Cryptogamie, Algol., 2002, 23 (1): 39-49

Taxonomy and distribution of *Paralemanea* (Lemaneaceae, Rhodophyta) in Central Mexico

Javier CARMONA Jimenez[a] *& Orlando NECCHI Jr*[b]*

[a] *Laboratorio de Ficología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, A.P. 70-620, Coyoacán, 04510, México, D.F. Fax: (52) 5622-4828; e-mail: jcj@hp. fciencias. unam. mx.*

[b] *Departamento de Zoologia e Botânica, Universidade Estadual Paulista, Rua Cristóvão Colombo, 2265 - 15054-000 - São José do Rio Preto, SP, Brazil. Fax: 55 (17) 224-8692; e-mail: orlando@bot. ibilce. unesp. br.*

(Received 7 November 2000, accepted 10 April 2001)

Abstract — Three collections of *Paralemanea* from Central Mexico included two species. *Paralemanea mexicana* is large (length ≥ 4.0 cm; diameter > 400 µm) and generally branched (≥ 40 % of plants branched), with whorled branches, of first to second order. *Paralemanea annulata* is small (length < 5.0 cm ; diameter < 500 µm), generally unbranched (≤ 5 % of plants branched), with branches of first order. Spermatangial sori contained obovoid spermatangia, formed from cells of the outer cortical layers, extending above the thallus surface. Carpogonial branches are described for the first time in *P. mexicana*. They develop on lateral filaments at nodes or internodes and have ovoid to globular cells, abundantly branched at the basal portion, penetrating the cortex towards the thallus surface. Carposporophytes are sessile on the inner portion of the cortex and produce carpospores in chains of up to twelve. The '*Chantransia*' stage was observed in *P. mexicana*. *Paralemanea annulata* is described for the first time from Mexico and *P. mexicana* is endemic from this country. Both species were collected in cold (temperature 12-16°C), acidic (pH 5.5-6.0), shallow (depth 1-60 cm) and moderate to fast flowing waters (> 35 cm s^{-1}), in shaded or partly shaded river segments, on rocky substrata (mostly bedrock).

Batrachospermales / distribution / freshwater algae / Lemaneaceae / Mexico / *Paralemanea* / Rhodophyta / taxonomy

Résumé — Taxinomie et distribution de *Paralemanea* (Lemaneaceae, Rhodophyta) au Mexique central. Trois récoltes de *Paralemanea* du Mexique central comprennent deux espèces. *P. mexicana* est grand (longueur supérieure ou égale à 4 cm ; diamètre supérieur 400 µm) et généralement ramifié (au moins 40 % de plantes ramifiées) à ramifications verticillées, de premier ou de deuxième ordre. *P. annulata* est petit (longueur de moins de 5 cm ; diamètre inférieur à 500 µm) généralement non ramifié (5 % ou moins de 5 % de plantes ramifiées), ramifications de premier ordre. Les sores mâles contiennent des spermatocystes obovoïdes, formés à partir de cellules des couches corticales externes, s'étendant au-dessus de la surface du thalle. Les rameaux carpogoniaux sont décrits pour la

* Author for correspondence

première fois chez *P. mexicana*. Ils se développent sur des rameaux latéraux aux nœuds ou dans les entrenœuds et ont des cellules globuleuses à ovoides, abondamment ramifiées à la base, pénétrant le cortex vers la surface du thalle. Les carposporophytes sont sessiles, sur la partie interne du cortex, produisant des carpospores en chaînes de 12 cellules au plus. Le stade « *Chantransia* » a été observé chez *P. mexicana*. C'est la première fois que *P. annulata* est observé au Mexique alors que *P. mexicana* est endémique de ce pays. Les deux espèces on été récoltées dans des eaux froides (12-16 ºC), acides (pH 5,5-6,0), peu profondes (1-60 cm), à courant modéré ou rapide (> 35 cm s^{-1}), sur substrat rocheux, dans des sections de rivières ombragées ou partiellement ombragées.

algues d'eau douce / Batrachospermales / distribution / Lemaneaceae / Mexique / *Paralemanea* / Rhodophyta / taxinomie

INTRODUCTION

The freshwater red algal family Lemaneaceae is characterized by uniaxial, cartilaginous and pseudoparenchymatous gametophyte thalli (Vis & Sheath, 1992). The two subgenera of the genus *Lemanea* (*Lemanea* and *Paralemanea*) were raised to generic status by Vis & Sheath (1992). The genus *Psilosiphon*, formerly classified within the family, was segregated in the Psilosiphonaceae (Sheath *et al.*, 1996). Thus, two genera are presently recognized in the family and these can be separated on the basis of the following characters (Vis & Sheath, 1992; Sheath *et al.*, 1996; Necchi & Zucchi 1995). *Paralemanea* includes plants without stalks; without hair cells in the inner cortex; with rhizoidal filaments surrounding axial filaments; with simple ray cells, consisting of two layers, the proximal ones not touching the outer cortex and the distal ones generally "Y" branched and connected to the cortex; and nodal spermatangial sori in rings. *Lemanea* has hair cells in the inner cortex; axial filaments without rhizoidal filaments; ray cells T- or L-shaped, closely applied to the outer cortex; and nodal spermatangial sori in patches. According to the molecular phylogeny of *Paralemanea*, based on *rbc*L gene (Vis *et al.*, 1998), the genus could not be recognized at any taxonomic level because it was paraphyletic. However, due to its well-defined morphology, those authors retained it at the generic level pending corroboration from nuclear gene sequences.

