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Variations in Cystocarp Structure in *Pterocladia* (Gelidiales: Rhodophyta)[1]

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ABSTRACT: Unilocular cystocarps distinguish *Pterocladia* from the morphologically similar *Gelidium*, which exhibits bilocular cystocarps. Unequally developed locules, regarded as exceptional, have been found in two species assigned to *Pterocladia*. This study describes the patterns of morphological variation found during cystocarpic development in *Pterocladia musciformis* Taylor and in *P. capillacea* (Gmelin) Bornet & Thuret. About 70% of the cystocarps of *P. musciformis* are *Gelidium*-type. The remaining exhibit unequally developed locules with a longitudinal septum displaced off-center, sometimes producing spores on only one side of the cystocarp and with one or a few ostioles only on the most protruding face of the frond or blade. In a Brazilian population of *Pterocladia capillacea* the internal cystocarpic structure changes with age. Young cystocarps exhibit the typical structure of the genus. In more mature cystocarps the septum is located close to the middle of the cystocarp, splitting the cavity, which then appears as two unequal locules. A few of these larger cystocarps show pericarps protruding equally on both surfaces of the frond and with ostioles on each surface. It is concluded that the origin of the placenta seems to be the only consistent reproductive difference that distinguishes *Gelidium* from *Pterocladia*. It spite of the comparative scarcity of gametophytes, this distinction is the only important one. Under this concept, the new combination *Gelidium musciforme* is proposed. The pattern of cystocarpic development exhibited by *Pterocladia capillacea* is clearly different from the one shown by *P. lucida* (R. Brown) J. Agardh, the type species of the genus. However, additional studies of interspecific and intraspecific variation in cystocarpic development in the genera *Pterocladia* and *Gelidium* seem desirable before erecting a new genus.

TRADITIONALLY (J. Agardh 1851, Bornet and Thuret 1876, Fan 1961), the number of locules in the cystocarp has been recognized as the most important character segregating the genera *Gelidium* and *Pterocladia*. The cystocarps of *Pterocladia* are unilocular, while those of *Gelidium* are bilocular. A few external differences in cystocarpic structure also apply to a number of species. The mature cystocarps of *Pterocladia* protrude on only one of the surfaces of the sporophyll and exhibit one or more openings only on that surface. The mature cystocarps of *Gelidium* protrude more or less equally on both surfaces and exhibit one or several openings on each of the two surfaces of the sporophyll.

However, not all species follow the above pattern. Cystocarps with two unequally developed locules opening to only one surface were found by Fan (1961) in two species of Gelidiales. These were considered to be exceptions and both species were placed in the genus *Pterocladia*. Some of these materials were thought to belong to an already known Japanese species, *P. nana* Okamura, while others were described as representing a new species, *P. lindaueri* Fan from New Zealand. Both species resemble closely some of the morphological variants of the widespread *Pterocladia capillacea* (Gmelin) Bornet & Thuret.

By assigning the species *nana* and *lindaueri*

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to the genus *Pterocladia*, Fan (1961) in fact changed the segregation character from an absolute (one versus two locules) to a relative (unequally developed locules) difference. However, relative differences require considering degrees of variability of the character when identifying species. Yet studies of variation in cystocarpic structure have never been made for any population of *Gelidium* or *Pterocladia*. The common scarcity of sexual thalli in these species probably has limited such analysis. In addition, the controversy over the ordinal status of the group (see Santelices 1988, 1990 for reviews) has determined that most of the studies dealing with reproductive biology of the Gelidiales (e.g., Kylin 1923, Dixon 1959, Fan 1961, Kaneko 1968, Hommersand and Fredericq 1988) have focused primarily on immediate postfertilization events, with less attention to late cystocarpic development.

While identifying herbarium materials from several collections, I noticed individual and ontogenetic variations in cystocarpic structure in specimens of *Pterocladia musciformis* and in *Pterocladia capillacea*. This study describes the pattern of variation found in these two species. For comparative purposes, changes in late ontogenetic stages of cystocarpic structure of *Pterocladia lucida* (R. Brown) J. Agardh, the type species of the genus, also are described and illustrated.

MATERIALS AND METHODS

Data were obtained from herbarium specimens (Table 1). Each fertile female gametophyte was examined under a stereomicroscope for cystocarps. Whenever possible, a sample of 10 to 20 cystocarps of different sizes, and presumably of different ages, was gathered from each specimen. A total of 30 cystocarps of *Pterocladia musciformis*, 100 of *P. capillacea*, and 50 of *P. lucida* were used in this study.

