Cyclolejeunea accedens*. – A Shoot with papillae only developed at the margin of the lateral leaves, postical view. – B Gemma which formed a caracteristically ligulate thallus consisting of three parts upon germination, young shoot with cells at the dorsal side of the lobe conical with papillae. – C Lateral leaf with characteristically crenulate border and young gemmae. – D Lobule with tooth and hyaline papilla. – E Median cells with oil bodies and chloroplasts. – F Gemma with rhizoids projecting from the margin to the convex side.

at the dorsal side of the lobe conical with papillae, but sometimes smooth and papillae developed only at the border of the leaves. Cell walls thin,

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sometimes with small trigons or intermediate thickenings. Oil bodies finely granular under oil-immersion (magnification 1000×), about 7–15 per cell, rounded to oblong about 3.5–8 µm. Ocelli lacking. Underleaves orbicular, 0.15–0.25 mm long 0.13–0.25 mm wide, bifid with triangular erect lobes, sinus narrow and obtuse, margin crenulate to denticulate from projecting cells. Gemmae rounded and domed like a watch-glass, 0.10–0.15 mm in diameter, usually with two marginal rhizoids projecting from the margin of the gemma to its convex side. Upon germination the gemma first forms a characteristically ligulate thallus consisting of three parts (Fig. 1B).

Plants autoicous. Perianth triangular-obovate, 0.7–0.8 mm long, 0.4–0.6 mm wide in the upper part, born on a short lateral branch, rarely on a leading branch, innovating on one side, the innovation sterile or fertile with a androecium or gynoecium, the gynoecium again innovating on one side. Lateral keels of the perianth extended upwards as auricles with the margin crenulate to dentate, rarely spinose, borderd by narrow wings; cells of the perianth surface smooth; beak very indistinct. Female bracts obovate-oblong (0.25) 0.5–0.7 mm long, (0.2) 0.3–0.5 mm wide with the margin weakly to strongly crenulate to denticulate by projecting cells. Lobule rectangular, reaching about 20–25 % of the lobe length. Bracteole ovate, bilobed with the sinus narrow, 0.27–0.35 mm long 0.18–0.25 wide. Androecium terminal or on a lateral branch, bracts in 5–7 pairs, 1–2 male bracteoles present at the base of the branch. Antheridia in pairs, rarely single.

Specimens examined: Costa Rica. – Limon: Braulio Carrillo-National Park, Botarrama-Trail, epiphyllous, on *Ctenitis subincisa*, leg. BERNECKER-LÜCKING, 92–472 (Be); ibid. on *Welfia georgii*, 92–210; ibid. on *Calyptrogyne condensata*, 92–37, 92–394; ibid. on *Rhodospatha wendlandii*, 92–36, 92–38; ibid. on *Ocotea atirrensis*, 92–35; ibid. on *Miconia hamelii*, 92–431; (all of the foregoing specimens Be). – Puntarenas: Cocos Island, trail to the summit of Cerro Iglesias, ca. 550 m, epiphyllous, on *Dicotyledoneae*, leg. BERNECKER-LÜCKING, s.n. (Be); ibid. on *Araceae*, 92-366 (Be); ibid. on *Araceae* s.n. (Be); ibid. on Fern s.n. (Be) – Cartago: Tapanti National Park, epiphyllous, on *Dicotyledoneae*, leg. BERNECKER-LÜCKING, s.n. (Be).

This species can only be confused with *C. luteola*. In both of the species the underleaves have a similar shape and the margin of the lateral leaves is crenulate to serrulate. However, in *C. accedens* cells at the dorsal side of the lobe of the lateral leaves are frequently conical and have papillae and ocelli are absent, whereas in *C. luteola* cells are smooth and ocelli are present at the basal part of the lateral leaves. Gemmae also serve to distinguish the two species. In *C. accedens* they are rounded and domed like a watch-glass with two marginal rhizoids projecting from the convex side of the gemma, whereas in *C. luteola* they are oval in shape with a median constriction and have marginally spreading rhizoids.

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Cyclolejeunea chitonia (TAYLOR) A. EVANS (Fig. 2)

Bull. Torrey Bot. Club 31: 194 (1904); STEPHANI, Sp. Hep. 5: 190 (1913); STEPHANI, Sp. Hep. 5: 194 (1913). – *Lejeunea chitonia* TAYLOR, in GOTTSCHE, LINDENBERG & NEES, Syn. Hep.: 339 (1845), nom. inval. (Art. 75.1 Sydney Code). – *Lejeunea clitonia* TAYLOR ex LEHMAN, in LEHMANN, Nov. Stirp. Pugillus 8: 27 (1844), (typografical error). – Type: Guyana, Demerara River, s. n., hb GREVILLE (FH).

