

PARALEMANEA SPECIES (RHODOPHYCEAE) IN CALIFORNIA

John L. Blum
University of Wisconsin-Milwaukee
Milwaukee, Wisconsin 53201

ABSTRACT: The practice of applying European names to the American species of *Paralemanea* is questioned. New parameters, in large part not previously employed in the taxonomy of *Paralemanea*, are introduced. Five new species of *Paralemanea* from streams in the Western States are described, and recommendations for the future delimitation of species are made.

KEY WORDS: Rhodophyceae, red algae, *Paralemanea*, *Paralemanea brandegeei*, *Paralemanea californica*, *Paralemanea gardnerii*, *Paralemanea parishii*, *Paralemanea tulensis*.

INTRODUCTION

Paralemanea, formerly a subgenus of the genus of freshwater red algae, *Lemanea*, was recently elevated to the rank of genus (Vis and Sheath, 1992). Three species, *Paralemanea catenata*, *P. annulata*, and *P. mexicana*, were included in the new genus. Both *P. catenata* and *P. annulata* were recorded from eastern North America, while *P. annulata* was recorded from California.

Since early in the last century, American workers have customarily used names based on European types for North American collections of *Lemanea* (Subgenus *Paralemanea*). From 1887 on (Vis and Sheath, 1992), a few new names were added to apply to collections of American provenance. The European names have not proven, even in Europe, to refer to clearly and reliably separate entities. Most of the descriptive texts deal with the gametophyte axis, which is more frequently seen and collected, than with the sporophyte or "chantransia" stage, which is essentially a plant of winter. The descriptions, utilizing adjectives such as nodose-torulose, undulate-constricted, etc., are subject to a degree of personal interpretation as marked as the structural variability to which they apply.

The gametophyte body plan of *Paralemanea* (P. Silva) Vis and Sheath consists of a cylinder or axis with successive enlargements (nodes) and elongate intervening segments (internodes) attached by a stipelike basal end, usually to a rocky substratum in a stream. Many specimens are markedly nodose and have a beaded appearance, but in some collections, especially in the early growth stages and in the lower portions of the axis, the nodes are not visible externally. The degree of nodosity and the outline of the nodes are considered diagnostic characters (Pascher, *et al.*, 1925), but it remains to be seen if this character is geographically and temporally consistent and if it correlates with characteristics of the "chantransia" and the spores.

The gametophyte axis is so variable in form that it appears fruitless to attempt to identify a single plant or even several plants on the basis of axis outline alone. Other characters must be studied, and even then, at certain ages, the attempt to determine the species of a clump of gametophyte axes is likely to be futile. Nodal variability may be due to age, position on the plant, or other factors. In summer

collections, the lowest 2-6 nodes are generally narrower than the upper nodes and have smaller spermatangial areas or lack them altogether. The main portion of the axis, starting around node 4-6 and extending distally for 10-20 and potentially for 100 or more internodes, can be considered as a unit inasmuch as one internode repeats another with little structural variation. The term *mesothallus* will be used for this region. Above the mesothallus during much of the growing season, the axis becomes progressively narrower toward the tip, the internodes become shorter, the nodes become more prominent, and the axis ends distally in a minute filamentous embryonic region. Internally, these changes are accompanied by other changes in both vegetative and reproductive anatomy. Within the young mesothallus, a body cavity is present between the axis wall and the central strand; this cavity may ultimately be filled with carpospores. In the mesothallus, little change is observed in the central (axial) strand from its upper to its lower end. However, in the subtending stipe and the lowermost internodes, the central strand usually becomes more massive and the internal space or body cavity, which is characteristic of the greater part of the gametophytic axis, is absent. Hence, the axis wall is in direct contact with the central strand. In the upper axis above the young mesothallus, the central strand is narrower, reflecting the juvenile status of the distal tip. In this region, the beginnings of rhizoidal cortication of the axial filament are evident. In the mesothallus, the rhizoidal cortication is denser. Likewise, in the mesothallus, the number of cystocarps per internode, while variable, tends to be higher than in the basal 4-6 internodes (Figure 10) or in the distal portion of the axis where fertilization (if any) is more recent and cystocarp growth more jejune.

The foregoing discussion depicts the variability of a typical gametophyte axis in summer. As the plants grow and mature, pronounced seasonal changes in form occur. During this time, the problems of description due to intra-axis variability are compounded by maturation and senescence (i.e., by month-to-month variation in form during the growing period).

The early efforts to differentiate the species of *Paralemanea* centered on the gametophyte. The "chantransia" stage (presumably diploid in California *Paralemanea* (cf. Magne, 1967)) has been studied in European material by Sirodot (1872), and Bourrelly (1970) maintains that the "chantransia" may be necessary for species determination. For certain species, this may be true. Nevertheless, most of the various growth stages have the potential of providing diagnostic features; for example, the spermatangial bands exhibit a range of characteristic dimensions and outlines, and they have been used to delimit species (cf. Pascher, *et al.*, 1925); the cystocarps probably have characteristic ranges in number per internode within certain species; and the spores have been utilized by Blum (1993) for *Paralemanea* and by Jao (1941) for *Lemanea* in the description of new species.

The above remarks suggest a flaw in the original species descriptions from Europe. Due to the observed variation from winter to fall, the identification process becomes one of applying terms wanting in accuracy to plants subject to wide morphological changes over the growing season. Keying-down becomes inconclusive or delusive. The range of names (which appears adequate to provide a systematic framework for this genus) may lull one into a sense of security and

satisfaction vis-a-vis the genus as it appears in standard manuals, when actually it is fair to ask whether anyone is capable of utilizing these descriptions with understanding and precision (cf. Israelson, 1942, p. 16).

The contention advanced in this paper is that the California flora does not include taxa of *Paralemanea* named (as species of *Lemanea*) from Europe or eastern North America. The California species are considered distinct from those of eastern North America. Thus, other American species can be ignored, and our attention focused on the European species. If the European species are based on type specimens, each of which represents only one stage of development in a continuum of morphological change, a stage not necessarily comparable with the stages of development represented by the other species; if the descriptions are unclear, and the unique characters of the taxa have not been recorded; if imperfections in the original descriptions of the older, 19th century species now assigned to *Paralemanea* (excepting *Lemanea mexicana* Kütz.= *P. mexicana* (Kütz.) Vis and Sheath) are not removed either in the illustrations provided by the original author or in later manuals utilizing these species; then any precise resolution of the nomenclature is rendered impossible, and the California entities should receive new names. The demonstration of unique features in the California material, when compared with a broad sampling of European material, is an important and abetting factor in the contention that, as regards this genus, the European and the California floras appear to be mutually exclusive. Taxa based on collections from California are differentiated from other American and European taxa in this paper. For five taxa, new names in the genus *Paralemanea* are proposed.

MATERIALS AND METHODS

The material studied in this work came from herbarium specimens supplemented by collections made by the author in the period 1988-1993. Dried specimens of both the gametophyte and the "chantransia" were found to return readily, upon hydration, to a natural appearance and very nearly to natural size. Specimens preserved in formol or other preservatives were used, if available. An appreciable number of the herbarium specimens were too fragmentary for instructive study.

Hydrated gametophyte axes were stained with dilute rose bengal solution and cleared in 50% Karo to produce semipermanent slides. "Chantransias" were similarly treated, following separation-dissection and repeated washing of the dissected material. Occasionally, good "chantransia" material could be found at the base of a gametophyte axis. All sections of gametophyte thalli were made freehand from dry or slightly hydrated axes. If available, three axes were sectioned together until approximately 60 sections were obtained. These sections were stained, cleared, and mounted together on the same slide. Spores, if sufficiently ripe, were studied from such sections or from crushed, stained, and cleared axes. Five characters were utilized as part of this study.

Rhizoids in the axial strand. Sections of the axis were used when counting (at 440x) the number of rhizoids surrounding the axial filament. Since corticating rhizoids are rare in the California specimens and since the central strand tends to follow a sinuous path through the thallus cavity, many sections were unsuitable

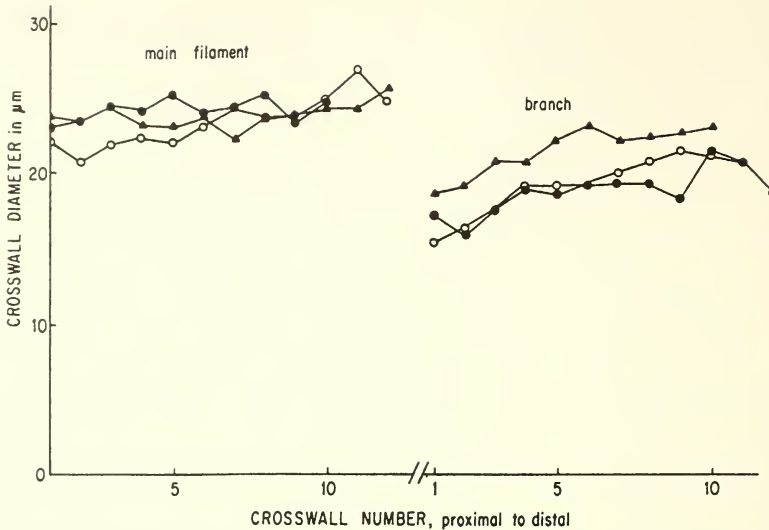


Figure 1. The crosswall diameters of three California "chantransias" having a main filament with primary branches distinctly inferior in thickness; the x-axis shows crosswall (i.e., cell) number. The collections represented are: *P. gardnerii*, F.R. Fosberg, T107, Borrego Valley, San Diego County, California (black circles; n=8; UC); *P. brandegeei*, Mrs. T.S. Brandegee, New York Ravine near Clarksville, Eldorado County, California (triangles; n=18; UC); and *P. californica*, C.L. Anderson, Santa Cruz, Santa Cruz County, California (open circles; n=7; FH).

for making such a count. Therefore, a variable number of useful sections (usually 10-20 from each collection) were used for rhizoid counts, which were then averaged. Rhizoid number in a collection varied within wide limits, and no statistical validity, based on such counts, can be claimed for the results from individual collections.