Cystocarps were gradually rehydrated avoiding tissue damage, then fixed using a

TABLE 1

CYSTOCARPIC SPECIMENS USED IN THIS STUDY

SPECIES	LOCALITY	DETERMINED BY	COLLECTIONS NUMBERS*
P. musciformis	Playitas, near La Unión, Golfo de Fonseca, El Salvador	E. Y. Dawson	N.H.S.I. (ex BF) 3488
P. capillacea	Praia Grande, Arraval del Cabo (Cabo Frio), Brasil	Yocie Yoneshige-Valentin	Y.Y. 2185, 2187, 2188
	Ensenada de Lomo, Cabo Frio, Brasil	Yocie Yoneshige-Valentin	Y.Y. 2519, 2521
	Saco de Inglés, Brasil	Yocie Yoneshige-Valentin	Y.Y. 2652, 2653, 2656, 2657, 2658
	E. S. Mateus, Cabo Frio, Brasil	Yocie Yoneshige-Valentin	Y.Y. 2473
P. lucida	Whararikí Beach, New Zealand	N. M. Adams	D.M. A 3717
	Otaki Beach, New Zealand	N. M. Adams	D.M. A 3707
	Alderman Islands, New Zealand	W. Nelson	D.M. A 13767
	Mataikona, E. Wairarape	N. M. Adams	D.M. A 4313a, A 736
	Wha Wha (north of Mercury Bay)	U.V.D.	D.M. A 2136

*N.H.S.I. (ex BF) = National Herbarium, Smithsonian Institution (ex Beaudette Foundation); Y.Y. = private collection of Yocie Yoneshige-Valentin; D.M. = Herb. Dominion Museum, Wellington, New Zealand.

10% formaldehyde solution in seawater. Fixed cystocarps were embedded in gelatine and cut using a Leitz freezing microtome. The material was cut 30–40 μm thick to avoid destruction of the sporogenous tissues. Sections were stained with methyl blue. Photographs were taken using a Nikon Biophot microscope.

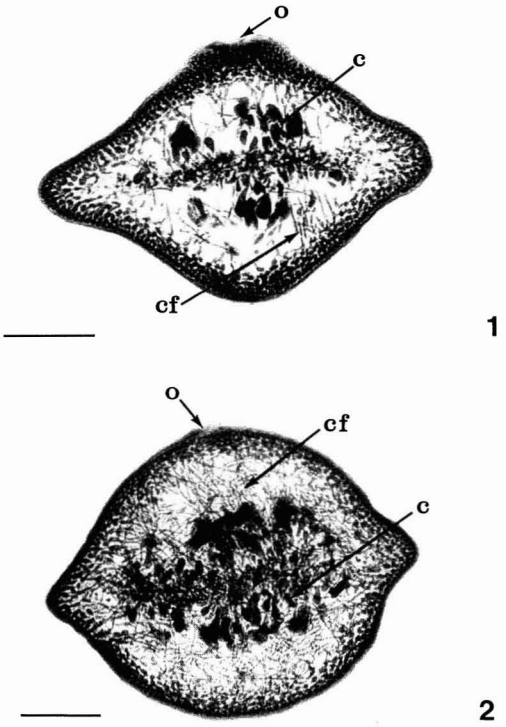
OBSERVATIONS AND DISCUSSION

Pterocladia musciformis *Taylor*

This species was first described by Taylor (1945) from specimens collected at Golfo Dulce, in Costa Rica. The plants formed a mosslike turf about 1 cm tall and were abundant on the rocks. Because the materials collected contained vegetative and tetrasporangial individuals only, Taylor (1945) assigned the species to the genus *Pterocladia* based on hyphae ("rhizines") distribution. Several authors (e.g., Okamura 1934, Feldmann and Hamel 1936) had earlier concluded that in *Pterocladia* the internal hyphae appeared only in the central (medullary) tissue of the thallus in dense or scattered groups, whereas in *Gelidium* they were usually thickly congested in the cortex. Although hyphae distribution is no longer accepted as a segregation character (see Santelices 1988 for a review), it was in use at the time that Taylor described this species.