Plants epiphyllous or corticolous, green to brownish when dry. Shoots with leaves 1.4–3.0 mm wide. Stems 130–190 µm in diameter. Lateral leaves imbricated, 0.6–1.5 mm long 0.5–1.0 mm wide, the margin weakly to sharply denticulate. Lobule inflated, ovate-oblong to tubular, 0.34–0.55 mm long, 0.14–0.27 wide, keel weakly crenulate, free margin involute. Apical tooth 1-celled, very short and curved. Mouth obliquely lunulate, consisting of 4 cells. Cells of the lobe at the margin 18–24 µm and in the middle 24–35 µm, isodiametric-polygonal, at the base slightly elongate 34–45 µm. Cell walls thin, sometimes thicker and with trigons. Oil bodies coarsely granular under oil-immersion (magnification 1000×), about 5–6 per cell, botryoidal 4–5 µm × 8–10 µm. Ocelli 1–2 (3) situated at the base of the lateral leaves but separated from the line of insertion by 1–2 rows of cells. Underleaves broadly orbicular to reniform 0.3–0.6 mm long 0.35–0.7 mm wide, emarginate at the apex with broadly rounded or apiculate lobes, sinus rounded or obtuse; margin entire on creeping shoots, slightly to strongly denticulate on erect shoots. Gemmae reniform, usually plane, rarely slightly vaulted, usually without, rarely with one or two marginal rhizoids, 0.3–0.55 mm long 0.35–0.65 mm wide.

Plants dioicous. Perianth triangular-obovate, 1.1–1.5 mm long, 0.85–0.95 mm wide in the upper part, born on a lateral branch, innovating on one side, the innovation repeatedly fertile. Lateral keels of the perianth extended upwards as truncate auricles with the margin minutely to sharply denticulate, sometimes bordered by narrow wings; cells of the perianth surface smooth; beak very indistinct. Female bracts obovate to spathulate 1.1–1.3 mm long, 0.55–0.8 mm wide, with the margin weakly to strongly denticulate. Lobule ligulate, sometimes bilobed at the apex, reaching about 50–60 % of the lobe length. Bracteole obovate, shortly bifid at the apex, 0.7–0.85 mm long, 0.45–0.7 mm wide. Androecium terminal or on a lateral branch, bracts in 6–14 pairs, 1 male bracteole present at the base of the branch. Antheridia single or in pairs.

Fig. 2: *Cyclolejeunea chitonia*. – A Creeping shoot, postical view. – B Erect shoot with strongly dentate lateral leaves and underleaves and perianth, postical view. – C Underleaf on creeping shoot. – D Underleaf on erect shoot. – E Median cells with oil bodies and chloroplasts. – F Lobule with tooth and hyaline papilla. – G Gemma without rhizoids. – H Cross section of stem.

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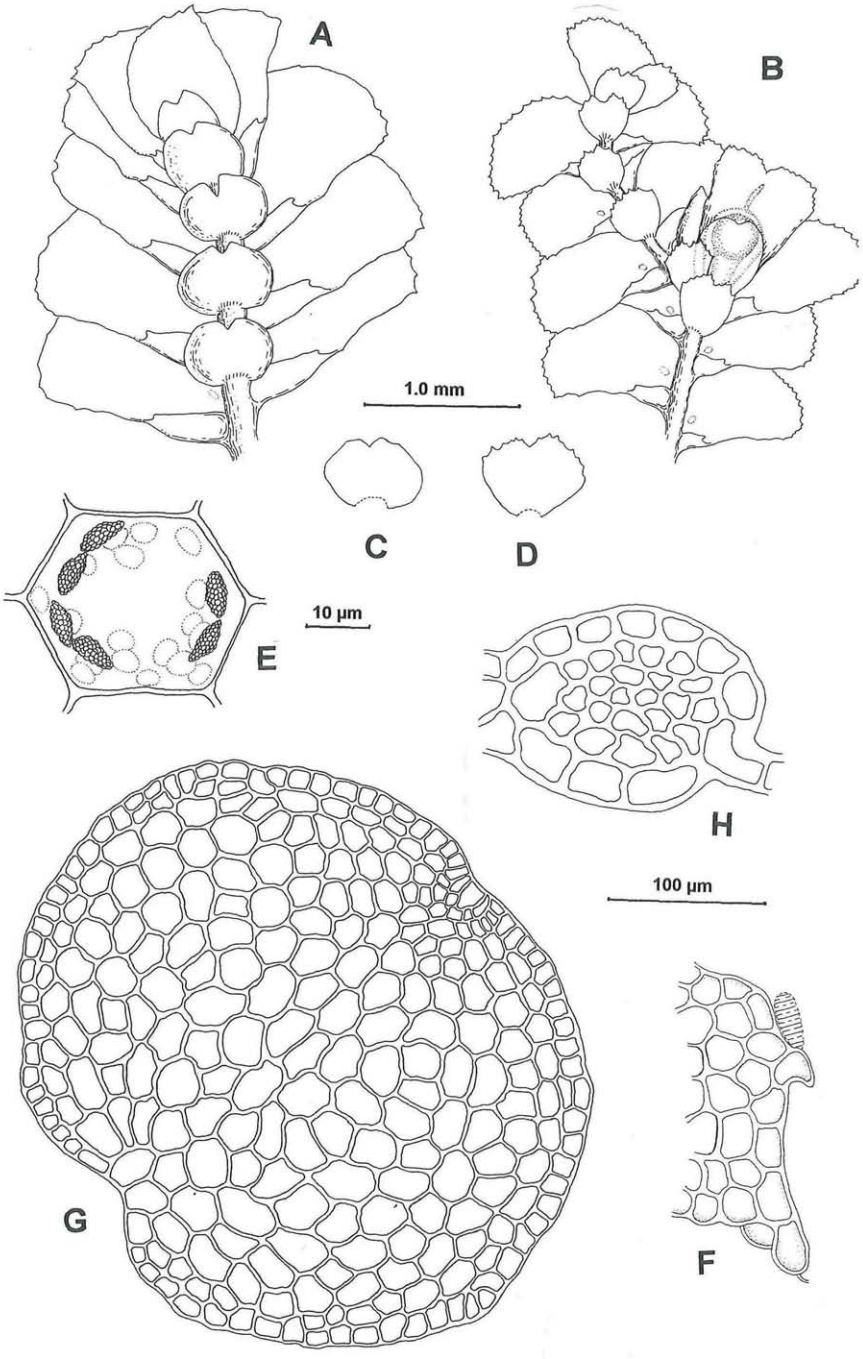