Distance from the Base of the Gametophyte to the Lowest Spermatangial Node. This distance was measured (at 440x), after the position of the lowest spermatangial node (which does not necessarily correspond with the first nodal enlargement) had been determined. The presence of at least 10 spermatangial cells was required to identify the lowest spermatangial node. The *Paralemanea* thallus, especially in the California specimens, is sufficiently translucent in the first few nodes and internodes to allow clusters of spermatangial cells to be observed through the thallus. Nevertheless, some error is introduced because the lowest spermatangial area, frequently a single spot, may occur where the curving edge of the mounted thallus obscures the epidermal structure. In addition, an entire axis (or at least its entire lower end) must be used in preparing a semipermanent mount. If the specimen packet contains only a few complete thalli, randomizing is impossible, and error is inevitable in the few counts which a single collection yields. For collections made expressly for this study, adequate numbers of thalli were generally available, but for many of the herbarium specimens, only 2-5 counts could be made.

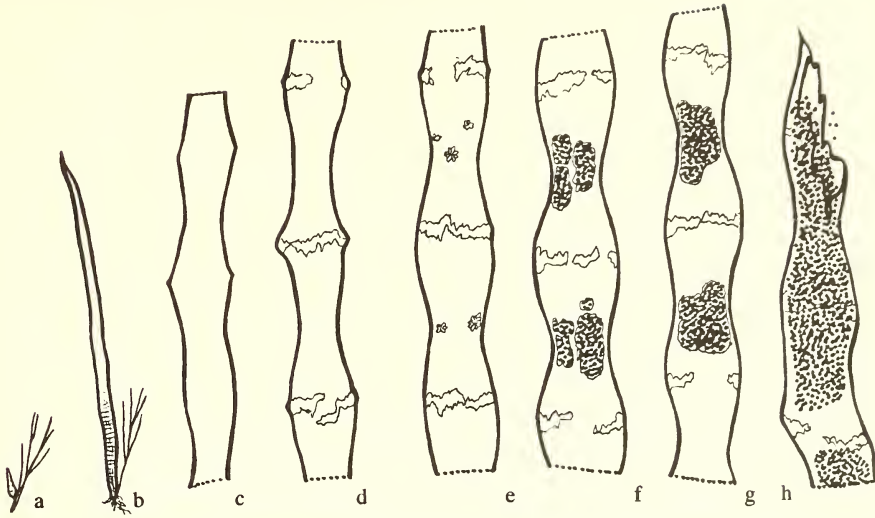


Figure 2. Diagrams representing “chantransias” and gametophytic thalli of *Paralemanea* at successive times in their growth. The “chantransia” at a has a juvenile gametophyte axis; at b, the gametophytic axis is older. Diagrams c-h show only a few nodes on progressively older axes. At c, the spermatangial bands are not yet visible. At d, the bands are visible, while at e, following fertilization, the beginning of cystocarp growth can be seen in the internode, if the axis has been cleared and stained. Much larger cystocarps are shown in f, and in g, the cystocarps have merged so that individual cystocarps can no longer be identified. In h, the spore masses from the cystocarps have conjoined, the decaying thallus wall has eroded, and the carpospores are being released.

Spermatangial Disposition. The spermatangial areas, consisting near the axis base of epidermal spots or sori, become complete rings about the upper nodes, and their width varies. Their width was measured using an ocular micrometer. An average of four to ten readings from random placements of the scale at each node from 1 through 14 or 15 were made. Spermatangial areas were recorded as spots, broken bands, or complete bands. The first two categories were regarded as incomplete; they included bands made up of a series of spermatangial areas forming a broken ring about the circumference of the node as well as those bands which completely encircled the node but were broken in such a way that their ends did not meet (Figure 2d). If the thalli from collections assigned to a single species gave conflicting results as to the number of the node representing the beginning of complete bands (*P. californica* and *P. gardnerii*), an average of the readings was taken (Figure 18). In the species descriptions in this paper, nodes 1-3 were disregarded when stating the limits of spermatangial band width, because the lowermost nodes frequently exhibit narrower bands, unrepresentative of the bands on superior nodes. An occasional incomplete band does sometimes interrupt an otherwise “complete” series; this incomplete band was disregarded in designating divisions of the thallus. Occasional outliers are encountered; i.e., spermatangial spots lateral to a band which are not connected to the band itself.

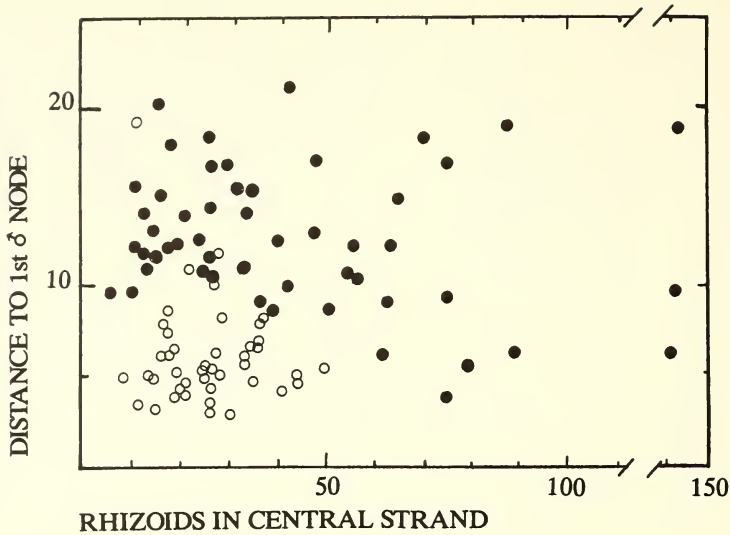


Figure 3. The rhizoids in the central strand (x -axis) plotted against the distance from the axis base to the lowest (1st) spermatangial area (y -axis). The black circles represent European collections; the open circles, California collections.

These outliers are most common in large specimens; they were measured and recorded as part of the spermatangial band, if the random line selected happened to cross them.

“Chantransia” Morphology. The young “chantransia” plant consists of an erect, uniseriate, unbranched, photosynthetic filament, whose basal end terminates in a colorless rhizoid. Additional rhizoids grow out of the lowermost cells of the photosynthetic filament. Both the photosynthetic axis and the rhizoids branch and rebranch. After branching begins, short photosynthetic branches, each initiated by an apical cell, form the young gametophytic axes. Certain “chantransia” plantlets become heavily tufted with many thickly-bunched branches. As the gametophytic axes grow rapidly in length, greatly surpassing the “chantransia,” the latter undergoes changes indicative of senescence: its filaments elongate, become crooked, and lose much of their pigmentation, approximating the rhizoids in appearance. The “chantransia” filaments may become colonized by a variety of epiphytes, and breakage and erosion occur. By late spring, the “chantransia” is likely to be greatly modified or completely gone.

The branching habit of the “chantransia” frustrates easy comparative description. Opposite branching and unilateral branching have been used as points of distinction (Sirodot, 1872), but for the California material, both these branching patterns appear to be universally present.

The presence or absence of a main filament to which the branches are both subsidiary and smaller as well as conic filaments which taper significantly from one end to the other appear to be potential diagnostic characters. These two traits were investigated by taking width measurements of successive cells at their crosswalls. Basal filaments (photosynthetic) were defined as those with free rhizoids attached at their base or whose base itself was becoming rhizoidal. The

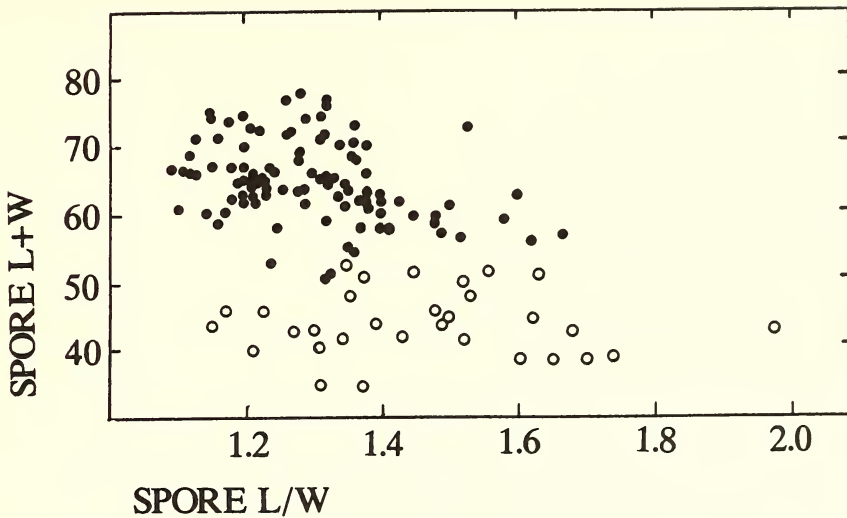


Figure 4. The ratio of spore length to width (μm , x -axis) plotted against the sum of spore length and width (μm , y -axis). The black circles represent collections from the eastern United States (essentially from the Missouri-Kansas boundary to the Atlantic); the open circles represent California collections plus a few from Oregon, Idaho, and Nevada.

diameter of the cells, if any, between the base and the first photosynthetic branch was recorded. The cross wall immediately above the first photosynthetic branch was considered the beginning of the main filament (although some main filaments were no greater in diameter than their branches). After measuring the crosswalls of all the cells in the main filament, a branch was selected, and similar measurements were made on the cells of the branch. For such measurements, plantlets were sought which had both an intact main filament and an intact branch of several cells apiece. Plants with broken tips were, insofar as possible, rejected, and older "chantransias" with elongate, crooked cells were considered atypical and were not measured. An outline sketch of each plantlet chosen was made after taking its measurements.

