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The species of *Ceramium* (Ceramiaceae, Rhodophyta) around Taiwan

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Abstract

A taxonomic study was recently carried out on the species of *Ceramium* occurring around Taiwan. One hundred and fifty-one collections were made from January 1993 through spring 1994 at 75 sites distributed around the island. A total of thirteen species were found, including three for which names cannot currently be assigned: *Ceramium aduncum, C. ciliatum, C. cimbricum, C. cliftonianum, C. flaccidum, C. gracillimum* var. *byssoideum, C. mazatlanense, C. nakamurai, C. paniculatum, C. tenerrimum* and unidentified species 1, 2 and 3. Among these are three new records for Taiwan, *C. cimbricum, C. cliftonianum*, and *C. mazatlanense*. This paper summarizes the taxonomic characters of these species and presents a key for their identification. Distribution records of all 42 species reported from the tropical western Pacific are compared. This report is the first detailed record of the genus for Taiwan.

Introduction

The benthic marine algal genus *Ceramium* is well represented amongst the floras of the world, either growing as a luxuriant turf or as an epiphyte. Including synonyms, over 190 species have been described (Boo & Lee, 1994). The genus *Ceramium* was established by Roth in 1797 on the basis of its gesticular habit and presence of capsular fruits. Taxa delimited on the basis of those characters include some species now placed in *Polysiphonia. Ceramium* has remained distinct by two features: its monosiphonous construction, and its incomplete cortication at the nodes.

In the course of recent laboratory culture studies, several of the traditional characters used to distinguish species of *Ceramium* have come into question (Suh & Lee, 1984; Migita, 1988; Meñeses, 1990). Two previously important characters that have now become taxonomically unreliable are internode distance and the presence or absence of spines. Even cortication pattern, which has always been of primary taxonomic importance in distinguishing *Ceramium* species, has been found to change in laboratory culture (Suh & Lee, 1984). When three Hawaiian species were cultured under a variety of conditions, Meñeses (1990) demonstrated that the external morphology of one changed sufficiently for the species designation to change. These findings clearly challenge species concepts, and indicate the need for a taxonomic reevaluation of the genus.

The historical record of *Ceramium* studies in Taiwan is too sparse to be taken as taxonomically representative. From the records compiled in the Lewis & Norris (1987) Taiwan seaweed catalog, *Ceramium* research history can be traced to an 1894 report of *C. tenuissimum.* This species was reported a total of only eight times, yet it is the most frequently reported of the *Ceramium* species in Taiwan. Seven other species have been reported: *Ceramium aduncum* (5 records), *C. ciliatum* (3), *C. flaccidum* (2), *C. gracillimum* (2), *C. nakamurai* (4), *C. paniculatum* (1) and *C. tenerrimum* (6). The total number of published records for this genus for all of Taiwan is only 31.

In addition to floristic interest, this genus is also of economic importance. It is known to produce agar, and studies on *Ceramium* phycocolloids have been conducted by Matsuhiro (1982) and Boo & Lee (1994). It also occurs as a nuisance alga. *Ceramium* is a common epiphyte on cultured genera (Friedlander *et al.*, 1990, 1991; Buschmann *et al.*, 1992). Fouling studies also cite it amongst the fouling flora (Fletcher, 1980; El-Komi, 1991).

This paper presents the taxonomic results of research undertaken to clarify the species richness of the *Ceramium* flora in Taiwan. Results are presented here on the distinguishable species collected and their taxonomic characters. A key is presented to distinguish these species. Species found in this study are compared to those reported in the literature for the tropical western Pacific. This is a contribution to the flora of Taiwan, and it is expected to be of use in applied and ecosystem research in the tropical western Pacific.