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Specimens examined: Costa Rica. – Limon: Braulio Carrillo-National Park, Botarrama-Trail, epiphyllous, on *Ctenitis subincisa*, leg. BERNECKER-LÜCKING, 92–483 (Be); ibid. on *Salpichlaena volubilis*, 92–347; ibid. on *Welfia georgii*, 92–219, 94–22; ibid. on *Ocotea atirrensis*, 92–89, 92–565; ibid. on *Besleria notabilis*, 91–93; ibid. from the canopy on *Iriartea deltoidea*, 91–91, 91–92, 91–94; ibid. on bark, 94–21; (all of the foregoing specimens Be). – Heredia: "La Selva" Biological Station, SCH-Trail, epiphyllous on palm, leg. BERNECKER-LÜCKING, February 1997, s.n. (Be); ibid. Arboretum, corticolous on small tree (Be).

Cyclolejeunea chitonia is the largest species of the genus, with emarginate underleaves as distinctive character. Poorly developed, small specimens can be confused with *C. convexistipa* if only erect shoots are compared. Using creeping shoots, the two species can be easily separated by looking at the underleaves which are clearly emarginate in *C. chitonia*, and rounded, sometimes reniform but never emarginate in *C. convexistipa*. They also can be distinguished by their lobule shape and structure, which is oblong with a very short curved tooth in *C. chitonia* whereas in *C. convexistipa* the lobule is square in shape with a short but mostly straight tooth. If gemmae are present they are reniform and nearly flat without or rarely with 1–2 rhizoids in *C. chitonia*, rounded and domed with three or more rhizoids in *C. convexistipa*.

According to SCHUSTER 1992 the species does not fit very well into this genus because of the stiff erect gemmiparous shoots with dense leaves but in Costa Rican specimens these shoots are also very common in *C. peruviana*. As discussed above the degree of modification of these shoots depends largely on microclimatic conditions. Thus *C. chitonia* is a typical member of the genus.

Cyclolejeunea convexistipa (LEHM. & LINDENB.) A. EVANS (Fig. 3)

Bull. Torrey Bot. Club 31: 198 (1904); STEPHANI, Sp. Hep. 5: 184 (1913). – *Jungermannia convexistipa* LEHM. & LINDENB., in LEHMANN, Nov. Stirp. Pugillus 6: 43 (1834). – Lectotype (GROLLE 1984): Lesser Antilles, St. Vincent, "in monte Sancti Andreae", hb HOOKER (BM).

Plants mostly epiphyllous, forming large patches but also growing on bark, pale green to olive or brown when dry. Shoots with leaves 0.5–1.5 mm wide. Stems 50–120 μm in diameter. Lateral leaves imbricated, (0.35) 0.5–0.75 mm long (0.2) 0.35–0.5 mm wide, the margin weakly dentate on

Fig. 3: *Cyclolejeunea convexistipa*. – A Creeping shoot with perianth, postical view. – B Erect shoot with strongly dentate lateral leaves and underleaves, postical view. – C Median cells with oil bodies and chloroplasts. – D Ocellus. – E Lobule with tooth and hyaline papilla. – F Gemma with rhizoids projecting from the margin to the convex side and marginal incision opposite the apical region. – G Cross section of stem.