The presence or absence of a main filament is not an easy distinction to make in *Paralemanea*. Of the filaments in a tuft, one or two, older than the rest, may be perceptibly larger. This perception could be verified using the measurements described above. In the California "chantransias," such measurements revealed the presence of a principal filament in three of the species described here (Figure 1).

Size of "Chantransia" Terminal Branches. Since the branching pattern of the "chantransia" offered few reliable characters and the comparative study of basal and intermediate cell size appeared to promise no useful results, the terminals of the youngest photosynthetic "chantransia" filaments were chosen for diameter determination. Their diameter was measured at the most distal crosswall; where possible, fifteen determinations were made and averaged for each of the 27 California collections studied as well as for the 29 collections from the eastern United States and the 18 collections from Europe. No broken, pale,

Table 1. Average distance determinations (gametophyte thallus base to lowest spermatangial areas) in the various collections ranked by size class. N is variable in each collection ((2-) 5-10 (-30)).

California Collections	Eastern U.S. Collections	European Collections	Size Classes (mm)
8	0	0	2.1-4
29	7	1	4.1-6
16	33	4	6.1-8
7	28	6	8.1-10
3	22	9	10.1-12
0	33	21	12.1-14
0	22	11	14.1-16
0	11	5	16.1-18
0	2	3	18.1-20
0	0	3	20.1-22
0	0	0	22.1-24
Total	63	158	63

or elongated (senescent) terminals were included in the measurements. "Chantransias" not associated with any gametophytic parts were also avoided.

GROWTH OF THE GAMETOPHYTE

The growth of the gametophyte of *Paralemanea* can be summarized in a series of diagrams (Figure 2a-h). These stages can sometimes be recognized *in vivo*; however, whole mounts are usually needed to identify them. A young gametophyte axis consists of a few cells, one of which is the apical cell. This axis, growing from and attached to the "chantransia," is shown in Figure 2a. In b, the axis has grown to several hundred cells and retains its apical cell, but as yet, nodes and internodes are not externally visible.

Stages c-h represent a series of internodes in the mesothallus. Stages a-c have no recognizable spermatangial areas. A typical spring stage, d, is somewhat unpredictable in southern California due to the frequent and irregular desiccation of the stream beds. This stage (d) shows recognizable spermatangial areas but no visible cystocarps, which are small and subspherical in e. In f (approximately early summer), the cystocarps have enlarged but can still be counted. Later, the tip of the thallus thickens as the lower portions of the axis have previously done. In g, the cystocarps, after further growth, have joined into a mass of developing spores, usually more or less central in each internode. The spores mature, acquire a thick wall, and normally lose their attachment to other spores in the cystocarp. In h (July-November), the mass of enlarging spores has joined other spore masses creating at least locally a continuous internal column of spores. Then, the axis is broken and/or eroded, and the spores are disseminated by water.

The above sequence can be modified or interrupted at any time in an intermittent stream. The desiccated plants remain for a few weeks or perhaps until winter with or without having matured their spores. In some species, vegetative growth can resume from viable holdfasts which remain in or on the rocky substrate (Stewart, 1983).

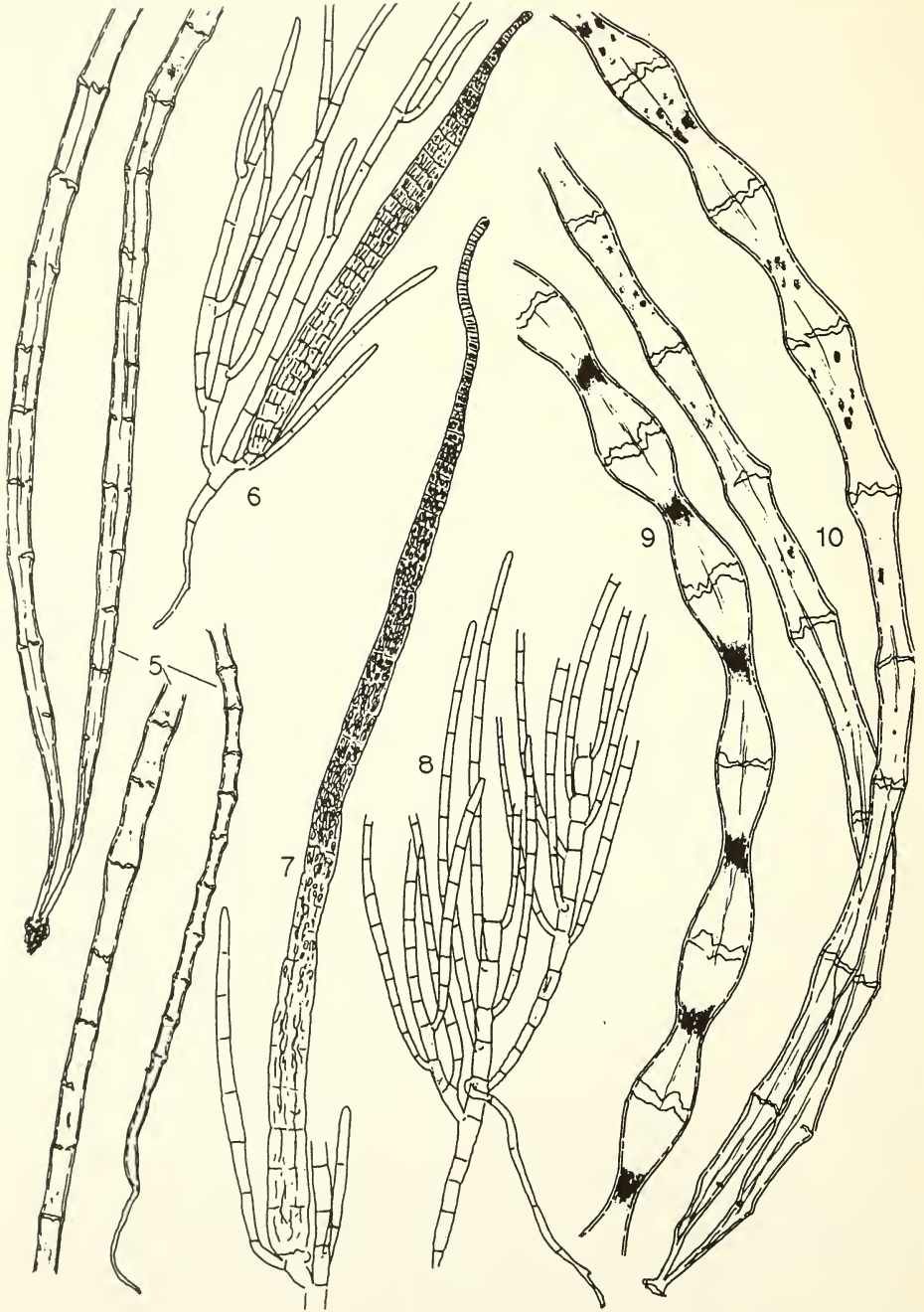
While stages a-h are defined by morphological events and structural features, the maturation of the gametophyte generally involves changes in shape. Frequently, the deformations may materially modify many or most of the axes in a collection. Some axes may mature before others. Certain internodes may produce spores, while others do not. The extent of these changes will affect the ultimate appearance of an internode and/or the entire axis. Therefore, this series (a-h) will not apply with accuracy to an entire collection or to any one species. The series (a-h) represents a schematized average of the appearance of the axes in any collection at certain times during the growing season.

DISTINGUISHING CHARACTERISTICS

The American Pacific Coast species differ from others with which they might be confused in three important characters: 1) the gametophyte axis bears spermatangial areas relatively close (4-8 mm) to its base, whereas in the European species, the spermatangial areas are farther away (8-21 mm; Table 1); 2) the corticating rhizoids of the central strand in the mesothallus are few (5-25 (-35)) in number, as seen on the cross-section, and show little tendency to cohere, whereas in species from the eastern United States, the corticating rhizoids are more abundant (20-250) and are regularly united about the axial filament in a coherent mass (the European species are similar to the West Coast species in this regard); and 3) the gametophyte of the West Coast species exhibits a banded appearance throughout the mesothallus during most of the warmer season when spores are present, the lighter nodal areas alternating with the darker, spore-bearing internodes (Figures 5, 9, 11, 14, 16). This phenomenon, with few exceptions, is not seen in material from the eastern United States or Europe. The banded appearance is particularly obvious after staining and clearing, but it is also visible in some dried specimens. In senescent California populations in the autumn, this character may be lost as the expansion of the spore mass ultimately fills the cavities of both the nodal and internodal areas (e.g., *P. tulensis* sp. nov.)