Materials and methods

To accommodate possible geographic and seasonal variations, collections were made around Taiwan from January 1993 through June 1994. Seventy-five sites were collected a total of 151 times. These sites were distributed in eight geographic areas: the north, south, east and west coasts of Taiwan, as well as the offshore islands of Penghu (also known as the Pescadores), Orchid Island, Green Island and Xiao Liu Qiu. In all collections, the specific objective was to document all *Ceramium* species present in a given area. In this study, samples of all visually distinguishable epiphytic and turf-forming *Ceramium* species were collected from intertidal and subtidal habitats, using snorkel or SCUBA techniques.

On the basis of gross external morphology, specimens from each site were separated into bottles shortly after collection, fixed initially in 10% formalin/seawater, then transferred to 5% formalin/seawater or processed as dry specimens. Under a Zeiss dissecting scope distinctive material from each bottle was located and separated. Selected material was observed and compared with information on taxonomic features assembled from the taxonomic literature. At the same time, all specimens were sorted for female, male and tetrasporic material.

For critical developmental observations, specimens were stained with hematoxylin stain (Wittmann, 1965) to emphasize cellular connections, then mounted in Hoyer's medium. Cross sections were made under a dissecting scope, and photographs were taken with a Zeiss photomicroscope using Kodak black and white film. Specimens of each taxon recognized in this study are housed in the herbarium of the Taiwan Provincial National Museum of Natural Science (NMNS: A-0886–A-0898).

Results

Although *Ceramium* was present in all eight geographic regions, in seven of the 75 sites (29 collections) it was not found at any time. From the remaining 123 collections, 172 specimen bottles were made. Successful sorts of this material resulted in 122 samples of recognizable *Ceramium* species. After observation, thirteen species were identified. Each species was represented by from 2–28 individual specimens, and each species was found growing in from two to five of the eight geographic areas (Table 1). Three of the species, *C. cimbricum*, *C. cliftonianum* and *C. mazatlanense*, are new records for Taiwan. Despite the relatively low number of samples, complete life history phases were collected for four of the species. Tetrasporangia were observed in all taxa except *C. mazatlanense, C. nakamurai* and *C. paniculatum.*

Taxonomic features were carefully observed to determine those most reliable. The morphological feature of primary importance in characterizing *Ceramium* is the pattern of cortication. To trace these patterns, one begins by noting the number of cortical initials per periaxial cell and the number of periaxial cells per node, here ranging from 3–5, and from 5–12, respectively (Table 2, Figures 1–25). Other morphological characters that were found to be reliable included degree of branching, shape of growing tips, the presence of uniquely-shaped cells (diamond or triangular), and the presence and/or structure of rhizoids and spines. Features that have been widely used by other investigators but are rejected here as being insufficiently stable in most cases include: cell size, relative width of thallus, cortical filament cell number, branching style (dichotomous, alternate, etc.), and tetrasporangial number and position.

Key to the *Ceramium* species of Taiwan

1. Spines present... 2
1. Spines absent... 3
2. Spines 4- or 5-celled throughout...*C. ciliatum*
2. Young branchlets with 6- or 7-celled spines... *C. paniculatum*
3. Tetrasporangia immersed... *Ceramium* species 1
3. Tetrasporangia on the surface... 4

Table 1. Specimen number by species and their geographic distribution. For geographic distributions: N (north), S (south), E (east), W (west), PH (Penghu Islands), XLQ (Xiao Liu Qiu), GI (Green Island) and OI (Orchid Island).

Number of specimens	Species	N	S	E	W	PH	XLQ	GI	OI
28	*C. flaccidum*	5	12	4			3	4	
24	*C. gracillimum* var. *byssiodeum*	3	14	3		3			1
14	*C. tenerrimum*	2	10	2					
12	*C. cimbricum*[1]	5	5	2					
11	*C. aduncum*	2	6	1				1	1
5	*C. cliftonianum*[1]	1	2	2					
8	*C. mazatlanense*[1]	1	6						1
2	*C.* sp. 1	1	1						
6	*C. nakamurai*		3	1		2			
2	*C.* sp. 3		1			1			
4	*C. ciliatum*		2	2					
4	*C.* sp. 2		1	1					2
2	*C. paniculatum*			1					1

[1] New records for Taiwan.