Atkinson (1890) provided the most comprehensive taxonomic treatment of the Lemaneaceae worldwide, including detailed morphological descriptions of seven species (three of *Lemanea* and four of *Paralemanea*). The recent studies on the systematics of family members include morphological as well as ultrastructural characters (Vis & Sheath, 1992; Blum, 1994; Necchi & Zucchi, 1995; Sheath *et al.*, 1996). Differentiation among species of this family has been problematic (Vis & Sheath, 1992), with species circumscriptions based on subjective and variable characters or morphometric characters not clearly disjunct among species. Thus, taxonomic treatments on Lemaneaceae are still required in order to delimit species, including morphological features of vegetative and reproductive, as well as ultrastructural and molecular information.

Two species of Lemaneaceae have been reported from Mexico: *Lemanea fluviatilis* (Linnaeus) C. Agardh from one locality in northwestern Mexico (Ortega, 1984), and *Paralemanea mexicana* (Kützing) Vis *et* Sheath (= *Lemanea mexicana* Kützing; *L. feldmannii* Sanchez-Rodríguez et Huerta) from two sites from Mexico Valley (Sanchez-Rodríguez & Huerta, 1969; Sanchez-Rodríguez, 1974; Vis & Sheath, 1992). However, information on some anatomical (both veg-

etative and reproductive) characters and environmental distribution is scarce. This investigation was undertaken to describe in detail the anatomical structure of the Mexican species and to compare it with that of nomenclatural types. The habitat and the geographic distribution of the Lemaneaceae populations from the central region of Mexico are also described.

MATERIAL AND METHODS

The three populations of Lemaneaceae analysed in this study were collected from the central region of Mexico (17-20° N, 96-100°W) from three among 51 sites with the presence of red algae (Carmona, 1997) at altitudes of 1,900-2,300 m (Fig. 1). The samples were preserved in 4 % formaldehyde and included in the herbaria FCME (Holmgren *et al.,* 1990). The following environmental variables were recorded for each sampling site (according to procedures described in Carmona, 1997) : temperature, pH, depth and type of substratum. In addition, shading and current velocity were estimated for each collecting site according to procedures described by DeNicola *et al.* (1992) and Johansson (1982), respectively.

In addition, two nomenclatural types from Herbarium L (Holmgren *et al.,* 1990) were examined for comparison:

(1) *Paralemanea annulata* (Kützing) Vis et Sheath (holotype) ; Germany, Halle, "am wehr unter des Bruthe", 31.v.1832, Herb. Kützing (L 8978, no. 1).

(2) *Paralemanea mexicana* (Kützing) Vis *et* Sheath (holotype) ; Mexico, unknown locality, no date, Herb. Kützing (L 8917, no. 1).

We have included all quantitative and qualitative morphological characters previously considered to be of taxonomic importance at generic and specific levels in relevant studies (Sirodot, 1872; Atkinson, 1890; Israelson, 1942; Sánchez-Rodríguez & Huerta, 1969; Vis & Sheath, 1992; Necchi & Zucchi, 1995; Sheath *et al.*, 1996). Microscopical analyses followed the procedures described by Vis & Sheath (1992) and Necchi & Zucchi (1995). Taxonomic descriptions incorporate the characteristics observed in Mexican specimens and those described in recent papers using the same methodology (Vis & Sheath, 1992; Necchi & Zucchi, 1995). Two staining procedures were applied: 0.3 % alcian blue (AB) in 3 % acetic acid at pH 2.5 (Sheath & Cole, 1990) and safranin combined with Astra blue (safra-blue, SB) (a variation of safranin + fast green staining, Grimstone & Skaer, 1972). Plants were embedded in paraffin for preparation of cross and longitudinal sections, made with a Leitz Wetzlar microtome. Specimens were observed, measured and photographed with a BHS Olympus microscope equipped with a PM-10 AD photomicrographic system, and a Reichert Jena microscope equipped with an interference phase contrast illumination system.