The California collections as a whole were compared with the European collections as a whole in preparing Figure 3, which contrasts their differences in the number of rhizoids and spermatangial position. While the accuracy of such a procedure is dependent on the number of collections sampled, and the 44 European collections are a meager group to represent either Europe or the rest of the world, the evidence suggests that none of the European names formerly applied to the California collections (e.g., *Lemanea torulosa* (Roth) Ag. or *L. catenate* Kütz.) are applicable to the material collected and studied to date.

The species from California and the eastern United States can be distinguished using two relatively simple measurements: 1) when carpospore size and shape are compared, the California spores are clearly smaller (Figure 4) and tend to be more elongate; and 2) the terminal cells of the primary and secondary branch filaments in the "chantransia" are narrower than those from eastern collections (Table 2).



Figures 5-10. 5. *Paralemanea gardnerii*, mature, spore-bearing gametophytes, TYPE (x10). 6. *P. gardnerii*, "chantransia" with juvenile gametophyte axis, TYPE (x150). 7. *P. californica*, young gametophyte axis showing proboscoid tip (x150). 8. *P. californica*, "chantransia" (x150). 9. *P. californica*, gametophyte axis, Blasdale collection (x10). 10. *R. californica*, gametophyte axes, TYPE (x10).

Table 2. The total number of “chantransias” arranged in size classes based on average terminal crosswall diameter. The populations from California are contrasted with the populations from the eastern United States.

California	Eastern U.S.	Size classes (µm)
0	0	10.0-10.9
2	0	11.0-11.9
4	0	12.0-12.9
2	0	13.0-13.9
5	0	14.0-14.9
4	1	15.0-15.9
4	3	16.0-16.9
0	2	17.0-17.0
0	12	18.0-18.9
1	5	19.0-19.9
0	3	20.0-20.9
0	3	21.0-21.9
0	5	22.0-22.9
0	3	23.0-23.9
0	0	24.0-24.9
0	1	25.0-25.9
0	0	26.0-26.9
0	0	27.0-27.9
0	0	28.0-28.9
0	0	29.0-29.9
0	0	30.0-31.9
0	1	31.0-31.9
Total	22	39

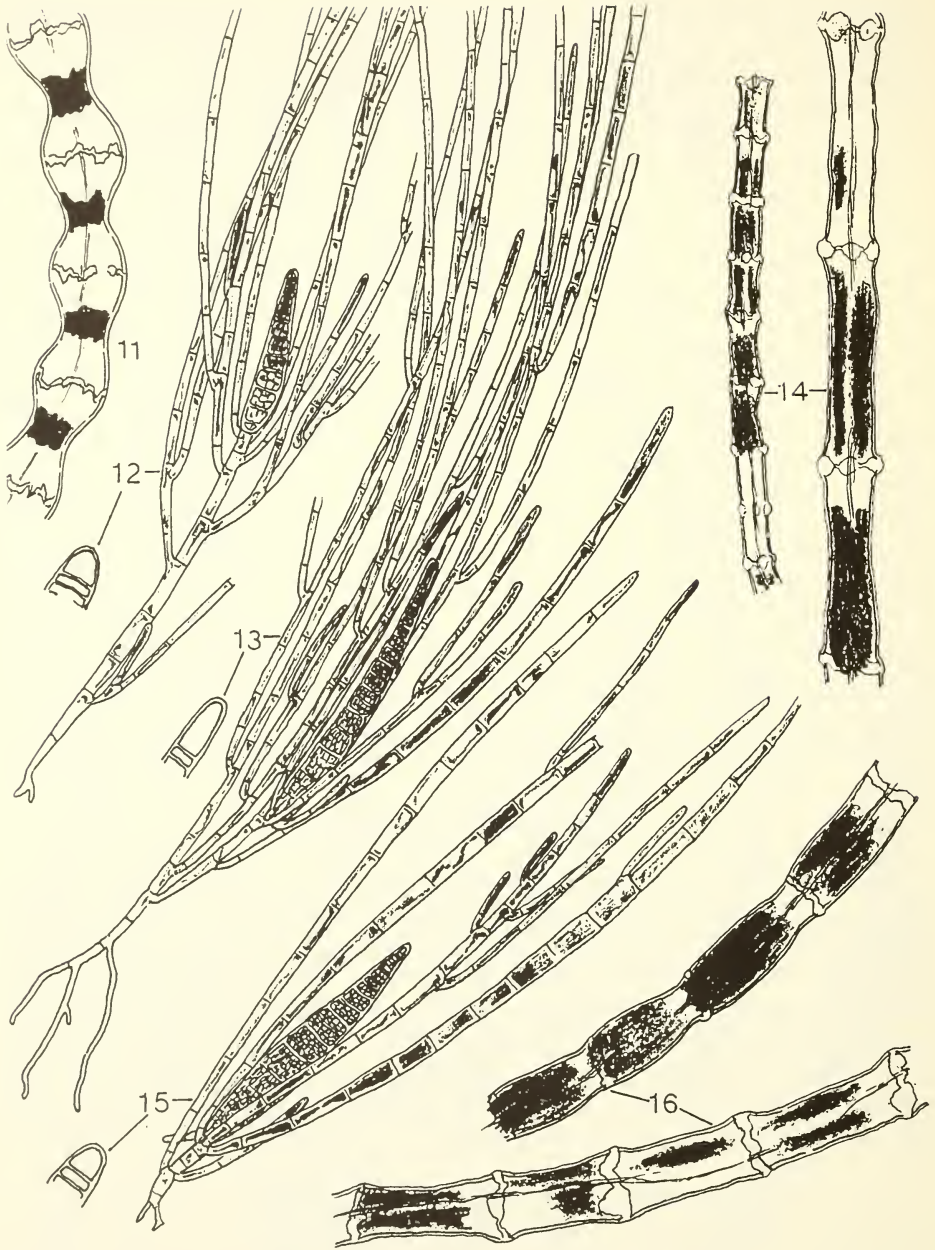
SPECIES DESCRIPTIONS

Five new species of *Paralemanea* from California are described below. These species are based on both herbarium specimens and the author’s collections. Some specimens from the western United States could not be assigned to any one of these five species, but whether these specimens represent hybrids or additional new species will have to await further collecting. All the descriptions are of gametophyte type specimens which have at least a portion of the “chantransia” present. These descriptions are supplemented by observations made on younger or older gametophytic material from other sites or collections. Each description includes measurements of the mature spores from the type specimen.

Paralemanea gardnerii Blum sp. nov.

Figures 5, 6, 20, 21

Axis gametophyti tenuis, internodia ca. 1.0-1.9 mm longa; saepe internodium cylindricis et nodis leviter amplificatis. Filum centrale in parte media thalli e 20-50 rhizoideis corticatis constans. Pars infima spermatangialis (ad primum nodum) ca. 4.3-7.2 mm super basem rhizoidalem. Taenia spermatangialia valde confectis aut annuli raro adsunt vel omnino absunt, sed ab nodo 15+ cum adsunt, ca. 25-90 µm lata, et non latiora distaliter. Multi nodi alveis annularibus non profundis positos quasi cum taeniis spermatangialibus. Cystocarpis plerumque 2-6 per internodium. Aspectus fasciatus typicus cum sporis. Sporae 13.2-28.6 x 15.4-33 µm. Caespites “chantransia” sine filamentis valde conicis aut filamento claro principali. In locis valde caespitosis, filamenta basalia 11-20 µm diametro ad septa.



Figures 11-16. Mature gametophyte axes; "chantransias" each bearing one juvenile gametophyte axis; the apical cell of the juvenile gametophyte of each "chantransia" (Figures 12, 13, and 15) is enlarged at the left (x900). **11.** *Paralemanea brandegeei*, mature gametophyte axis, TYPE (x10). **12.** *P. brandegeei*, "chantransia" (x150). **13.** *P. parishii*, "chantransia" (x150). **14.** *P. parishii*, mature gametophyte axis, TYPE (x10). **15.** *P. tulensis*, "chantransia" (x150). **16.** *P. tulensis*, mature gametophyte axis, TYPE (x10).