4. Apices of young axes strongly involute... *C. mazatlanense*
4. Apices of young axes erect or little involute... 5
5. Number of periaxial cells >7...*C. aduncum*
5. Number of periaxial cells <7... 6
6. Number of cortical initials = 3... 7
6. Number of cortical initials >3... 8
7. Tertiary cortical initials may divide several ways...*C. flaccidum*
7. Tertiary cortical initial only divides transversely... *C. gracillimum* var. *byssoideum*
8. Hairs present... 9
8. Hairs absent... 10
9. Hairs present on all cortical cells... *Ceramium* species 3
9. Hairs present only on the youngest cortical cells... *Ceramium* species 2
10. Number of cortical initials = 5... *C. cimbricum*
10. Number of cortical initials = 4... 11
11. Periaxial cell is immersed with 1 pseudo-periaxial cell... *C. nakamurai*
11. Periaxial cells not immersed... 12
12. Pseudo-periaxial cells present... *C. tenerrimum*
12. Pseudo-periaxial cells absent...*C. cliftonianum*

Discussion

Thirteen species are reported here from the Taiwan flora. Seven of the eight species previously reported for Taiwan are included. Three other species – *C. cimbricum, C. cliftonianum*, and *C. mazatlanense* – are new records for Taiwan. An additional three taxa (*Ceramium* sp. 1, 2 and 3) could not be clearly assigned to any existing species.

It is interesting that *C. tenuissimum*, the most commonly reported species from early records, was not found in this study. This species has been characterized by a typically straight tip, disc-like rhizoidal cells, very slim proportions and tetrasporangia single or in groups of no more than 4. We have no specimens that reliably match these features, and would suggest that the earlier records may be taxonomically suspect and in need of verification. The most careful taxonomic investigation of *Ceramium* done in this region (Itono, 1977) does not list *C. tenuissimum* as present in the very well studied southern islands of Japan.

The three unidentified species are likely to represent three new species of *Ceramium*. Literature search, discussion with other scholars and examination of all *Ceramium* holdings in the E. Yale Dawson Herbarium failed to link these three species with previously known species. Of these, all three life history stages were collected for *Ceramium* sp. 2. This taxon was collected on six occasions, all critical taxonomic characters are present in the specimens, and it is clearly morphologi-

Table 2. Taxonomic characters of the *Ceramium* species collected in this study. Abbreviations: cc or CC = cortical cell; ci or CI = cortical initial, N = node, pa or PA = periaxial cells, tc = triangular cell, tta = tetrasporangia, 1°, 2°, 3° = primary, secondary, tertiary.

Species	CI per PA	PA per N	Other distinguishing characters
C. aduncum Nakamura [Figures 1–2]	4	12	Several rhizoids per pa; cortex with row of triangular cells; tta derived from cc
C. ciliatum (Ellis) Ducluzeau [Figures 3–5]	4	6	2° ci become pseudo-pa; apex very strongly incurved; cortex w/several 4–5-celled spines
C. cimbricum[1,2] H. Petersen in Rosenvinge [Figures 8–9]	5	6–7	Unicelluar filamentous rhizoid
C. cliftonianum[1] J. Agardh [Figures 6–7]	4	6	Plant w/ few branchlets; pa diamond-shaped; short cortical filament
C. flaccidum[2] (Kützing) Ardissone [Figure 10]	3	7	3° ci transversely divided; rhizoid discoid
C. gracillimum[2] var. *byssiodeum* (Harvey) G. Mazoyer [Figure 11]	3	6–7	Several rhizoids/pa/N; 3° ci develops into a 3-celled filament w/ transverse division
C. mazatlanense[1] Dawson [Figure 12]	4	12	Some 2° ci become pseudo-pa; pa immersed; cortex w/ 2 rows of gland cells; apex strongly inrolled
C. nakamurai Dawson [Figures 13–14]	4	5	2° ci become pseudo-pa; pa immersed; N width ca 3–4x length
C. paniculatum Okamura [Figure 15]	4	6	1° ci become pseudo-pa; 6–7 cell/spine in young portion of thallus; apex incurved
C. tenerrimum Okamura [Figures 16–17]	4	6	Pa rectangle-shaped; youngest cells regular and deeply staining; young axes with spine-like abaxial cortical filaments
C. sp. 1 [Figures 18–19]	4	6	Plant w/ few branchlets; apex almost completely covered with cortication; tetrasporangia immersed and large
C. sp. 2[2] [Figures 20–22]	4	8–10	2° ci become pseudo-pa; cortex w/ row of tc; tc is smallest cell, each with 1 hair; cortex length ca. 2x internode
C. sp. 3 [Figures 23–25]	4	5–6	CC rounded and of uniform size; 1 hair/cc; rhizoids - multicellular, filamentous