RESULTS AND DISCUSSION

Morphological analyses

Two groups of populations were recognized, both with characteristics ascribed to the genus *Paralemanea*: plants unstalked (internodal/basal diameter ratio ≤ 1.0, Figs 2, 10), spermatangial sori arranged in rings around the nodes (Figs 4, 11), rhizoidal filaments present around the axial cell, and ray cells composed of

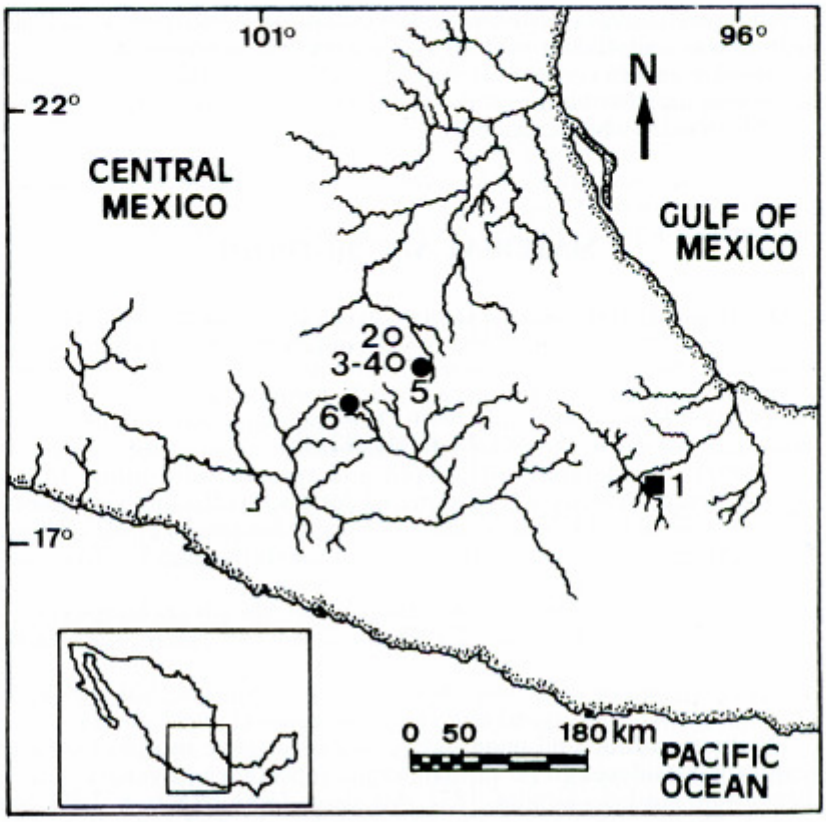


Fig. 1. Known distribution of *Paralemanea* in Central Mexico. ■ *P. annulata*; ● *P. mexicana*; ○ previous records of *P. mexicana*.

two layers, the proximal ones not touching the outer cortex (Figs. 5, 12). The morphometric characters of populations and type specimens are summarized in Tab. 1.

The first group included populations 1 and 2 and the type specimen of *P. mexicana*. It was characterized by the following characteristics (in agreement with those described for the species by Vis & Sheath, 1992) : plants long (≤ 9.0 cm) and generally branched (≤ 40 % of branched plants) and branches of first and second order usually whorled (Tab. 1, Figs 2-9).

We observed sexual reproductive structures in populations 1 and 2. In cross section and staining with SB, spermatangial sori with obovoid spermatangia were observed, which were formed from cells of the outer cortical layers and extended above the thallus surface (Fig. 6). Generally, these characteristics are similar to those described for *P. annulata* (as *L. australis* Atkinson) by Atkinson (1890) and for *P. mexicana* by Sheath *et al.* (1996). However, we did not observe the development of spermatangial sori from distal cortical cells and formed on the apices of column cells, as reported by Atkinson (1890). In addition, the number of inner cortical cells was lower than previously reported (1-2 × 2-4).

In cross section and interference phase contrast, we observed a novelty for this species: the development of carpogonial branches. Borne on lateral filaments at nodes or internodes, the structure consists of a filament with ovoid to

Tab. 1. Characteristics of Mexican freshwater populations and type specimens of *Paralemanea*. Measurements are in µm and represent ranges, mean and standard deviation.