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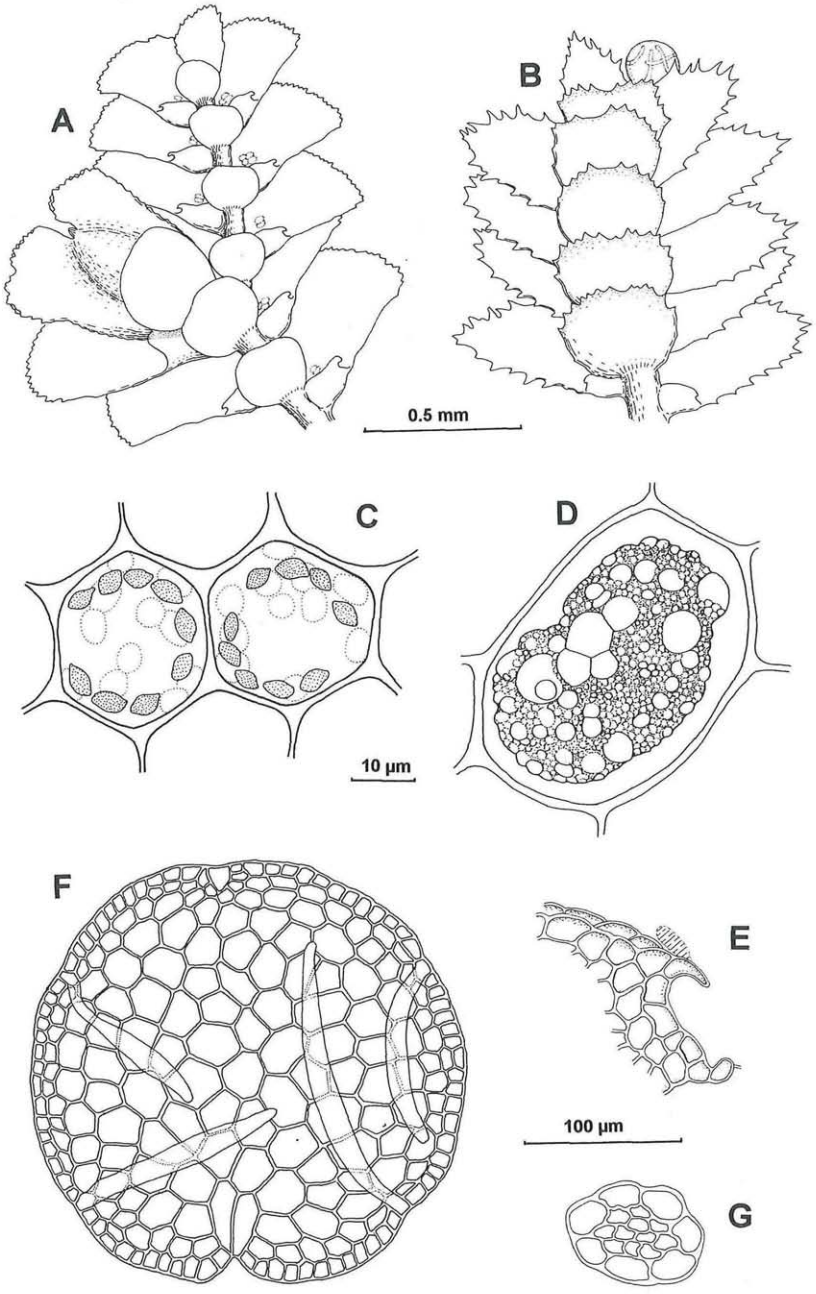

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creeping shoots to sharply dentate on erect shoots. Lobule inflated, ovoid to trapezoidal 0.13–0.17 mm long, 0.08–0.12 mm wide, keel weakly crenulate, free margin involute, rarely plane. Apical tooth 1-celled, long, straight or slightly curved in the basal region. Mouth lunulate or oblique and straight, consisting of 4 cells. Cells of the lobe at the margin 16–20 µm and in the middle 20–31 µm, isodiametric-polygonal, at the base elongate 17–31 × 27–44 µm. Cell walls thin, ocasionally with small trigons. Oil bodies finely granular under oil-immersion (magnification 1000×), about 6–12 per cell, short botryoidal 3–5 µm × 6–8 µm. Ocelli brownish, 1–2 (3) situated at the base of the lateral leaves but separated from the line of insertion by 1–2 rows of cells, slightly larger or as large as the surrounding cells. Underleaves broadly obovate to reniform 0.12–0.3 mm long 0.17–0.45 mm wide, margin entire on creeping shoots, slightly to strongly dentate on erect shoots. Gemmae rounded and domed, like a watch-glass, 0.18–0.3 mm in diameter, with a marginal incision opposite the apical region, usually with three or more rhizoids projecting from the margin to the convex side of the gemma.

Plants dioicous. Perianth triangular-obovate, 0.6–0.95 mm long, 0.45–0.7 mm wide in the upper part, born on a lateral branch, innovating on one side, the innovation repeatedly fertile. Lateral keels of the perianth extended upwards as truncate auricles with the margin minutely to sharply denticulate, sometimes winged; cells of the perianth surface smooth; beak short but distinct. Female bracts ovate to obovate 0.5–0.7 mm long, 0.25–0.4 mm wide, with the margin weakly to strongly dentate. Lobule ligulate, reaching about 20–25 % of the lobe length. Bracteole obovate to oblong, 0.3–0.4 mm long, 0.2–0.35 mm wide. Androecium terminal or on a lateral branch, bracts in 6–13 pairs, male bracteole present throughout the branch. Antheridia in pairs.