[1] New record for Taiwan.
[2] Species with all three life history phases represented in the collections.

Table 3. Ceramium distribution around Taiwan and other locations in the tropical western Pacific. FLD = results from this study; NDA = recent studies from this laboratory of Nan Sha (N) and Dong Sha (D) Archipelagos in the South China Sea; other comparative data from Lewis (1990) citing literature reports of species from Taiwan (TW), southern Japanese islands (Ryu), the Philippines (PH), Vietnam (VN) and northern Australia (NAus).

Species Location	FLD	NDA	TW	Ryu	PH	VN	NAus
C. aduncum Nakamura	X	D	X	X	-	-	-
C. affine Setchell *et* Gardner	-	-	-	X	X	-	-
C. amamiense Itono	-	-	-	X	-	-	-
C. camouii Dawson	-	-	-	-	-	-	X
C. ciliatum (Ellis) Ducluz	X	-	X	X	-	-	-
C. cimbricum H. Petersen	X	-	-	-	-	-	-
C. cingulalum Setchell *et* Gardner	-	-	-	-	-	X	-
C. clarionense Setchell *et* Gardner	-	-	-	-	-	X	X
C. cliftonianum J. Agardh	X	D	-	-	-	-	X
C. codii (Richards) Mazoyer (= *C. cimbricum)*	-	N	-	X	-	-	X
C. cruciatum Collins *et* Hervey	-	-	-	-	X	-	-
C. equisetoides Dawson	-	-	-	-	X	-	-
C. fastigiatum (Wulfen) Harvey (= *C. cimbricum?)*	-	-	-	X	X	X	-
C. fimbriatum Setchell *et* Gardner	-	-	-	X	-	X	-
C. flaccidum (Harvey) Ardissone	X	ND	X	-	X	-	X
C. gracillimum (Kützing) Zanardini	X	-	X	X	X	X	-
C. howei Weber-van Bosse	-	-	-	-	-	X	-
C. huysmansii Weber-van Bosse	-	-	-	X	-	X	X
C. leptozonum Howe	-	-	-	X	-	-	-
C. loureiri C. Agardh	-	-	-	-	X	-	-
C. luetzelburgii O. Schmidt	-	-	-	-	X	-	-
C. marshallense Dawson	-	-	-	X	X	-	-
C. maryae Weber-van Bosse	-	-	-	-	X	X	X
C. mazatlanense Dawson	X	-	-	X	X	X	X
C. multijugum Jaasund	-	-	-	-	X	-	-
C. nakamurai Dawson	X	-	X	X	-	-	-
C. nitens (C. Agardh) J. Agardh	-	-	-	-	X	-	-
C. ornatum Setchell *et* Garner	-	-	-	X	-	-	-
C. paniculatum Okamura	X	-	X	X	-	-	-
C. personatum Setchell *et* Gardner	-	-	-	-	X	-	-
C. procumbens Setchell *et* Gardner	-	-	-	X	-	X	X
C. punctiforme Setchell	-	-	-	-	-	-	X
C. serpens Setchell *et* Gardner	-	-	-	X	X	-	-
C. setchellii Lucas	-	-	-	-	-	-	X
C. sinicola Setchell *et* Gardner	-	-	-	-	X	-	-
C. taylorii Dawson	-	-	-	-	X	X	-
C. tenerrimum (Martens) Okamura	X	-	X	X	X	-	-
C. tenuissimum (Roth) Areschoug	-	-	X	-	X	-	X
C. vagabunde Dawson	-	-	-	-	-	-	X
C. vagans Silva	-	-	-	-	X	-	-
C. vietnamense Pham-hoang Ho	-	-	-	-	-	X	-
C. zacae Setchell *et* Gardner	-	-	-	-	X	-	-