In his studies of the marine algae of the Pacific Costa Rican gulfs, Dawson (1957) did not find additional materials of *Pterocladia musciformis*. However, he reexamined the type materials described by Taylor and illustrated a specimen from the type collection (Dawson 1957, fig. 4*A*). Later, Dawson (1960, 1961*a*) reported the species from Bahia Carrizal, Colima, Pacific Mexico, gathered subtidally between 20 and 45 ft, and from two intertidal localities in El Salvador (Dawson 1961*b*). One such sample comes from Playitas, close to La Unión, in Golfo de Fonseca and the other from El Cuco, close to Rio Achiate, in San Miguel. Surprisingly, in this last study Dawson (1961*b*) cited the species as *Pterocladia musciformis* (Taylor) Dawson, with no explanation for the change of authors. Dawson (1961*b*, pl. 21, fig. 3) also illustrated a tetrasporangial individual of *P. musciformis* from El Salvador, morphologically very similar to the type materials from Costa Rica.

The plants collected by Dawson in the intertidal localities of El Salvador were first deposited in the Beaudette Foundation Herbarium and are now in the U.S. National Herbarium at the Smithsonian Institution (US). These materials are identified in Dawson's writing (J. N. Norris, pers. comm.) as "*Pterocladia musciformis* (Taylor) Dawson." The materials from Playitas are indicated by Dawson as containing tetrasporangial and spermatangial specimens. New examination of these last materials also yielded cystocarpic thalli.



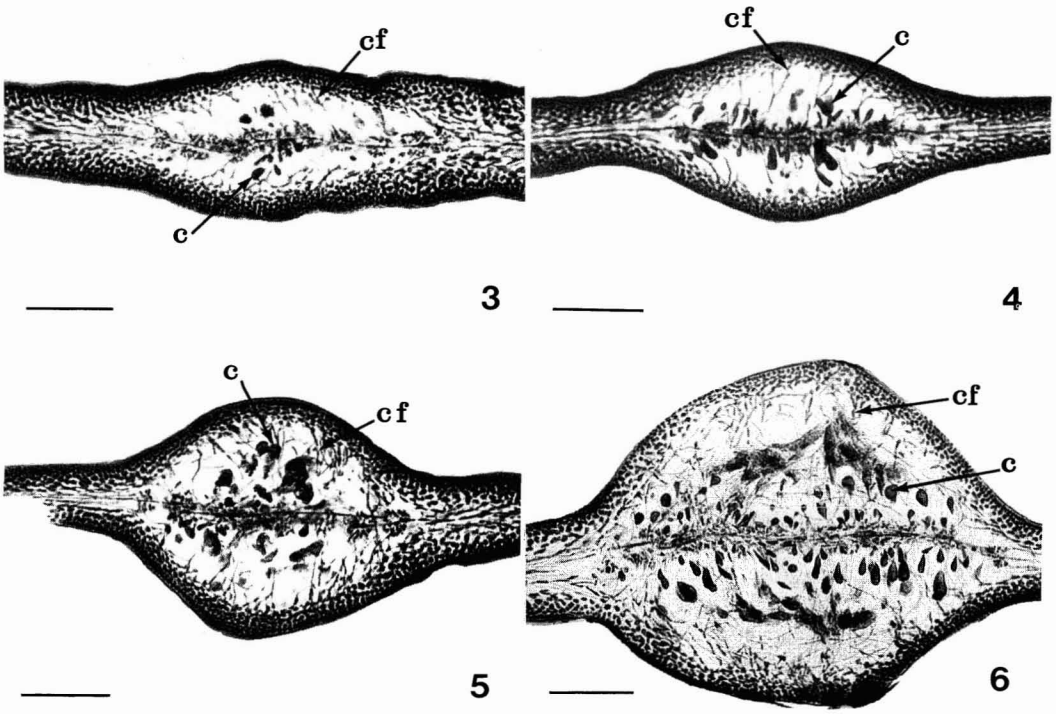
FIGURES 1–2. (1) Transection through a young cystocarp of *Gelidium musciforme* showing one ostiole (o), carpospores (c), and internal cortical filaments (cf). The bar measures 100 μm. US (ex Hancock) 3488. (2) Transection through a mature cystocarp of *Gelidium musciforme*. One of the ostioles (o) is slightly behind the plane of transection. The bar measures 100 μm. Symbols (c, cf) as in previous figure. US (ex Hancock) 3488.

Cross sections through young and mature cystocarps (Figures 1 and 2) show two opposite locules separated by a longitudinal septum and with placentae paired along both sides of the septum. This structure is typical of *Gelidium*. The following new combination is proposed: *Gelidium musciformis* (Taylor) Santelices. Basionym *Pterocladia musciformis* Taylor, 1945, p. 159.