Specimens examined: Costa Rica. – Limon: Braulio Carrillo-National Park, Botarrama-Trail, epiphyllous, on *Prestoea decurrens*, leg. BERNECKER-LÜCKING, 91–111 (Be); ibid. on *Chamaedorea tepejilote*, 91–51; ibid. on *Welfia georgii*, 91–54, 91–56; ibid. on *Calyptrogyne condensata*, 92–108, 94–23; ibid. on *Geonoma cuneata*, 91–109; ibid. on *Rhodospatha wendlandii*, 91–55, 92–66, 92–105, 92–111; ibid. on *Araceae*, 91–108; ibid. on *Ocotea atirrensis*, 92–65; ibid. on *Miconia hamelii*, 91–110; ibid. on *Guarea kunthiana*, 92–107; ibid. on *Schlegelia sulfurea*, 92–103; ibid. on *Vismia billbergiana*, 92–109; ibid. from the canopy on *Iriartea deltoidea*, 91–53, 91–57; ibid. from the canopy on *Dicotyledoneae*, 92–67; (all of the foregoing specimens Be). – Cartago: Tapanti National Park, epiphyllous, leg. M. I. MORALES 2264 (USJ); ibid. leg. B. RODRÍGUEZ, 28. June 1992 (USJ); ibid. leg. BERNECKER-LÜCKING, on *Dicotyledoneae* 97–50, 97–51, 97–52 (Be). – Alajuela: San Ramón Reserve, epiphyllous, leg. A. ZAMORA, 5. May 1991 (USJ); ibid. leg. G. DAUPHIN & U. WAGNER, 9–10 May 1992 (USJ); ibid. leg. BERNECKER-LÜCKING 97–48, 97–49 (Be). – Puntarenas: Monteverde Reserve, epiphyllous, leg. A. CONEJO, 12. Juli 1991 (USJ). – Puntarenas: Cocos Island: gallery vegetation along Rio Pittier (Iglesias Bay), epiphyllous, on *Dicotyledoneae*, leg. BERNECKER-LÜCKING, 92–364 (Be); ibid. gallery vegetation along Rio Genio, on *Spati-*

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phyllum, s.n. (Be); ibid. trail to the summit of Cerro Iglesias, ca. 550 m, on *Dicotyledoneae* 92–365 (Be).

C. convexistipa is a very common species mostly forming large patches on living leaves. The variability of morphological characters is very high, but the species can be easily recognized by its rounded underleaves. On erect shoots the underleaves may be slightly emarginate, in which case the species is similar to poorly developed, small plants of *C. chitonia*. Nevertheless, appressed shoots serve to separate the two, as already discussed under *C. chitonia*. The gemmae of *C. convexistipa* are very similar to those of *C. peruviana*, both rounded and with usually 3 or more marginal rhizoids. They differ in *C. convexistipa* having a marginal incision opposite the apical region, whereas in *C. peruviana* the gemmae are evenly rounded with a mucus-papilla at the apical region. According to SCHUSTER 1992 scattered ocelli are present throughout the lobes of the lateral leaves in some specimens of *C. convexistipa* from Dominica. This condition was never found in specimens from Costa Rica.

Cyclolejeunea luteola (SPRUCE) GROLLE (Fig. 4)

Wiss. Zeitschr. Friedrich-Schiller-Univ. Jena, Math.-Nat. Reihe 33: 761 (1984). – *Lejeunea luteola* SPRUCE, "*Cerato-Lejeunea*", in SPRUCE, Trans. Proc. Bot. Soc. Edinburgh 15: 205 (1884). – *Ceratolejeunea luteola* (SPRUCE) STEPH., STEPHANI, Spec. Hep. 5: 422 (1913) – Lectotype (GROLLE 1984): Venezuela, Terr. Fed. Amazonas, Rio Negro, San Carlos, SPRUCE L 407 (MANCH).

Plants epiphyllous or corticolous, pale green to yellowish or brownish when dry. Shoots with leaves 0.9–1.5 mm wide. Stems 65–100 μm in diameter. Lateral leaves imbricated, 0.45–0.75 long 0.35–0.55 wide, the margin weakly to sharply serrulate or denticulate from projecting cells. Lobule inflated, ovoid, 100–150 μm long, 90–120 μm wide, keel slightly crenulate, free margin involute. Apical tooth 1-celled, elongate and sharp, straight or slightly curved. Mouth straight to lunulate, consisting of 4 cells. Cells of the lobe at the margin 10–17 μm and in the middle 20–31 μm, isodiametric-polygonal, at the base elongated 17–31 × 31–45 μm. Cell walls thin to thick, with or without trigons and intermediate thickenings. Oil bodies not seen. Ocelli bright or brown, (2) 3–6 situated side by side at the base of the lateral leaves but separated from the line of insertion by one or two rows of cells. Underleaves orbicular (0.12) 0.14–0.17 mm long (0.12) 0.18–0.2 wide, bifid with triangular erect lobes, sinus lunulate to broadly acuminate, margin entire to crenulate often angular-dentate on the sides. Gemmae oval to elongate in shape with a median constriction and marginal rhizoids streching out in the same plane.