Populations and type specimens	*Plant Length (cm)*	*Nodal diameter ND*	*Internodal diameter ID*	*ND/ID*	*Percentage of branched plants*	*Carpospores*	
						Length	*Diameter*
1. PA2L	2.0-9.0	263-2280	184-739	1.0-2.5	49	23.7-39.2	12.4-23.9
San Luis Ayucán	5.5 ± 2.0	691 ± 302	484 ± 162	1.3 ± 0.2		31.3 ± 3.8	19.4 ± 3.3
N = 30*							
2. BALE1942	1.5-7.6	200-628	158-486	1.0-1.5	40	18.4-33.3	14.8-24.8
Arroyo Meyuca	3.9 ± 2.1	412 ± 124	349 ± 100	1.1 ± 0.1		27.1 ± 4.1	18.9 ± 4.1
N = 17*							
3. PAP758	0.5-4.0	175-588	136-544	0.9-1.6	5	28.8-54.3	14.4-27.9
Totontepec	1.2 ± 0.4	386 ± 92	323 ± 93	1.1 ± 0.1		38.5 ± 6.7	21.3 ± 4.8
N = 7*							
P. mexicana	0.8-5.3	520-920	360 ± 660	1.0-1.5	40	40.0-56.0	22.0-38.0
(type)	2.2 ± 1.4	724 ± 123	540 ± 93	1.3 ± 0.1		47.6 ± 53.0	32.6 ± 3.6
N = 20*							
P. annulata	1.0-4.0	340-1100	220-900	1.1-1.6	0	26.0-44.0	16.0-26.0
(type)	2.8 ± 1.1	781 ± 224	621 ± 197	1.2 ± 0.1		31.7 ± 4.1	22.4 ± 2.6
N = 5*							

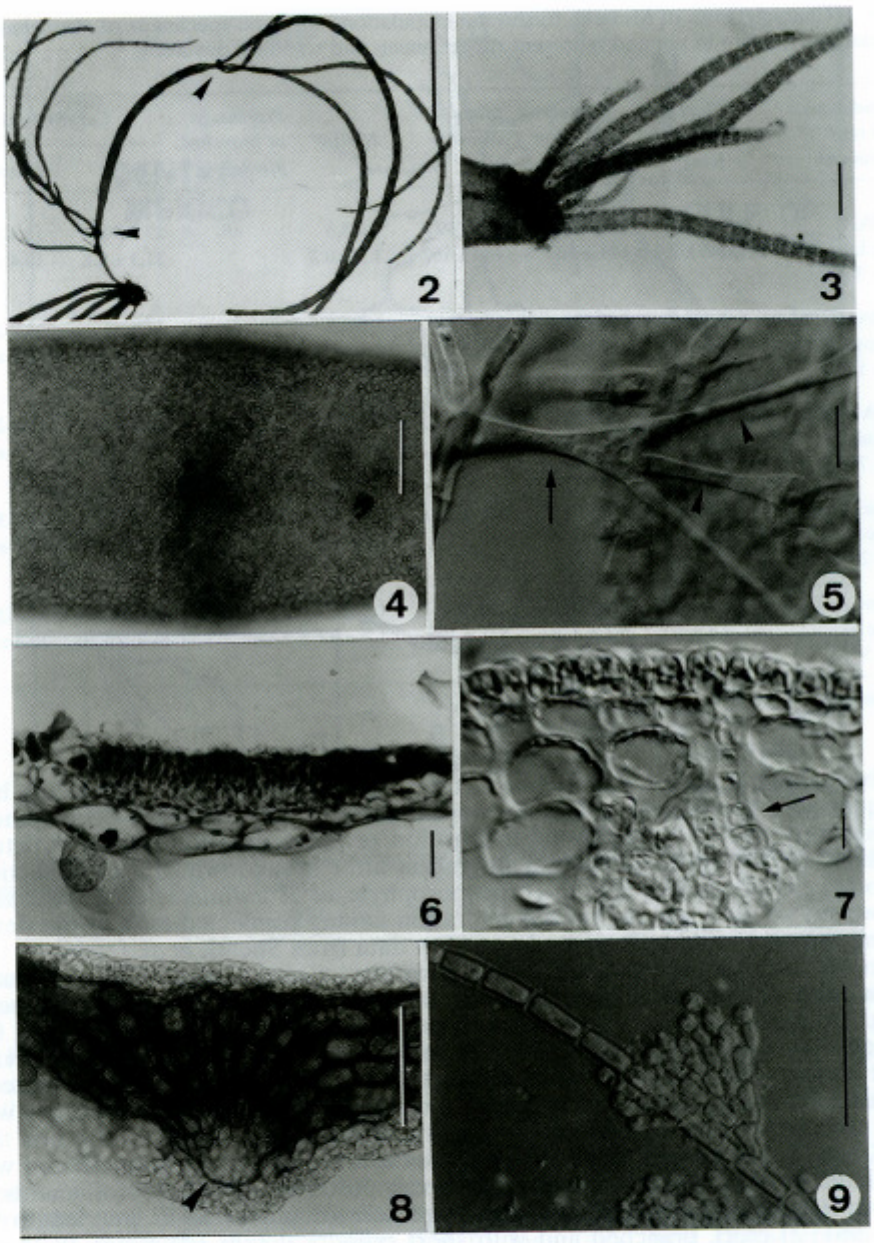
* number of plants examined.

globular cells, abundantly branched at the basal portion (Fig. 7). Despite the high frequency of gonimoblast filaments, we did not observe trichogyne development, presumably due to a synchronic maturation or short duration of this structure. Mullahy (1952) observed nuclear migration after breakdown of pit connections among cells of the developing carposporophyte of *P. annulata* (as *L. australis*). However, we observed no nuclear migration among connected cells of the developing carposporophyte, in accordance with data from Sheath *et al.* (1996).