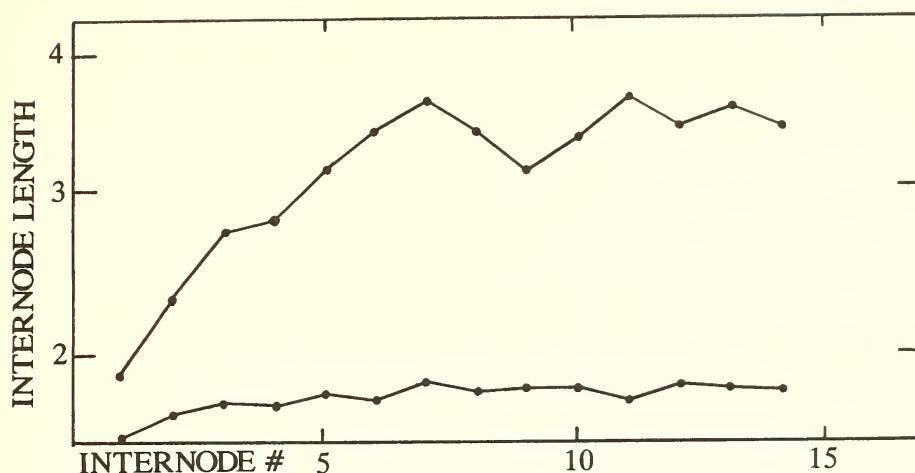


Figure 17. The internode length (mm) of *Paralemanea californica* shown from internode 1 through 14 on the upper line and for *P. gardnerii* on the lower line. The upper line is an average of four collections (7 axes) of *P. californica* (see Figure 18). The lower line is an average of four collections (8 axes) of *P. gardnerii*.

Gametophyte axis slender, often cylindric; internodes mostly 1.0-1.9 mm in length, sometimes with gently swollen nodes; central strand in the mesothallus of ca. 10-30 corticating rhizoids. Lowest spermatangial area (at node 1) ca. 4.3-7.2 mm above the rhizoidal base but with ostensibly complete annular bands or rings starting only at node 15 or higher; the annular bands ca. 25-90 μ m in width, not increasing in overall width on superior nodes; many nodes showing shallow annular troughs approximately coinciding in position with the spermatangial bands. Cystocarps usually 2-6 per internode; banded appearance typical, if spores are present. Spores ca. 13-31 x 19-42 μ m. "Chantransia" without markedly conical filaments, but sometimes with an identifiable main filament wider than the primary branches; the basal filaments 13-26 μ m in diameter at the crosswalls, branch filaments 13-17 μ m.

Type. San Francisquito Creek, Santa Clara County, California, no date, *N.L. Gardner* 2846 (UC 27167).

Additional Collections. Palm Canyon, Borrego Valley, San Diego County, California, May 4, 1929, *F.R. Fosberg* (UC); Mill Valley, Marin County, California, July 20, 1906, *N.L. Gardner* 1792 (UC 94471, 276168); Mt. Tamalpais, Marin County, July 1906, *W.J.V. Osterhout* (UC 94470); Mill Creek, Marin County, California, July 18, 1925, *H.E. Parks* (UC 278342); Mill Creek, Marin County, California, July 1925, *W.A. and C.B. Setchell* (MO in UC 1018388).

Description. The type material has a few young gametophyte axes and was chosen partly for this reason. The other collections listed above include the type material of *Lemanea annulata* var. *franciscana* Atkinson (*Bot. Gaz.* 92(2): 232, 1931). There are parallels between *Paralemanea californica* and *P. gardnerii*,

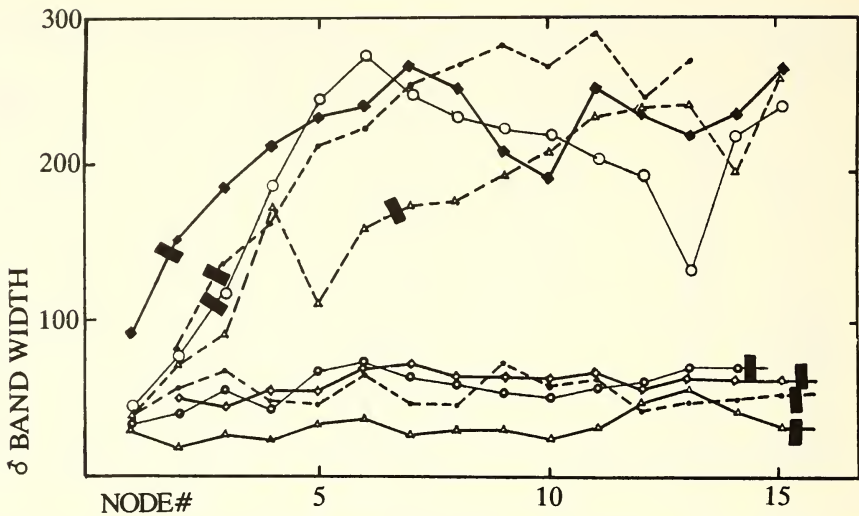


Figure 18. The width of the spermatangial band (μm) and the point at which it becomes complete are contrasted for *Paralemanea californica* (the four upper lines) and *P. gardnerii* (the four lower lines). The upper four lines show band width from node 1 through node 15 in *P. californica*; the heavy black bar indicates where on the axes the first complete nodes were recorded. The collections of *P. californica* represented are from: C.C. Parry, Santa Margarita (diamonds, heavy line; $n = 2$; CU); Blasdale collection (circles, light line; $n = 2$; UC); G.W. Hollenberg, 179 (dots, broken line; $n = 1$; US); R.S. Ferris and R. Bacigalupi, TYPE (triangles, broken line; $n = 2$; UC). The lower four lines show band width from node 1 through node 15 in *P. gardnerii*; the heavy black bars terminating the record indicate that complete bands were not recorded in this region of the axis (nodes 1-15), although higher nodes might have complete bands. The collections of *P. gardnerii* represented are from: N.L. Gardner, 2846, TYPE (dots, broken line; $n = 2$; UC); Osterhout collection (circles, narrow line; $n = 2$; US); Fosberg collection (diamonds, heavy line; $n = 2$; UC); Parks collection (triangles, heavy line; $n = 2$; UC).

thus the transfer of the varietal name *franciscana* to *P. californica* was considered. However, the nature of the juvenile gametophytes and of the spermatangial bands led to the conclusion that this transfer was unwise, and a new specific name is proposed.

Some of the collections had usable "chantransia" material, but the type appears to be the only collection having juvenile gametophytes on the "chantransia." Several of the collections are from the area of Mill Valley and may represent multiple samplings of a single population.

Paralemanea gardnerii shares with *P. californica* sp. nov. the occasional occurrence of a nodal trough (see below) and appears superficially to be a smaller and near-cylindric version of the latter. The narrower spermatangial band and the persistence of spotlike spermatangial areas and/or broken or incomplete bands

throughout much of the axis delimit *P. gardnerii* from *P. californica*. The tendency to show little or no distal increase in the width of the spermatangial band and practically no distal increase in internodal length constitute additional points of distinction. The patches of spermatogenous cells are seldom, if ever, raised above the general epidermal surface as they are in *P. parishii* sp. nov., and they are usually irregular and often angular, rather than rounded. The terminal initials of the young gametophytic axes bear some resemblance to those of *P. californica*; the type collection contains many examples of these, but the terminal initials offer no obvious contrast with *Paralemanea* axes from the eastern United States or Europe.

***Paralemanea californica* Blum sp. nov.**

Figures 7-10, 19

Axis gametophyti robustus. Internodia plerumque 2-4 mm longa, saepe nodis valde tumidis. Filum centrale in parte media thalli e 20-50 rhizoideis corticatis constans. Pars infima spermatangialis (ad primum nodum) circa 2.9-5.4 mm super basem rhizoidalem et ex una vel pluribus maculis spermatangialibus constans, sed taeniis valde confectis aut annulis ab secundo aut tertio (-8) nodo et taeniis annularibus circa 110-300 μ m latis crescentibus distaliter latitudine post nodes spermatangiales 1-7. Multi nodi alveis annularibus non profundis positos quasi cum taeniis spermatangialibus. Cystocarpis plerumque 5-8 per internodium. Massa sporae maturae internodium non replens. Aspectus fasciatus typicus cum sporis. Sporae ca. 13.2-28.6 x 15.4-33 μ m. Caespites "chantransia" in locis valde caespitosis, filamenta basalia 11-20 μ m diametro ad septa. Initia axis juvenis in portionem elongatam et cylindricam distaliter terminantia.

Gametophyte axis robust; internodes mostly 2-4 mm in length, often with clearly swollen nodes; central strand in the mesothallus comprising ca. 20-50 corticating rhizoids. Lowest spermatangial area (at node 1) ca. 2.9-5.4 mm above the rhizoidal base and consisting of one or more spermatophorous spots, but with complete annular bands or rings starting at node 2 or 3 (-8), the annular bands ca. 110-300 μ m in diameter, increasing distally in width after the initial series (nodes 1-7) of spermatangial nodes (Figure 18); many nodes showing shallow annular troughs approximately coinciding in position with the spermatangial bands. Cystocarps usually 5-8 per internode; mature spore mass not filling the internode. Banded appearance typical, if spores are present. Spores ca. 13.2-28.6 x 15.4-33 μ m. "Chantransia" in places heavily tufted; the basal filaments 11-20 μ m in diameter at the crosswalls; branch filaments mostly 11-15 μ m in diameter at the crosswalls. Young axis initials terminating distally in an elongate cylindric portion (Figures 7, 19).

Type. Four miles north of the Ben Hur Post Office, Mariposa County, California. May 29, 1941, *R.S. Ferris* and *R. Bacigalupi* (DS in UC 502456).