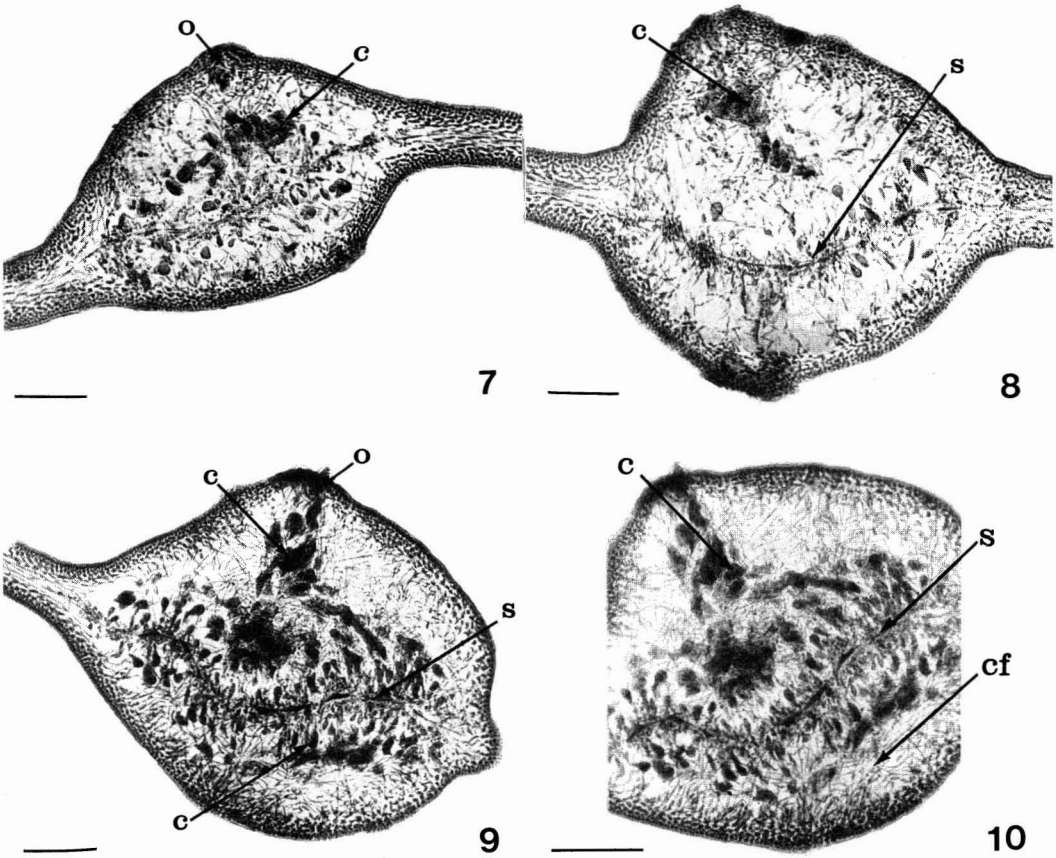
During cystocarp development (Figures 3 to 6) both locules enlarge gradually, the number of sporangia increases, and inner cortical cells elongate, forming a matrix of cortical filaments. In young cystocarps (Figures 3 and 4) this matrix is barely represented by a few parallel filaments that extend between the cortex and the placenta. In mature cystocarps this matrix is densely entangled, with filaments running in several directions.

Both locules in each cystocarp may expand at similar or at different rates. When they expand at an approximately similar rate (about 70% of the 30 cystocarps examined) the mature cystocarp becomes biconvex (Figures 2 and 6), with the longitudinal septum clearly placed at the center of the cystocarps, with paired placentae bearing carposporangia on both sides of the septum and with two locules that can be distinguished easily.

However, in about 30% of the cystocarps examined one locule expands more (or at a faster rate) than the other (Figures 7 to 10). Such cystocarps often are irregularly biconvex, as one side of the cystocarp protrudes more than the other. The longitudinal septum can be displaced off-center and become located very close to the base of the cystocarp. The size difference of the two locules can be extensive (e.g., Figures 8, 10). The placenta facing the larger locule often produces carposporangia earlier than the placenta facing the smaller locule, and the ostiole on the most



FIGURES 3–6. Longitudinal sections of the cystocarp of *Gelidium musciforme* at different stages of maturity. The two locules develop at approximately the same rate, the septum is centrally placed with paired placentae bearing carposporangia (c) on both sides of the septum. Bars in all figures are 100 μm long. cf, internal cortical filaments. US (ex Hancock) 3488.