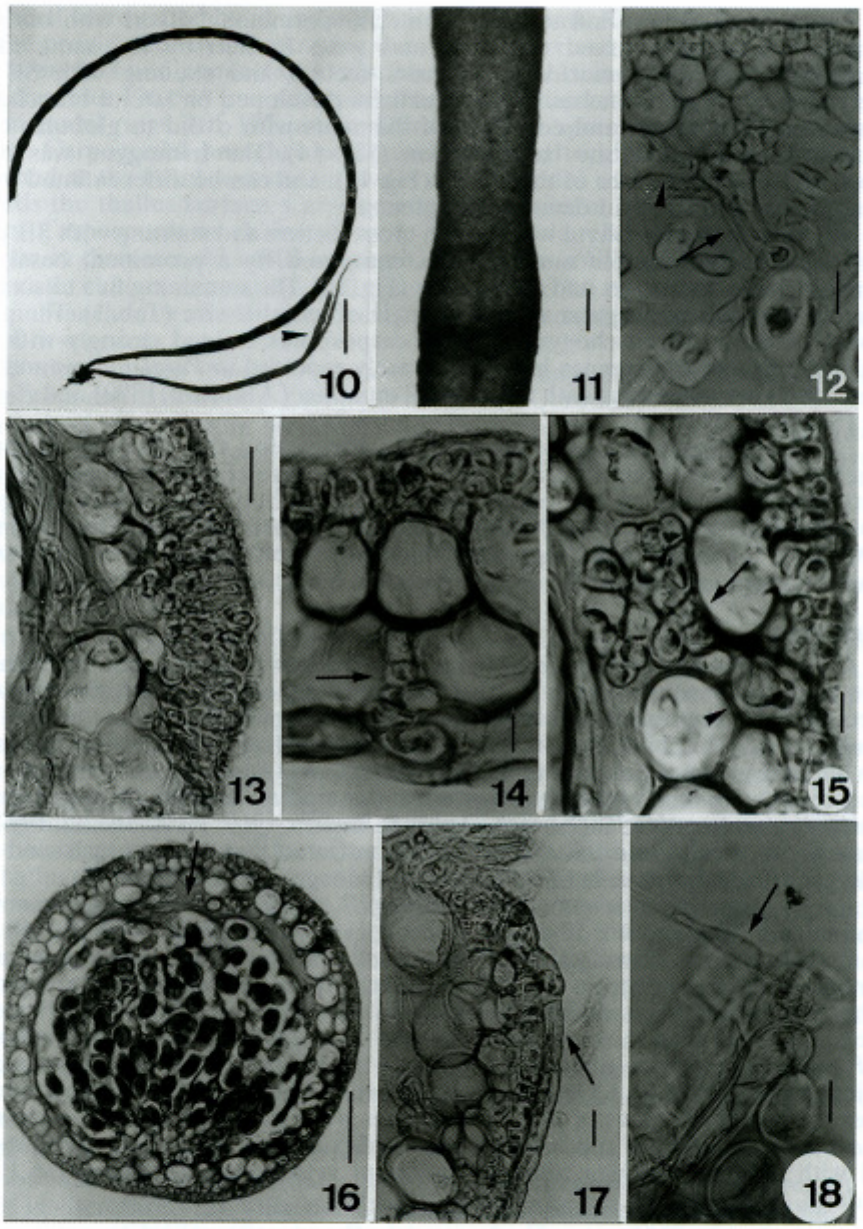
Carposporophytes were seen in cross sections of plants (SB), produced on a prominent basal cell and forming densely branched, moniliform filaments (Fig. 8). The first two to three cells were short and sterile and the remaining five to ten cells consisted of ellipsoid, obovoid to irregular carposporangia with variable sizes in the two populations (Tab. 1). The spermatangia and cortical cells exhibited a strong staining with SB, inner cortical cells stained more strongly with AB and carpospores stained both with SB and AB.

The '*Chantransia*' stage (Fig. 9) was observed in the field, associated with the basal portion of gametophytes. It was composed of two types of filaments: 1) prostrate, sparsely branched and with large cells (diameter 18-32 µm, length 96-224 µm); 2) erect, branched and with short cylindrical cells (diameter 18-24 µm, length 30-68 µm) and reproducing by spherical to sub-spherical monosporangia (diameter 14-18 µm). The presence of monosporangia has been rarely reported in the '*Chantransia*' stage of Lemaneaceae but confirms that it represents a common mode of propagation as in the other Batrachospermales (Sheath, 1984; Guiry, 1990).