Additional Collections. Oakland (no other data), *C.L. Anderson* (Herb. Atkinson) (UC); Santa Cruz, Santa Cruz County, *C.L. Anderson* (FH); Herb. Bolander (no data), *Anonymous* (US); Atlas, Napa County, California, May 1916, *W.C. Blasdale* (UC); Eastern Oregon, 1886, *W.C. Cusick 1353* (CU); Los Troncos Creek, woods near Palo Alto, Santa Clara County, California, 6-1-1932, *G.W. Hollenberg 179* (US); Santa Margarita, San Luis Obispo County, April, 1850, *C.C. Parry* (CU); Little Carson Canyon, Sonoma County, California, March

1917, *L.P. Rose* (UC); Japocha Springs, Cuyamaca Mountains, San Diego County, California, May 26, 1978, *J. Stewart 3318a* (LAM).

Description. The type was chosen because the collection included both juvenile and mature gametophyte material, spores, and "chantransia." Of the above collections, the Blasdale collection shows the general structure of the gametophyte the best, and the anonymous collection from the Bolander Herbarium (in US) shows the juvenile gametophyte axes the best. An additional collection (W.I. and E.B. Follett) from Seigler Canyon, Lake County, California (see below) is questionably referable to this species.

Paralemanea californica is one of the larger and more graceful species of the genus in North America. The large gametophyte axes, up to 15 cm or more in length and 1-2 mm in nodal diameter, are likely to be mixed with narrower and shorter axes. The elongate internodes and the obviously banded appearance, when spores are present, are characteristic of *P. californica*. Fresh material was not available, but for much of the herbarium material examined (largely early and mid-summer collections), the mass of maturing spores forms a mid-internodal plug, which is confined to a small portion of the internodal midsection. The spore mass is further constricted by the axis wall, which is, and apparently remains, narrowest at this approximate midpoint of the internode (Figure 9). Whereas substantial inflation of the nodes is typical, a slight depression (trough) often occurs at the midpoint (of the inflated area), which may, as in *P. gardnerii*, completely encircle the node (Figure 21). This trough usually corresponds with the area occupied in whole or in part by the spermatangial band.

Paralemanea californica is set off from other California species by its substantial internode length and by the increase in length of successive internodes, especially from spermatangial node 1 through 3 (Figure 17). *Paralemanea gardnerii* shows only a slight increase in internode length in this area (Figure 17).

A broad spermatangial annulus is characteristic of *P. californica*. The annulus is regularly present as a complete ring, starting at about spermatangial node 2 or 3 (Figure 18) and continuing to the distal end of the axis. Apart from the inflation of the entire nodal area, little or no elevation of the spermatangial sorus occurs above the epidermal level. The basal node bears 1-3 spermatangial sori.

The most pronounced morphological peculiarity of *Paralemanea californica* is the proboscoïd distal end of the young gametophyte at about the 300-800 cell stage. A terminal uniseriate cylinder below the apical cell is typical, consisting of 10-20 cells which are undivided periaxially, the entire uniseriate cylinder remaining for a time narrower than the remainder of the axis. In all the collections of *P. californica* studied, the elongate uniseriate tip appears to be a temporary phenomenon that is absent from juvenile gametophytes which have attained about 2 cm in length.

Paralemanea brandegeei Blum sp. nov.

Figures 11, 12, 22

Axis gametophyti robustus. Internodia plerumque 2-3 mm longa, saepe nodis valde tumidis. Filum centrale in parte media thalli e 30-40 rhizoideis corticatis constans. Pars infima spermatangialis (ad primum nodum) ca. 6-8.5 mm super basem rhizoidalem et ex una vel pluribus maculis spermatangiales constans; sed taeniis valde confectis aut annulis ab sexto (-9) nodo et taeniis annularibus ca. 80-150 μ m latis crescentibus

distaliter latitudine post nodes spermatangiales 1-7. Cystocarpia plerumque 5-8 per internodium. Massa sporae maturae internodium non replens. Aspectus fasciatus typicus cum sporis. Sporae 15.4-24.2 x 17.6-30 μ m. Caespites chantransiae flabelliformes; rami principales altiores e stipite basali 4-10 cellularum plerumque exorientes; rami usque ad 28 μ m diametro. Initia in chantransia gametophyti basalia aut comparate alta; cellula apicalis tholiformis.

Gametophyte axis robust, internodes mostly 2-3 mm in length with swollen, frequently inflated nodes; central strand in the mesothallus comprising ca. 30-40 corticating rhizoids; lowest spermatangial area (at node 1) ca. 6-8.5 mm above the rhizoidal base and consisting of one or more spermatophorous spots, but with complete annular bands or rings starting at about nodes 6-9; the annular bands ca. 80-150 μ m in diameter, increasing distally in width after the initial series (nodes 1-7) of spermatangial nodes. Cystocarps usually 5-8 per internode; mature spore mass not filling the internode; banded appearance is typical, if spores are present. Spores 15.4-24.2 x 17.6-30 μ m. "Chantransia" tufts without markedly conical filaments when reproductive, but sometimes with a main filament wider than the primary branches. Young axis initials without an elongate cylindric portion; apical cell dome-shaped.

Type. This species is known only from the type locality: New York River, Eldorado County, California, May 10, 1945(?), Mrs. Katherine Brandegee (UC 277581).

Supplementary Type (for "chantransia"). Same locale as above, December 12, 1993, *J.L. Blum* 5179.

Additional Collections. New York Ravine, Eldorado County, California, May 1907, Mrs. L.S. Brandegee (UC 447018); Same locale, September 17, 1988, *J.L. Blum* 4948; Same locale, July 29, 1990, *J.L. Blum* 5056; Same locale, March 10, 1991, *J.L. Blum* 5076.

Description. All of these collections except for the supplementary type were essentially devoid of juvenile gametophytes and included little "chantransia" material. The mature gametophyte of *Paralemanea brandegeei* has much shorter internodes than *P. californica*, but it was tentatively considered to be a form of the latter species until the December 1993 collection, when the locale yielded abundant "chantransia" with juvenile gametophytes, which were very different from those of *P. californica*. The dome-shaped apical cell is similar in shape to most *Paralemanea* apical cells, but the more mature gametophyte, because of its relatively short internodes and "banded" appearance, is unlike any other North American *Paralemanea* that the author has observed.

Paralemanea parishii Blum sp. nov.

Figures 13, 14, 23

Axis gametophyti tenuis et nodosus, saepe internodis cylindricis et nodis leviter amplificatis. Internodia ca. 1.0-1.5 mm longa. Filum centrale in parte media thalli ex rhizoideis 5-22 corticatis constans. Cystocarpis plerumque 2-6 per internodium. Massa sporae maturae paene internodium replens. Pars infima spermatangialis (ad primum nodum) ca (4.8-) 6.7-9.4 mm super basem rhizoidalem et ex una aut pluribus maculis rotundis elevatisque constans, interdum per 15 aut plures nodos saepe extendens. Sporae 11-20 x 15-31 μ m. Caespites "chantransia" sine filamentis valde conicis, interdum filamento claro principali quod latius est quam rami principales. Filamentum principale 19-22 μ m diametro ad septa. Rami 14-19 μ m diametro ad septa. Cellula apicalis gametophyti cylindrica.

Gametophyte axis narrow and nodose, often with cylindric internodes and slightly enlarged nodes. Internodes mostly 1.0-1.5 mm in length, the central strand in the mesothallus comprising 5-22 corticating rhizoids. Cystocarps 2-7 per internode. Mature spore mass filling the internode. Spermatangial areas beginning (node 1) with one or more rounded and raised spots at (4.8-) 6.7-9.4 mm above the rhizoidal base, this pattern of spots sometimes continuing distally for 15 or more nodes; the sequent spermatangial bands, ca. 50-100 μm in width, not increasing materially in width distally. Spores 11-20 x 15-31 μm . "Chantransia" without markedly conical filaments but sometimes with an identifiable main filament wider than the principal branches. Main filament 19-22 μm in diameter, its branches 14-19 μm in diameter. Apical cell cylindric.

Type. Tahquitz Creek about 0.6 km below Tahquitz Falls, Palm Springs, Riverside County, California, December 9, 1993, *J.L. Blum 5175* (UC).

Additional Collections. West Cañon at Palm Springs, 1-10 April 1896, *S.B. Parish 4055* (UC 205366); In hills 2 miles southwest of Bloomington in the vicinity of San Bernardino, San Bernardino County, California, March 23, 1897, *S.B. Parish* (UC 94473).

Description. The author's attention was directed to the Tahquitz area (formerly called West Cañon at Palm Springs) by S.R. Parish's collections there nearly a century ago. My collections include both "chantransia" and gametophyte material, including juvenile material, which appears to be totally lacking in Parish's collections.

Parish's locality near San Bernardino could not be located with precision. Both of Parish's collections consist of relatively small gametophyte axes with cylindric internodes. The nodes, as in the Tahquitz Creek material, tend to be enlarged, producing an axis which can be compared to a knotted cord with considerable space between the knots. The axes are further characterized by raised spermatangial areas, which may appear as circular mounds, frequently four in number, at a node. The mounds may be separate from each other, at least in the first fifteen nodes, or joined by narrow connections. The presence of spermatangial areas is suggestive of the spermatangial protuberances in *Lemanea* (as opposed to *Paralemanea*), but usually these areas are less pronounced and, in the mesothallus, tend to become somewhat fused. No significant increase in spermatangial band width or internode length occurs within the mesothallus, and the spermatangial band appears as a broken ring at many of the lower nodes. The number of cystocarps is 2-7 per node, but 2 appears to be the most common number (which is often the case in relatively narrow *Paralemanea* axes). The species characteristically shows considerable size variation in the gametophyte axes. In the mature gametophyte, the spore mass fills much of the internode and sometimes extends proximally, thus occupying much of the subtending nodal area as well.