FIGURES 7–10. Longitudinal sections of cystocarps of *Gelidium musciforme* at different stages of maturity with inner cortical filaments (cf), carpospores (c), and unequally developed locules. Figure 10 is an enlargment of Figure 9. Cystocarps in Figures 7 and 8 exhibit two ostioles (o), but only one is shown in the cystocarp in Figure 9. Bars in all figures measure 100 μm. s, septum. US (ex Hancock) 3488.

protruding side often opens earlier (e.g., Figure 9) than the ostiole on the other face. The matrix of elongated filaments in mature cystocarps sometimes (Figure 10) fills the smaller locule.

Such a description of cystocarpic structures shown by specimens with locules growing at different rates approaches closely the characters chosen by Fan (1961) for *Pterocladia*, where he described two unequally developed locules opening on only one surface for *Pterocladia nana* and *P. lindaueri*. These arrangements are shown also in *Gelidium musciforme*. The similarity with *Pterocladia* is still closer if such cystocarps simultaneously exhibit strongly excentric septa formed when placenta produce spores only on one side and internal cortical filaments fill the cavity of the smaller locule.

The observations given here on *Gelidium musciforme* suggest, in addition, that the origin of the placentae seems to be the only consistent difference in reproductive characters between *Gelidium* and *Pterocladia*. As already described by J. Agardh (1851), *Pterocladia* bears placenta along the base of the locule while *Gelidium* bears it paired along both sides of the septum. However, to be certain of such differences, a larger number of studies on morphological development of cystocarps must be made before taxa can be critically distinguished. This is a difficult task because,

as already indicated, sexual thalli are infrequently found.

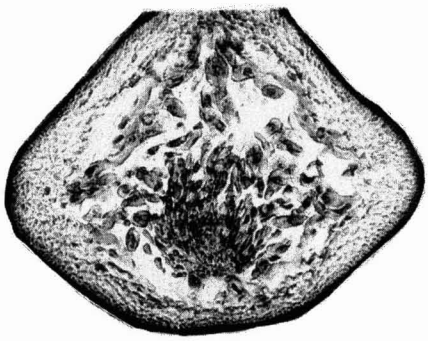
Pterocladia capillacea *(Gmelin) Bornet & Thuret*

In recent years this species has been the subject of numerous studies dealing with its vegetative and reproductive morphology (Dixon 1958, 1959), phenotypic plasticity (Stewart 1968), phenology (Oliveira and Sazima 1973), and geographic distribution (Santelices 1977, Stewart and Norris 1981, Santelices and Stewart 1985). The species is known to occur in temperate and subtropical waters. In the Pacific Ocean the species extends from Santa Barbara, California to Pacific Baja California, Gulf of California, Mexico, Galápagos Islands, northern Peru, Easter Island, northwestern New Zealand, southeastern coast of Australia, New Caledonia, Taiwan, Japan, China, and the Hawaiian Islands. In the Atlantic, it is known from the southern coast of England south to North Africa and the Mediterranean. Also it has been found in the Caribbean, Brazil, and Uruguay.

Pterocladia capillacea was regarded as a variety of *Gelidium corneum* until Bornet and Thuret (1876) studied the structure of the cystocarp. They found that, as in *Pterocladia lucida* J. Agardh, the cystocarp exhibited the placenta along the base of the cystocarp and the carpospores were formed in short chains. Bornet and Thuret (1876, p. 60) also recognized that some of the cystocarps of *P. capillacea* showed variations. For example, they described cystocarps with pericarps protruding on both sides of the frond, separated by a septum bearing spores on both faces and exhibiting two ostioles. However, they considered this to be exceptional. The placenta and the spores almost always developed from only one side of the axis, with the pericarp protruding on only one surface and the placenta remaining in close contact with the bottom wall of the cystocarp during cystocarp development. The illustrations provided by Bornet and Thuret (1876, figs. 1 and 2) showed these characters in addition to a few elongated internal cortical filaments running between the internal wall of the locule or ending before reaching the placenta.

Examination of cross sections of young cystocarps from a Brazilian population of *Pterocladia capillacea* shows the typical unilocular structure of the genus (Figure 11). Spores are produced in short chains and with placenta in close contact with the bottom of the cystocarp. Longitudinal sections of these cystocarps (Figure 12), however, show a few, elongated cortical filaments extending from the internal cortex at the bottom of the cystocarp to the placenta.