Plants dioicous. Perianth cuneiform, 0.75–0.85 mm long, 0.55–0.7 mm wide in the upper part, born on a leading branch, rarely on a short lateral

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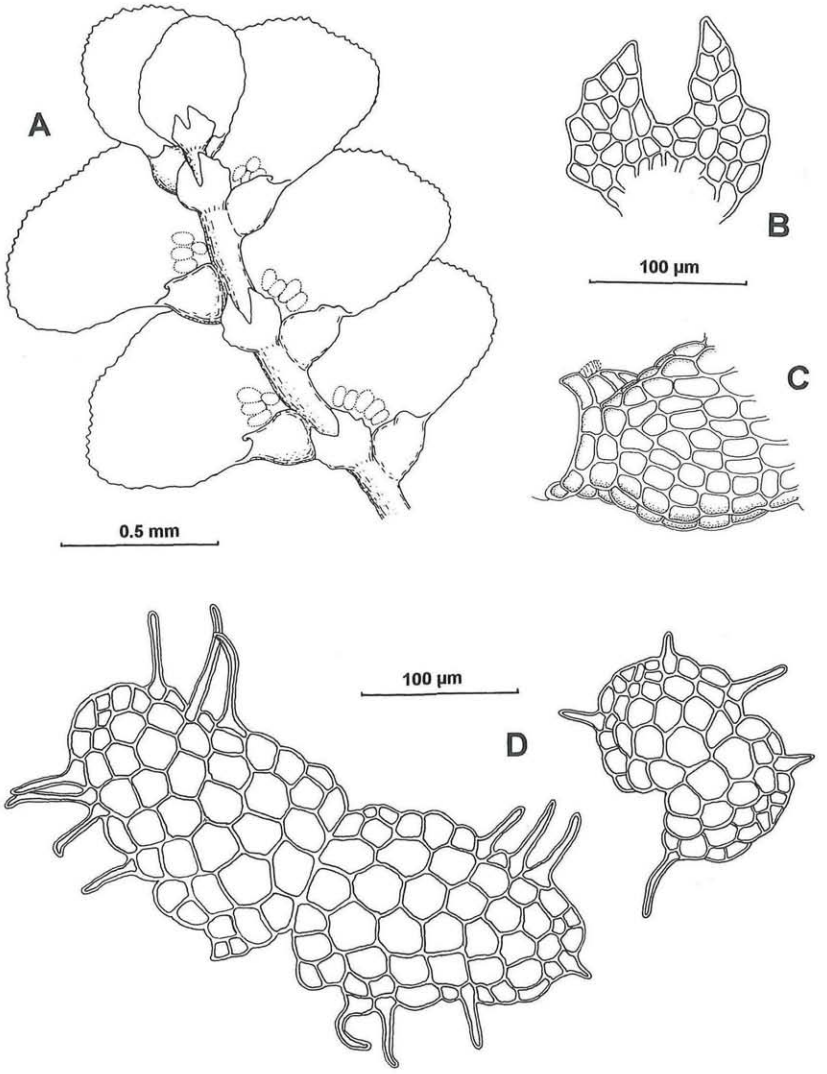

Fig. 4: *Cyclolejeunea luteola*. – A Shoot, postical view. – B Underleaf. – C Lobule with tooth and hyaline papilla. – D Gemmae with median constriction and marginal rhizoids streching out in the same plane.

branch, innovating on one side, sometimes floriferous. Lateral keels of the perianth extended upwards as truncate auricles borderd by narrow wings, the margin crenulate-dentate; cells of the perianth surface smooth; beak distinct but short. Female bracts ovate to obovate, rounded at the apex 0.45–0.75 mm long, 0.25–0.35 mm wide with the margin weakly to strongly

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crenulate-papillous. Lobule lanceolate, reaching about 50–70 % of the lobe length. Bracteole ovate to oblong, bilobed with the sinus narrow, 0.4–0.55 mm long, 0.2–0.35 mm wide. Androecium terminal or on a lateral branch, bracts in 3–9 pairs, 2 (3) male bracteoles present at the base of the branch. Antheridia mostly in pairs.

Specimens examined: Costa Rica. – Limon: Braulio Carrillo-National Park, Botarrama-Trail, epiphyllous, on *Prestoea decurrens*, leg. BERNECKER-LÜCKING, 91–111 (Be); ibid. on *Chamaedorea tepejilote*, 91–51; ibid. on *Welfia georgii*, 91–54, 91–56; ibid. on *Calyptrogyne condensata*, 92–108, 94–23; ibid. on *Geonoma cuneata*, 91–109; ibid. on *Rhodospatha wendlandii*, 91–55, 92–66, 92–105, 92–111; ibid. on *Araceae*, 91–108; ibid. on *Ocotea atirrensis*, 92–65; ibid. on *Miconia hamelii*, 91–110; ibid. on *Guarea kunthiana*, 92–107; ibid. on *Schlegelia sulfurea*, 92–103; ibid. on *Vismia billbergiana*, 92–109; ibid. from the canopy on *Iriartea deltoidea*, 91–53, 91–57; ibid. from the canopy on *Dicotyledoneae*, 92–67; (all of the foregoing specimens Be). – Puntarenas: Cocos Island: corticolous, leg. G. DAUPHIN A-4/17 (USJ); gallery vegetation along Rio Pittier (Iglesias Bay), epiphyllous, on fern, leg. BERNECKER-LÜCKING, 92–367 (Be).