The "chantransia" filaments are narrower and longer than in the other California species, and they often bear the juvenile gametophytes a short distance (4.5 mm) above the rhizoidal base. The apical cell of the young gametophyte is greatly elongated in comparison with the apical cells of the other species.

***Paralemanea tulensis* Blum sp. nov.**

Figures 15, 16

Axis gametophyti cellulis epidermicis comparate parvis quorum 170-210 transectum 1 mm scindunt. Axis leviter nodosus internodiis, diameter axis, ubi repletus sporis, diametrum nodi frequent superans. Internodia ca. 1.0-1.8 mm longa. Filum centrale in parte mesothalli ex rhizoideis 20-30 corticatis constans. Pars infima spermatangialis (ad primum nodum) ca. 4.3-7.2 mm super basem rhizoidalem, taeniis annularibus valde confectis aut annulis ad nodes distales ab nodes 3-5. Taenia annularia spermatangialis ca. 85-230 μ m late, valde latiora a nodo 3 distaliter. Massa sporae maturae paene internodium replens. Sporae ca. 8-24 x 15-31 μ m. "Chantransia" filamenta valde conica, includens quae distaliter amplificant ab 13 usque ad 33 μ m. Cellula apicalis tholiformis.

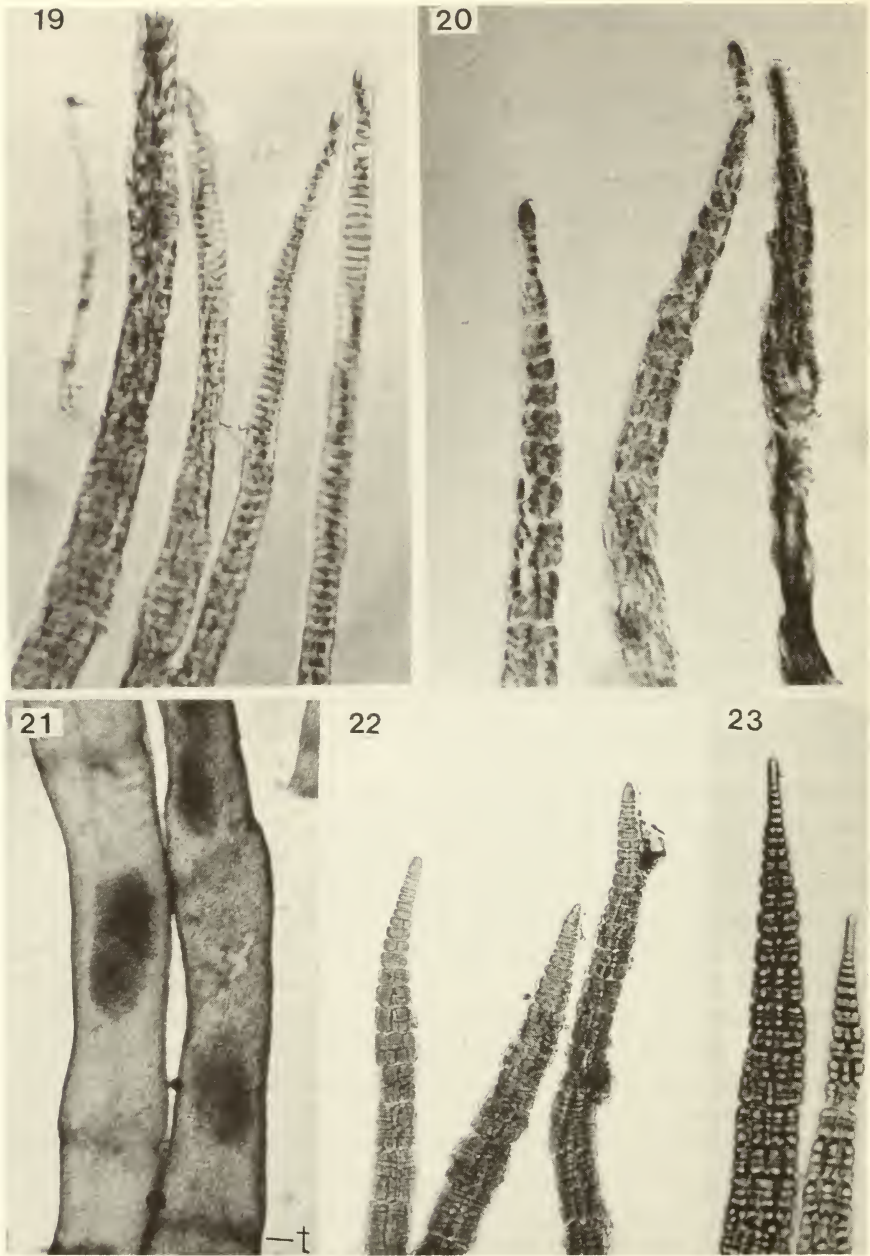
Gametophyte axis with relatively small epidermal cells of which 170-210 occur on a 1 mm transect; slightly nodose with internodes, where spore-filled, frequently exceeding in diameter the nodal diameter. Internodes ca. 1.0-1.8 mm in length. Central strand in the mesothallus comprising ca. 20-30 corticating rhizoids. Lowest spermatangial area (node 1) ca. 4.3-7.2 mm above the rhizoidal base but with ostensibly complete annular bands or rings at the nodes distally from nodes 3-5; the annular bands showing a substantial increase in width from node 3 distally. Mature spore mass approximately filling the internode. Spores ca. 8-24 x 15-31 μ m. "Chantransia" with markedly conical filaments which enlarge distally from 13-33 μ m. Apical cell dome-shaped.

Tape. North Fork of the Tule River on large rocks at the crossing of Highway 190, Springville, Tulare County, California, December 11, 1993, *J.L. Blum 5176* (UC).

Additional Collections. On rocks in the Tule River, Burnett Park, east of Porterville, Tulare County, California, October 5, 1941, *F. Drouet and M.J. Groesbeck 4502* (MICH 20707); In the North Fork of Tule River above Springville, Tulare County, California, September 20, 1988, *J.L. Blum 4963* (UC); Same locale, July 28, 1990, *J.L. Blum 5054* (UC); In the Tule River above Springville, Tulare County, California, June 15, 1985, *J. Stewart 4514-a* (in the author's collection).

Description. To date, *Paralemanea tulensis* is known only from the Tule River in the area of Springville and Porterville, Tulare County, California. *Paralemanea tulensis* is a form of intermediate size with a clearly banded appearance at maturity. Its spores, by their growth, often enlarge the internode to such a degree that its diameter frequently or even regularly exceeds the nodal diameter, contrary to the usual relationship in *Paralemanea* (nodes larger than the internodes). This species is the only *Paralemanea* species encountered which shows this phenomenon regularly, although an occasional internode in other collections may approximate this condition. The spermatangial areas of *P. tulensis* form complete rings from node 3-5 on and show a slight but steady increase in width from node 1 through node 10. A similar increase in internode length is also typical (as in *P. californica*, Figure 17), but the internodes are in general much shorter than in *P. californica*.

Cystocarp number in *Paralemanea tulensis* has not been determined, as none of the extant material is of an appropriate maturity to show this. The spore mass enlarges longitudinally as well as laterally and, while remaining cohesive, pushes



Figures 19-23. **19.** *Paralentanea californica*, juvenile gametophytic axis (tips) at about the 800 cell stage; the tip of the left axis in the photograph is broken off; H.N. Bolander Herbarium, "California" (x300; US). **20.** *P. gardnerii*, juvenile gametophytic axis tips (x300), N.L. Gardner, 2846, TYPE. **21.** *P. gardnerii*, gametophytic axes (x 17; t = trough); Setchell collection (UC). **22.** *P. brandegeei*, juvenile gametophytic axis (tips x200); Blum collection, 5179 (UC). **23.** *P. parishii*, juvenile gametophytic axis (tips; x175); Blum collection, 5175, TYPE (UC).

past the subtending node and into the subjacent internode. Thus, for a time (as in *P. parishii*), the axis shows the remains of the spermatangial band from the internode above on the proximal flank of the spore mass (Figures 14, 16). As in other relatively small *Paralemanes*, the growth of the gonimoblasts and the form of the spore mass is linear and shows the restraining effect of the narrowly cylindrical thallus wall.

The "chantransia" of *Paralemanea tulensis* is characterized by occasional fusiform filaments, frequently one per tuft of the "chantransia." These filaments widen to a diameter of 30-33 μm in their middle portion. The terminal (narrower) portion is soon lost as a result of molar forces, so the result is an apparently tapered filament, narrower toward its base. The initials of the juvenile gametophytes are formed almost entirely at the base of the "chantransia" tuft.

DISCUSSION

For some time, a need for additional characters has existed by which the division of the genus (*Paralemanea*) as well as the species of long standing could be judged. Hopefully, the new characters, both of the gametophyte and the spores, introduced in this paper will help remedy this need. These new characters allow the identification of the California species, and their utilization for populations from the eastern United States and Europe may make it possible to work out the relationships of these species with greater success.