Internal cystocarpic morphology changes



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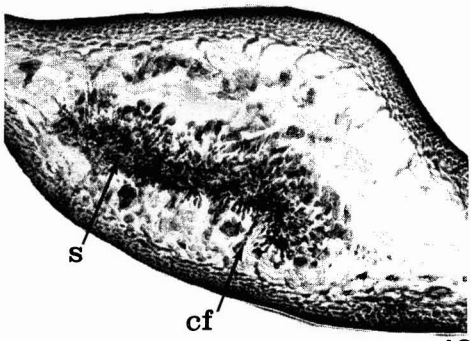

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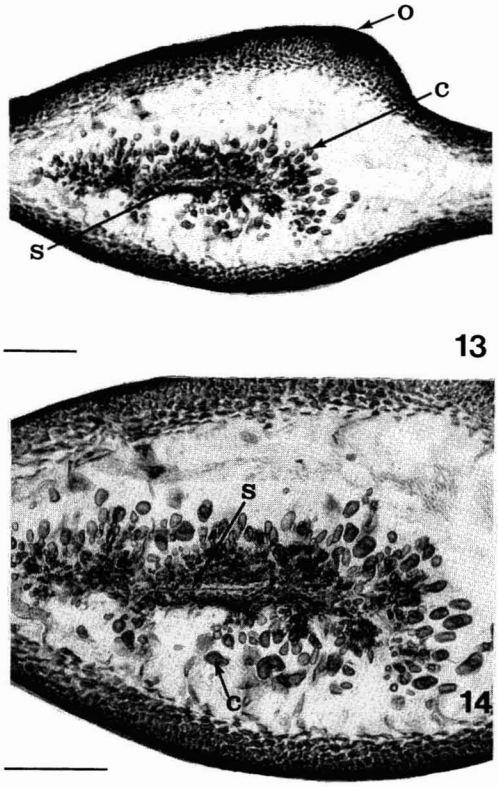
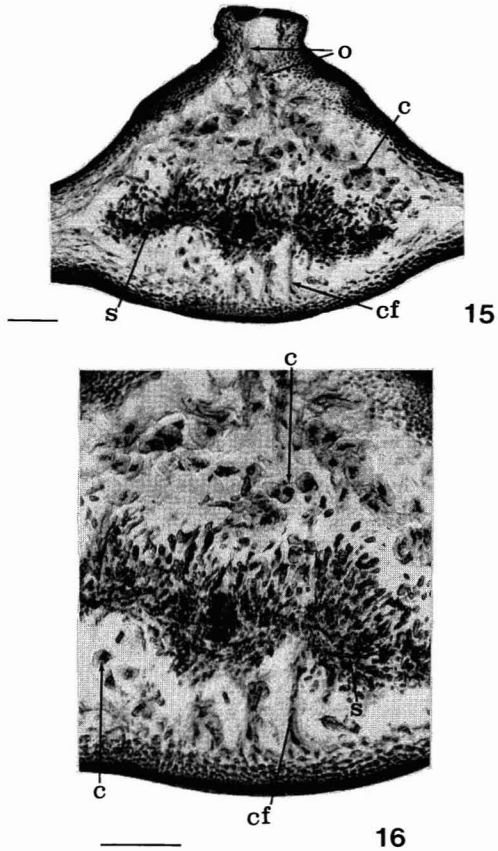
FIGURES 11–12. (11) Transection of a young cystocarp of *Pterocladia capillacea* with one locule, one ostiole, and placenta in close contact with the cystocarpic wall. Y. Yoneshige 2187. (12) Longitudinal section of a young cystocarp of *Pterocladia capillacea* with a few elongated cortical filaments (cf) extending from the bottom of the cystocarp to the placenta and a septum (s) separated from the bottom wall of the cystocarp. Y. Yoneshige 2187.

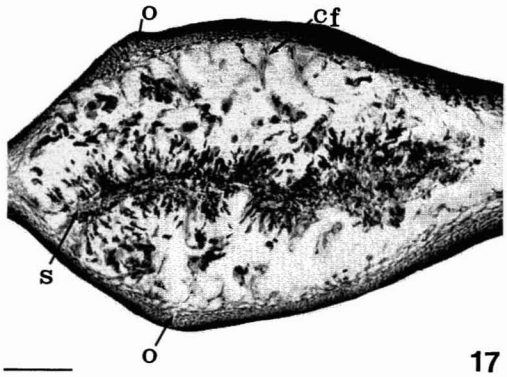


FIGURES 13–14. Longitudinal section through a more advanced state of cystocarpic development in *Pterocladia capillacea*. Figure 14 is an enlargement of Figure 13. Bars in both figures measure 100 μm. Cystocarps have one ostiole (o), a centrally placed septum (s), and carpospores produced in two directions. Y. Yoneshige 2187.