C. luteola can be confused only with *C. accedens*; the differences are discussed under *C. accedens* (above).

Cyclolejeunea peruviana (LEHM. & LINDENB.) A. EVANS (Fig. 5)

Bull. Torrey Bot. Club 31: 196 (1904); STEPHANI, Sp. Hep. 5: 190 (1913). – *Lejeunea peruviana* LEHM. & LINDENB., in GOTTSCHE, LINDENBERG & NEES, Syn. Hep.: 339 (1845). – *Jungermannia peruviana* LEHM. & LINDENB., in LEHMANN, Nov. Stirp. Pugillus 5: 18 (1833). – Type: Peru, s. loc., POEPPIG 1832, (S).

Plants mostly epiphyllous forming large patches but also growing on bark, yellowish to olive or brown when dry. Shoots with leaves 1.5–2.5 (3.0) mm wide. Stems 65–170 µm in diameter. Lateral leaves imbricated, 0.7–1.3 mm long 0.45–1.1 mm wide, the margin dentate. Lobule slightly inflated, rectangular to trapezoidal, 0.3–0.4 mm long, 0.15–0.3 mm wide, keel smooth to slightly crenulate, free margin plane to slightly involute. Apical tooth blunt, built up by an elongated straight cell lying side by side with the next cells of the lobule. Mouth nearly straight but oblique, consisting of 4 cells. Cells of the lobe all isodiametric-polygonal, at the margin 17–24 µm, in the middle 24–31 µm and at the base 31–37 µm. Cell walls thin, occasionally with small trigons. Oil bodies finely granular under oil-immersion (magnification 1000×), about 5–12 per cell, rounded to botryoidal 3–5 µm × 4–8 µm. Ocelli brownish, 1–2 situated side by side at the base of the lateral leaves but separated from the line of insertion by 1–2 rows of cells, larger than the surrounding cells. Underleaves ovate 0.2–0.55 mm long 0.25–0.7 mm wide, on creeping shoots bifid with triangular erect lobes, with the sinus narrow and acuminate and the margin denticulate; on

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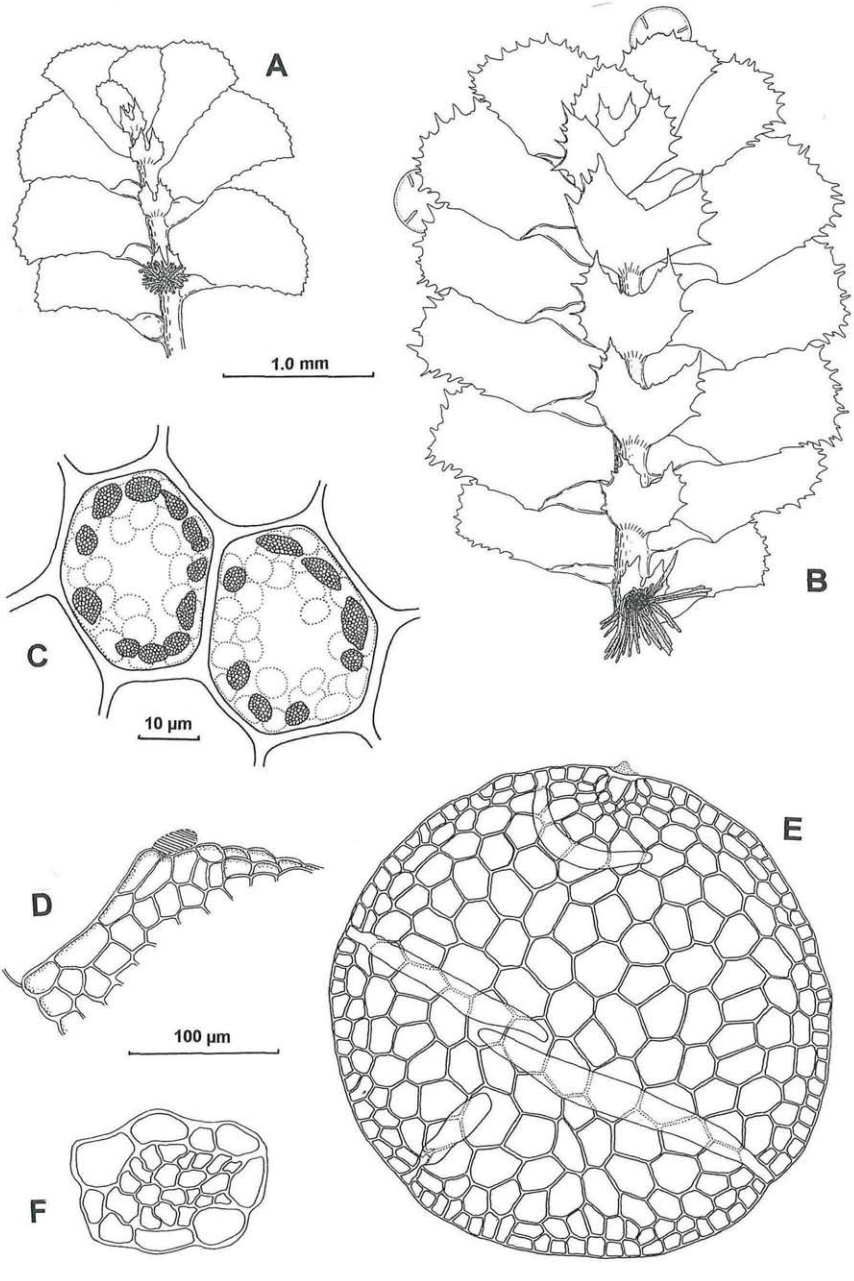