The second group contained one population (# 3) and the type specimen of *P. annulata*, characterized by smaller plants (≤ 4.0 cm) that are generally unbranched (≤ 5 % of branched plants) and branches, when present, are only of first order (Tab. 1, Figs 10-18).



Figs 2-9. Morphological features of *Paralemanea mexicana*. Fig. 2. General view of a plant showing whorled branches (arrowheads). Fig. 3. Detail of a young whorled branch. Fig. 4. Detail of a nodal spermatangial sorus in ring. Fig. 5. Ray cells forming two layers (interference phase contrast, IPC): proximal (arrow) and distal (arrowheads). Fig. 6. Cross section of a spermatangial sorus. Fig. 7. Cross section (IPC) of the outer cortex showing carpogonial branch (arrow). Fig. 8. Gonimoblast filaments before formation of carposporangia with a prominent basal part (arrowhead). Fig. 9. Detail of '*Chantransia*' stage (IPC). Scale bars: 10 mm for Fig. 2; 1 mm for Fig. 3; 100 µm for Figs 4, 8-9; 10 µm for Figs 5-7.



Figs 10-18. Morphological features of *Paralemanea annulata*. Fig. 10. General view of a plant showing a branch (arrowhead). Fig. 11. Detail of a nodal spermatangial sorus in ring. Fig. 12. Ray cells forming two layers: proximal (arrow) and distal (arrowhead). Fig. 13. Cross section of a spermatangial sorus. Figs 14-15. Cross sections of the outer cortex showing carpogonial branches (arrows) and trichogyne (arrowhead). Fig. 16. Cross section of the plant showing the outer cortex, carposporangia inside the plant cavity and mucilage stained with alcian blue (arrow). Fig. 17-18. Uniseriate filaments (arrows) arising from gonimoblast filaments. Scale bars: 1 mm for Fig. 10; 100 μm for Figs 11, 16; 10 μm for Figs 12-15, 17-18.

In cross section and staining with AB, spermatangial sori with obovoid spermatangia were observed (Fig. 13), and were formed by the same mode described above for *P. mexicana*. In cross section and staining with SB we observed carpogonial branches. These structures developed on lateral branches at the nodes or internodes and consisted of filaments with ovoid to globular cells, abundantly branched at the basal portion (Fig. 14). The trichogyne was pear-shaped, close to the surface of the cortex (Fig. 15), and can be differentiated by its distinct shape and size and dense cell contents.

The carposporophyte was seen in cross section and staining with SB, consisting of branched moniliform filaments, composed by a prominent basal cell forming three to four short and sterile cells (Fig. 16). The remaining five to six cells consisted of ovoid to irregular carposporangia of variable size (Tab. 1). The gonimoblast filaments, the trichogyne and the carpospores stained strongly with SB. Gonimoblasts and trichogynes have been rarely reported in *Paralemanea* and our observations are consistent with those for *P. annulata* (Atkinson, 1890) and *P. catenata* (Sheath *et al.*, 1996).

The inner space between the outer cortex and the rhizoidal filaments stained with AB, showing that it is filled with mucilage (Fig. 16). Uniseriate filaments were observed on the cortex surface arising from branches of the gonimoblast filaments (Figs 17-18). These structures were described by Atkinson (1890) in *P. annulata*, who suggested that they could represent a process of apospory or apogamy.

Distribution

Paralemanea annulata is described for the first time from Mexico, extending its distribution southward in North America. Based on this record, the species is expected to be also relatively widely distributed in South America, where it was recently found (Necchi & Zucchi, 1995), once more intensive collections are made from suitable regions (mountainous or cool regions). *Paralemanea mexicana* was collected in two rivers from high mountain and temperate regions, near and similar to the previous records (Sánchez-Rodríguez & Huerta, 1969; Vis & Sheath, 1992). It is endemic to Mexico and this study has demonstrated that it is not restricted to a single hydrological system but also occurs in drainage basins in the region.

In terms of environmental variables, *P. annulata* and *P. mexicana* were found in cold (temperature 12-16ºC), acidic (pH 5.5-6.0), shallow (depth 1-60 cm) and moderate to fast flowing waters (> 35 cm s^{-1}), in shaded or partly shaded river segments, on rocky substrata (mostly bedrock). The temperature data are similar to those reported by Vis & Sheath (1992) for these species. However, pH values were much lower than those recorded by those authors (6.8-8.6 for *P. annulata*, 8.3 for *P. mexicana*). Our results are consistent with the preference of Lemaneaceae for inorganic carbon as CO_2 (Raven & Beardall, 1981), the form predominant under the reported values of pH. Both species were collected with *Prasiola mexicana* J. Agardh, another species endemic to Mexico, and *P. mexicana* was associated with another red alga, *Batrachospermum gelatinosum* (Linnaeus) A.P. De Candolle.