FIGURES 15–16. Longitudinal section through a mature cystocarp of *Pterocladia capillacea*. Figure 16 is an enlargement of the placenta producing carpospores (c) in two directions. The pericarp has one ostiole (o). Elongated cortical filaments (cf) between the cystocarpic wall and the placenta are common. All bars are 100 μm long. s, septum. Y. Yoneshige 2187.

in more advanced stages of cystocarpic development. Median sections of more mature cystocarps (Figures 13 and 14) show a placenta detached from the bottom of the cystocarpic cavity and located in the middle region of the cystocarp. Carposporangia are produced on both sides of the septum (Figures 15 and 16), suggesting a gradual development of a paired placenta. Elongated internal cortical cells can be seen, especially between the placenta and the bottom of the cystocarp. Most of these cystocarps have only one ostiole. However, because of the central position of the septum and the production of carposporangia in two directions, the cystocarps appear to have two locules. About 5% of the cystocarps examined exhibit (Figure 17) two ostioles. Generally, these are the largest cystocarps in the plant. Some of the pericarps in these cystocarps are externally eroded and a few are greenish. Median sections (Figures 17 and 18) show a central septum producing sporangia in both directions. The cystocarp cavity thus appears incompletely divided into two locules. The pericarp protrudes equally on both sides of the frond and exhibits one ostiole on each frond surface. Production of carposporangia in short chains is not evident in these mature cystocarps.



FIGURES 17–18. Longitudinal section through a mature cystocarp of *Pterocladia capillacea* with two ostioles (o), a centrally placed septum (s), two locules, and placenta producing carpospores (c) in both directions. Internal cortical filaments (cf) are frequent. Figure 18 is an enlargement of the septum and the placenta. Bars are 100 μm long. Y. Yoneshige 2187.

The pattern of cystocarpic development in this Brazilian population indicates that the internal structure of mature cystocarps of *Pterocladia capillacea* resembles those of some species of *Gelidium*. Cystocarps that exhibit a centrally placed septum, a placenta producing spores in both directions, internal cortical filaments running from the cortex to the placenta, a pericarp equally raised on both sides, and with ostioles on each surface are difficult to distinguish from *Gelidium*-type cystocarps. As remarked above, the only consistent difference seems to be the origin of the placenta, a character with limited use because of the common scarcity in the field of plants exhibiting different stages of cystocarpic development.

Some of the above variations in cystocarpic structure of *Pterocladia capillacea* were noticed by Bornet and Thuret (1876), but they thought they represented exceptions. The Brazilian materials examined in this study suggest that in this species the changes in internal cystocarpic structure are part of a normal process of development. One locule and a basal placenta are the rule among young cystocarps. Unequally developed locules by displacement of the placenta at some distance away from the base are common among more mature cystocarps. The representation of cystocarps with pericarps protruding equally on both surfaces is rather low (5–10%). However, that would be expected for cystocarps in the last stage of development. Many cystocarps are probably lost in earlier stages because of release of their spore contents, grazing, sunlight-induced bleaching, and other disturbances.

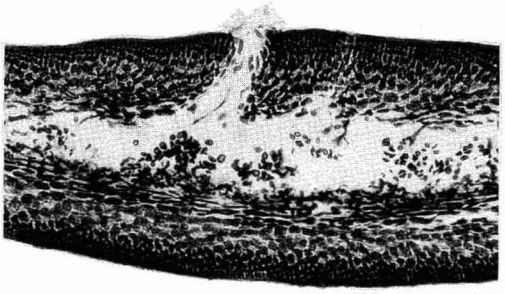
Some stages in the pattern of cystocarpic development found in the Brazilian specimens of *Pterocladia capillacea* are extremely similar to Fan's (1961) description of unequally developed locules of *Pterocladia lindaueri* and *P. nana*. The cystocarpic structure illustrated in Figures 13 and 15 essentially corresponds to those illustrated by Fan (1961) in his plate 42. The presence of cystocarps containing two locules of unequal size was included as a species character in the diagnosis of *P. lindaueri*. Therefore, the pattern of cystocarpic development described above seems to be common in more than one species of *Pterocladia*. Some authors (e.g., Stewart 1968, Santelices 1977, 1988) have shown that the morphological variability of natural populations of *P. capillacea* may include the taxonomic concepts of *P. nana*. However, *P. lindaueri* is still considered a valid species. Even if this last species had good correspondence with *P. capillacea*, the available data suggest that geo-

graphically discontinuous populations of this species exhibit a similar pattern of cystocarpic development. Such a situation can hardly be considered an exception, as characterized by Bornet and Thuret (1876).