The decisive contrasts between the California species as a whole and those of the eastern United States (Table 1) may appear to be based on rather insignificant characters. This appearance is misleading for three reasons: 1) researchers are unfamiliar with the characters because they are not the ones customarily used in *Paralemanea* taxonomy; 2) the characters are microscopic in contrast to those upon which the classification schemes of the last 150 years have been based; and 3) they call into question the historic approbation which has been accorded the external form of the gametophyte axis as a basis for classification. The new characters are based largely on the gametophyte; the characteristics of the "chantransia" are not stressed. Although abundant in many collections, the California "chantransias" were not taxonomically useful in most extant collections, because so few gametophyte initials were found.

When the California species as a whole were compared with the European species, the same decisive contrasts, except for spore size, apply. While some European collections were similar to the California material in the distance separating the lowest spermatangial area from the axis base, and others were similar in the number of corticating rhizoids, none of the European species agreed with the California species in both these characters.

Existing descriptions of and keys to *Paralemanea* species rely heavily on the size and shape of the gametophyte, but they are imprecise when describing nodal shape and other features. The author attempted to remedy this situation (Blum, 1993) by developing a series of comparative nodal diagrams. The variability of most *Paralemanea* axes and populations requires the use of abundant material, if meaningful identifications are to be made. Lack of material is the gravest drawback in the use of the type specimens from the 19th century in the genus *Lemanea* (*sensu* 1900). Most of these types consist of only a few axes, and

curatorial responsibility implies that they not be sacrificed. Yet the characters advanced in this paper require the sectioning and mounting of enough material to allow precise descriptions to be prepared and appropriate measurements to be taken. Another drawback is the lack of collection dates for most of the older type specimens. The existing herbarium material for *Paralemanea* is potentially a valuable resource, type specimen or not, but if the collection represents only one day out of the entire growing season, and if no follow-up specimens were taken, the collection's value is greatly reduced. Spring collections from the North Temperate Zone regularly show the young sexual axis, which may still have a portion of the "chantransia" at the base, but virtually none of these collections are supplemented by additional material from the same population obtained later in the year or early in the following year. For an undated specimen, an intelligent guess can be made as to the time of year the collection was made, but even then, such a sample, collected on a single visit to the habitat stream, can yield no information on characters which have not yet appeared in ontogenetic development, or which have already passed. Detailed comparison with a freshly collected specimen, even a dried one of greater or lesser maturity, is really impossible, and on this the naming process founders.

Fully as serious a flaw with the older types is the virtual absence of spore characters. Spore characters (measurements) have been shown to have geographic implications in this paper. That geographic localization, spore size, and other morphological characters show consistency in the California populations implies that these populations are genetically isolated, but the possibility remains that a cline in spore size may be found that is related to different weather and/or other environmental patterns.

The general variability in important characters and the possibility of hybridization are factors that should be studied when working with the California representatives of this group. *Paralemanea californica* and *P. gardnerii* are readily separable on a variety of characters, but at least one collection (W.I. and E.B. Follett, Seigler Canyon Creek, Lake County, California, April 17, 1961 (UC wet stacks)) seems intermediate. The width of the spermatangial band and the presence of complete spermatangial bands starting from low nodes (nodes 2-3) is in disagreement with both the type and other collections of *P. californica*. The only intact juvenile gametophytic axis found in the Follett collection had a terminal uniseriate cylinder as in *P. californica*; this, along with an increase in internode length relative to distance from the base (which this collection shows), led the author to identify it as *P. californica*.

Paralemanea gardnerii is basically cylindric, whereas *P. californica* is clearly nodose. Nevertheless, an affinity between these two species is apparent. They share the presence of a nodal trough, and the more nodose specimens of *P. gardnerii* suggest the outline of some *P. californica* specimens. Whereas the proboscoïd initials of the young gametophyte axes of *P. californica* are unmistakable, a somewhat similar terminus occurs in *P. gardnerii* but is not so marked. A five- to ten-celled uniseriate initial filament is normal in *P. gardnerii* (and in other species of *Paralemanea*).

Both *Paralemanea californica* and *P. gardnerii* have a substantial and wide geographic base in existing collections, but *P. brandegeei*, *P. tulensis*, and *P.*

parishii are much more limited. Additional collections of these taxa may yield some surprises requiring emendations of the species descriptions.

The descriptive characters utilized by Sirodot (1872) in his detailed and careful work on the "chantransia" generation of *Lemanea* included the following: 1) the presence or absence of a principal filament to which the other (branch) filaments are inferior in diameter; 2) unilateral and opposite branching; 3) branching basal on the main filament as against suprabasal; 4) position (high to low) of the young gametophytic axis on the filamentous system; and 5) position of the young gametophyte axes with respect to the supporting filaments (terminal to lateral). A sixth character can be added to these: the tendency of individual filaments to exhibit enlargement toward their tips, a phenomenon noted in the description of the American species, *Lemanea australis* Atkinson (1890).

These characters are best applied to material having young and vigorous "chantransias," but even so, when applied to individual California collections, these characters seldom permit easy identification. The presence of a principal filament is a character apparently offering little opportunity for error. Measurements and averaging, at least for the American material, is necessary to demonstrate the presence of a principal filament. The difference in diameter is slight, and primary branches regularly replace the primary filament, when it is damaged or broken, often equaling or surpassing it in length or diameter.

Where the gametophyte initials develop (i.e., their position relative to the main axis, if any, and the branches of the "chantransia") is considered a significant feature by Sirodot (1872). This character gave mixed results in nearly all the American material studied. Most gametophyte initials are basal on the "chantransia," but in some specimens, these initials can be found at higher levels. In herbarium material, their numbers are so low that no convincing assessment can be made as to their comparative position. Characters based on unilateral branching of the "chantransia," opposite and alternate branching, and basal branching of the main filament as opposed to suprabasal branching are equally dubious.

The "chantransia" characters discussed here may prove difficult to work with. Those collections made and studied by the author in December 1993 were in active growth, good condition, and bore relatively abundant juvenile gametophytes, but workers, who study *Paralemanea* "chantransias" from herbarium material, must reckon with the possibility of substantial modification in structure and appearance due to seasonal and/or other factors. Few extant herbarium specimens of the "chantransia" were in a state of active growth when collected, and few show abundant gametophytic initials. This unfortunately applies to the type material of *P. californica* and *P. gardnerii*. "Banding" is essentially a macroscopic character, which appears as a striking feature only in material from the Pacific seaboard of the United States. European material with relatively faint banding has been found in a few collections, mainly from southern Europe. The European material has all been disqualified on other grounds from conspecificity with the California material.

CONCLUSIONS

Three conclusions emerge from the study of the California species of *Paralemanea*. First, the California species of *Paralemanea* are structurally

distinct from both the species of Europe and the eastern United States. Hence, names applied to the species from Europe and the eastern United States are not applicable to the California material. Second, five species of *Paralemanea* are named and described. These species are based on specimens from California, and their diagnoses utilize morphological characteristics not previously used in the taxonomy of this family (Lemaneaceae). Finally, the descriptions of new species of *Paralemanea* should be based on more than one collection. Ideally, the collections should include both the young and mature gametophytes, mature carpospores, and young "chantransias." Unfortunately, few, if any, of the temperate-zone species named prior to 1890 meet this criterion of adequacy.

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LITERATURE CITED

- Atkinson, G.F. 1890. Monograph of the Lemaneaceae of the United States. *Ann. Bot.* 4: 177-229.
- Blum, J.L. 1993. *Lemanea* (Rhodophyceae, Florideophyceae) in Indiana. *Proc. Indiana Acad. Sci.* 102(1-2): 1-7.
- Bourrelly, P. 1970. *Les Algues d'Eau Douce III*. Editions N. Boubée & Cie, Paris, 516 pp.
- Israelson, G. 1942. The freshwater Florideae of Sweden. *Symb. Bot. Upsaliensis* VI(1): 134 pp.
- Jao, C.-C. 1941. Studies on the freshwater algae of China. VIII. A preliminary account of the Chinese freshwater Rhodophyceae. *Sinensia* 12: 245-290.
- Magne, F. 1967. Sur le déroulement et le lieu de la meiose chez les Lémanéacées. *C.R. Acad. Sci. (Paris)* 264D: 2632-2633; 265D: 670-673.
- Pascher, A., J. Schiller, and W. Migula. 1925. Heterokontae, Phaeophyta, Rhodophyta, Charophyta. In: A. Pascher (Ed.), *Die Süßwasserflora Deutschlands, Österreichs und der Schweiz*, pp. 134-206, Gustav Fischer Verlag, Jena, 11,250 pp.
- Sirodot, S. 1872. Etude anatomique, organogénique et physiologique sur les Algues d'eau douce de la famille des Lémanéacées. *Ann. Sci. Natur. Bot. Sec.* 16: 5-95.
- Stewart, J.G. 1983. *Lemanea* (Rhodophyta) in mountain streams of southern California. *Madroño* 30: 255-256.
- Vis, M.L. and R.G. Sheath. 1992. Systematics of the freshwater red algal family Lemaneaceae in North America. *Phycologia* 31: 164-179.