Descriptions of the Mexican material

Paralemanea annulata (Kützing) Vis et Sheath, *Phycologia* 31: 177, 1992.
(Figs 10-18)
Basionym: *Lemanea annulata* Kützing, *Phycol. Germ.* : 261, 1845.
Heterotypic synonyms: *Lemanea australis* Atkinson, *Ann. Bot.* 4: 218, 1890; *Lemanea grandis* Wolle, *Bull. Torrey Bot. Cl.* 6: 183, 1877.
Plants bambusiform, unstalked, cartilaginous, unbranched or rarely branched (≤ 5 % of branched plants), branches, if present, of first order, 0.5-4.0 cm high.

Axial cell surrounded by abundant rhizoidal filaments. Ray cells forming two layers: the proximal ones not touching the outer cortex and the distal ones generally "Y" branched and connected to the cortex. Nodal diameter 175-588 µm; internodal diameter 136-544 µm; ratio nodal/internodal diameter 0.9-1.6. Spermatangial sori in nodal rings, 105-175 µm in diameter; ratio spermatangial/nodal diameter 0.2-0.5. Carpogonial branches composed of ovoid to globular cells, abundantly branched at the basal portion, on nodes or internodes and penetrating the cortex towards the thallus surface. Carposporophyte sessile, on the inner portion of the cortex. Carpospores in chains of up to six, obovoid, ellipsoid or irregular, 14.4-27.9 µm in diameter, 28.8-54.3 in length. '*Chantransia*' stage not observed.

Diagnostic characters: plants small (mean length < 5.0 cm; mean diameter < 500 µm), unbranched or rarely branched (≤ 5 % of branched plants), branches, if present, of first order.

World distribution: North America (Mexico and U.S.A.), South America (Argentina and Brazil) and Europe (France and Germany).

Distribution in Mexico: in literature - first report of the species. Specimens examined: **1)** Oaxaca, Zacatepec, Road Totontepec-Zacatepec, km 790, coll. R. Tavera, 1.v.1983, PAP758 (FCME).

Paralemanea mexicana (Kützing) Vis *et* Sheath, *Phycologia* 31: 177, 1992.

Basionym: *Lemanea mexicana* Kützing, *Tab. Phycol.* 7: 34, 1857.

Heterotypic synonym: *Lemanea feldmannii* Sánchez-Rodríguez *et* Huerta, *Ciencia (Mexico)* 27: 27, 1969.

Plants bambusiform, unstalked, cartilaginous, abundantly branched (≤ 40 % of branched plants), branches whorled, of first to second order, 1.5-9.0 cm high. Axial cell surrounded by abundant rhizoidal filaments. Ray cells forming two layers: the proximal ones not touching the outer cortex and the distal ones generally "Y" branched and connected to the cortex. Nodal diameter 200-2,280 µm; internodal diameter 158-739 µm; ratio nodal/internodal diameter 1.0-2.5. Spermatangial sori in nodal rings, 65-202 µm in diameter; ratio spermatangial/nodal diameter 0.1-0.4. Carpogonial branches composed of ovoid to globular cells, abundantly branched at the basal portion, on nodes or internodes, and penetrating the cortex towards the thallus surface; trichogyne pear-shaped. Carposporophyte sessile, on the inner portion of the cortex. Carpospores in chains of up to twelve, obovoid, ellipsoid or irregular, 12.4-24.8 µm in diameter, 18.4-39.2 in length. 'Chantransia' stage microscopic, growing near the basis of gametophytic plants; basal system with cylindrical, large cells, diameter 18-32 µm, length 96-224 µm; erect system with cylindrical and short cells, diameter 18-24 µm, length 30-68 µm; monosporangia spherical to sub-spherical, diameter 14-18 µm.

Diagnostic characters: plants large (mean length ≤ 4.0 cm; mean diameter > 400 µm), branched (≤ 40 % of branched plants), branches whorled, of first to second order.

World distribution: endemic to Mexico.

Distribution in Mexico (herbaria abbreviations according to Holmgren *et al.*, 1990): in literature - **2)** Villa del Carbón, W of Villa del Carbón, iii.1968, coll. Huerta-Silva (ENCB) (Sanchez-Rodríguez & Huerta, 1969; Sánchez, 1974); **3)** Mexico State, Nicolás Romero, 1 km from Cahuacán, 28. iii.1965, coll. Sánchez-Rodríguez 87, 28. ix.1965, coll. Sánchez-Rodríguez 88 (ENCB), 21. vii.1968, coll. Sánchez-Rodríguez 222 (ENCB), 3. ix.1966, coll. Cruz-Cisneros 1120 (ENCB); **4)** Cahuacán, Route 21, 1.6 km west of Cahuacán, coll. R.G. Sheath, 22. ii.1990 (NFLD) (Vis & Sheath, 1992; Sheath *et al.*, 1996). Specimens examined: **5)** Mexico State, Ecatepec, San Luis Ayucán, 5.i.1989, coll. G. Montejano PA2L (FCME); **6)** Coatepec de las Harinas, arroyo Meyuca, 8. ix.1990, coll. M. Gold BALE1942 (FCME).