Pterocladia lucida *(R. Brown) J. Agardh*

In his morphological studies of the Gelidiales, Fan (1961, pl. 41) briefly described the pattern of cystocarp development of *Pterocladia lucida* and illustrated a longitudinal section through a mature cystocarp. The illustration and the description suggest clear differences with the aforementioned patterns of cystocarpic development of *P. lindaueri* and *P. capillacea*. Perhaps convinced that unequally developed locules in *Pterocladia* are rather exceptional, Fan (1961) did not elaborate further on these differences. The present studies suggesting that unequal locules are common in *P. capillacea* call for additional studies of cystocarpic development in *P. lucida*.

The conclusions from a study of materials of *Pterocladia lucida* examined here (Table 1) coincide with Fan's (1961) observations. In this species, cystocarps of different sizes and different degrees of development show the placenta at the bottom of the cystocarp (Figures 19 to 22). Elongated internal cortical cells could not be found in any section of the 50 cystocarps studied. Elongation of cells of the inner wall to produce a cystocarpic cavity occurs on only one side of the frond, hence the cystocarp protrudes from only one surface. Because the placenta remains in close contact with the bottom of the cystocarp, only one locule is found in all cystocarps, normally opening through one ostiole located at the protruding side of the cystocarp. Therefore, the pattern of cystocarpic development in *P. lucida* is clearly different from the one exhibited by *P. capillacea*.



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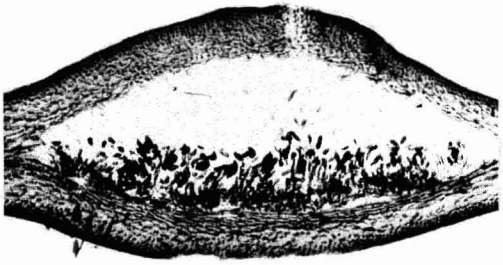

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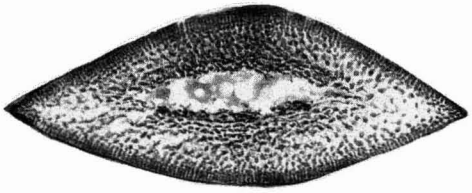
FIGURES 19–20. Longitudinal section of cystocarps of *Pterocladia lucida* at two stages of development. The placenta remains close to the bottom wall of the cystocarp at all times. Bars in both figures measure 100 μm long. D.M. 4313a.



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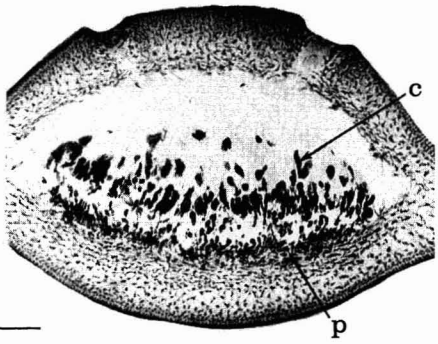

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FIGURES 21–22. Transection of young (Figure 21) and mature (Figure 22) cystocarps of *Pterocladia lucida* showing the placenta (p) in close contact with the bottom wall of the cystocarp and carpospores (c). Bars measure 100 μm long. D.M. A 736.

The basis of the above differences seems related to differences in early postfertilization events. In *P. lindaueri*, a species with unequally developed locules, Fan (1961) noticed that the carpogonial branches are produced on both surfaces of the fertile branchlet, while in *P. lucida* these branches usually develop on only one surface. Furthermore, in *P. lucida* the nutritive filaments are usually produced only on the side on which the carpogonial branches have developed, whereas in *P. lindaueri* they are produced on both surfaces. Later, the gonimoblast filaments fuse with the nutritive cells before and during formation of carposporangia.

The combination of observations gathered in this study suggests the need for segregating *Pterocladia capillacea* and other species of *Pterocladia* with unequally developed locules from the genus *Pterocladia* and erecting a new genus to accommodate them. However, several other studies seem highly desirable before making such a move. Additional studies on other populations of *P. capillacea* are required to know the relative constancy of the above pattern of development in the taxon now known as *Pterocladia capillacea*. Equivalent studies on other species of *Pterocladia* are necessary to evaluate the degree of interspecific variability in the pattern of cystocarpic development. Comparative studies with species of *Gelidium* also are required because in those taxa carpogonial branches and nutritive filaments also are produced on both surfaces of the fertile branchlet and unequally developed locules exist, at least in *G. musciforme*.

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