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erect shoots bifid with broad triangular obliquely spreading lobes with the sinus broadly obtuse and the margin slightly to strongly dentate. Gemmae rounded and domed, like a watch-glass, 0.25–0.4 mm in diameter, with a mucus-papilla at the apical region and usually three or more rhizoids projecting from the margin to the convex side of the gemma.

Plants dioicous. Perianth triangular-obovate, 0.75–1.3 mm long, 0.6–0.7 mm wide in the upper part, born on a long lateral branch or terminal, innovating on one side, the innovation repeatedly fertile. Lateral keels of the perianth extended upwards as truncate auricles with the margin denticulate; cells of the perianth surface smooth; beak indistinct. Female bracts oblong-ovate 0.7–1.1 mm long 0.35–0.7 mm wide with the margin dentate. Lobule ligulate, sometimes bilobed at the apex, reaching about 70 % of the lobe length. Bracteole ovate to obovate 0.3–0.55 mm long 0.4–0.5 mm wide. Androecium terminal or on a lateral branch, bracts in 6–20 pairs, 1–2 male bracteoles present at the base of the branch. Antheridia in pairs.

Specimens examined: Costa Rica. – Limon: Braulio Carrillo-National Park, Botarrama-Trail, epiphyllous, on *Ctenitis subincisa*, leg. BERNECKER-LÜCKING, 92–507 (Be); ibid. on *Chamaedorea tepejilote*, 91–15; ibid. on *Welfia georgii*, 91–9, 91–14, 91–17, 92–209, 94–39; ibid. on *Calyptrogyne condensata*, 94–40; ibid. on *Geonoma cuneata*, 91–13; ibid. on *Dieffenbachia longispatha*, 92–21; ibid. on *Rhodospatha wendlandii*, 91–11, 92–12, 92–18, 92–22; ibid. on *Ocotea atirrensis*, 92–553; ibid. on *Ardisia auriculata*, 91–18; ibid. on *Guarea grandifolia*, 91–19; ibid. on *Guarea kunthiana*, 92–19, 92–20, 92–392; ibid. on *Guarea* sp., 92–17; ibid. on *Vismia billbergiana*, 91–8; ibid. from the canopy on *Iriartea deltoidea*, 91–10; (all of the foregoing specimens Be). Braulio Carrillo-National Park, leg. G. DAUPHIN, 24. October 1991 (USJ). – Puntarenas: Cocos Island, Cerro Iglesias, epiphyllous, on *Elaphoglossum*, leg. BERNECKER-LÜCKING, 92–250 (Be). Las Cruces Botanical Garden, leg. R. MENJIVAR, January 1990 (USJ). – Alajuela: San Ramón Reserve, epiphyllous, leg. A. ZAMORA, 5. May 1991 (USJ); ibid. on *Dicotyledoneae*, leg. BERNECKER-LÜCKING, s.n. (Be). – Cartago: Refugio de Fauna Silvestre de Tapanti, epiphyllous, leg. M. I. MORALES 2158 (USJ); ibid. on *Dicotyledoneae*, leg. BERNECKER-LÜCKING (Be). – San José: Genesis II Cloud Forest Reserve, Cordillera de Talamanca, epiphyllous, on *Dicotyledoneae*, leg. BERNECKER-LÜCKING, s. n. (Be).

C. peruviana is a large and remarkable species. Unique within the genus is the reduced and blunt tooth of the lobule, built by an elongated, straight (never curved) cell, lying side by side with the adjacent cells. Erect gemmiparous shoots are common, with the leaves very dense and the

Fig. 5: *Cyclolejeunea peruviana*. – A Creeping shoot, postical view. – B Erect shoot with strongly dentate leaves and gemmae developing at the antical margin of the lateral leaves, postical view. – C Median cells with oil bodies and chloroplasts. – D Lobule with blunt tooth and hyaline papilla. – E Gemma with rhizoids projecting from the margin to the convex side and mucus-papilla at the apical region. – F Cross section of stem.

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postical margin of the lateral leaves involute. In this respect it is similar to *C. chitonia* but underleaves in *C. peruviana* are deeply bifid, whereas in *C. chitonia* they are only emarginate. The gemmae produced in *C. peruviana* are very similar to those of *C. convexistipa* as discussed under *C. convexistipa*.

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