Acknowledgements. This work was supported by DGAPA (UNAM) Postdoctoral Fellowship to JCJ and CNPq (300379/86-2) Research Grant to ONJ. The authors are indebted to: Maria Helena Carabolante, for the laboratory assistance; Willem F. Prud'homme van Reine, Algal Curator from Herbarium L, The Netherlands, for allowing ONJ access to the type specimens of freshwater red algae.

REFERENCES

ATKINSON G.F., 1890 — Monograph of the Lemaneaceae of the United States. *Annals of Botany* 4: 177-229.

BLUM J.L., 1994 — *Paralemanea* species (Rhodophyceae) in California. *Proceedings of the Indiana Academy of Science* 103: 1-24.

CARMONA J. J., 1997 — Estudio florístico (taxonómico, ecológico, biogeográfico) de las rodofitas de agua dulce en la región central de México. PhD Thesis, México, DF, Universidad Nacional Autónoma de México, 201 p.

DENICOLA D.M., HOAGLAND K.D. & ROEMER S.C., 1992 — Influences of canopy cover on spectral irradiance and periphyton assemblages in a prairie stream. *Journal of the North American Benthological Society* 11: 391-404.

GRIMSTONE A.V. & SKAER R.J., 1972 — *A guidebook to microscopical methods.* Cambridge, Cambridge University Press, 134 p.

GUIRY M.D., 1990 — Sporangia and spores. *In:* Cole, K.M. & Sheath. R.G. (eds), *Biology of the red algae*. Cambridge Cambridge University Press., pp. 347-376.

HOLMGREN P.K., HOLMGREN N.H. & BARNETT L.C., 1990 — *Index herbariorum. Part I. The Herbaria of the World*, 8th edition. New York, New York Botanical Garden, 693 p.

ISRAELSON G., 1942 — The freshwater Florideae of Sweden: studies on their taxonomy, ecology and distribution. *Symbolae Botanicae Upsaliensis* 6: 1-135.

JOHANSSON C., 1982 — Attached algal vegetation in running waters of Jämtland, Sweden. *Acta Phytogeographica Suecica* 71: 1-83.

MULLAHY J.H., 1952 — The morphology and cytology of *Lemanea australis* Atk. *Bulletin of the Torrey Botanical Club* 79: 393-406, 471-484.

NECCHI O. Jr & ZUCCHI M.R., 1995 — Record of *Paralemanea* (Lemaneaceae, Rhodophyta) in South America. *Algological Studies* 78: 33-38.

ORTEGA M.M., 1984 — Catálogo de algas continentales recientes de México. México, DF, Dirección General de Publicaciones, Universidade Nacional Autónoma de México, 566 p.

RAVEN J.A. & BEARDALL J., 1981 — Carbon dioxide as the exogenous inorganic carbon source for *Batrachospermum* and *Lemanea*. *British Phycological Journal* 16: 165-175.

SÁNCHEZ-RODRÍGUEZ M.E., 1974 — Rodofíceas dulceacuícolas de México. *Boletim de la Sociedad Botanica de México* 33: 31-37.

SÁNCHEZ-RODRÍGUEZ M.E. & HUERTA L.M., 1969 — Una nueva especie de *Lemanea* (Rhodph., Florid.), para la flora dulceacuícola mexicana. *Ciencia (México)* 27: 27-30.

SHEATH R.G., 1984 — The biology of freshwater red algae. *In:* Round, F.E. & Chapman, D.J. (eds), *Progress in phycological research, vol. 3*. Bristol, Biopress, pp. 89-157.

SHEATH R.G. & COLE K.M., 1990 - Differential alcian blue staining in freshwater Rhodophyta. *British Phycological Journal* 25: 281-285.

SHEATH R.G., MÜLLER K.M., VIS M.L. & ENTWISLE T.J., 1996 — A re-examination of the morphology, ultrastructure and classification of genera in the Lemaneaceae (Batrachospermales, Rhodophyta). *Phycological Research* 44: 233-246.

SIRODOT M.S., 1872 — Étude anatomique, organogénique et physiologique sur les algues d´eau douce de la famille des Lémanéacées. *Annales des Sciences Naturelles, Botanique, Série 5* 16: 1-95.

VIS M.L., SAUNDERS G.W., SHEATH R.G., DUNSE K. & ENTWISLE T.J., 1998 — Phylogeny of the Batrachospermales (Rhodophyta) inferred from *rbc*L and 18S ribosomal DNA gene sequences. *Journal of Phycology* 34: 341-350.

VIS M.L. & SHEATH R.G., 1992 — Systematics of the freshwater red algal family Lemaneaceae in North America. *Phycologia* 31: 164-179.