Figures 1–25. Figures 1 & 2. *Ceramium aduncum.* Figure 1. Young branches with straight tips and tetrasporangial (T) position on the inside of dichotomies (matching branch not shown). Figure 2. Cortex regular with lower row of triangular cells (tr). Figures 3–5. *C. ciliatum.* Figure 3. Tip inrolled and spines present throughout plant. Figure 4. Tetrasporangia (T) present only at tip. Figure 5. Mature cortex configuration with spines. Figures 6 & 7. *C. cliftonianum.* Figure 6. Thallus with few branchlets, young branches with straight tips and spermatangial (S) position limited to young tips. Figure 7. Periaxial cell (pa) diamond-shaped. Figures 8 & 9. *C. cimbricum.* Figure 8. Cross section, showing tetrasporangium (T) derived from periaxial cell (pa). Figure 9. Cortex with 5 cortical initial cells (ci) per periaxial cell (pa). Figure 10. *C. flaccidum.* In the same plant, different patterns of cortex cell derivation (arrows) from cortical initials. Figure 11. *C. gracillimum* var. *byssoideum.* Tertiary cortical initial cells only divide transversely to form a cortical filament. Figure 12. *C. mazatlanense.* Young branches with incurved tips. Figures 13 & 14. *C. nakamurai.* Figure 13. Young branches with straight apices, and node with width 3–4 times length. Figure 14. Periaxial cells (pa) with 4 cortical initial cells (ci). Figure 15. *Ceramium paniculatum.* Young branches with straight apices and spines with 6–7 cells. Figures 16 & 17. *Ceramium tenerrimum.* Figure 16. Young branches with incurved tip. Figure 17. Rectangular periaxial cell (pa) with 4 cortical initial cells (ci). Figures 18 & 19. *Ceramium* sp. 1. Figure 18. Young branches with straight tip. Figure 19. Tetrasporangium (T) immersed and width to half of thallus. Figures 20–22. *Ceramium* sp. 2. Figure 20. Young apex is incurved. Figure 21. Hair (h) present on all youngest cortical cells. Figure 22. The youngest cortical cells triangular (tr). Figures 23–25. *Ceramium* sp. 3. Figure 23. Thallus with few branchlets. Figure 24. Cortical cells uniform size and rounded, each periaxial cell (pa) with 4 cortical initial cells (ci). Figure 25. Tetrasporangia (T) are present only on erect branchlets. Scale bars in μm.

cally distinct from all known species. More specimens of species 1 and 3 will need to be collected to allow for their full characterization.

In Table 3, results from the present study are compared with the published records of this genus around the tropical western Pacific, and with unpublished 1994 investigations by this laboratory on the floras of the South China Sea islands. A total of 42 species are compiled for the region. Half (21) are reported for only one of the seven locations. One of these is from our field study (*C. cimbricum*).

The presence of *C. cimbricum*, often thought of as a temperate species, may seem surprising at first. This could simply be explained by the cold-water currents that extend south to the northern portions of Taiwan. More likely this record can be explained by a taxonomic confusion with a species of wide tropical distribution.

Rueness (1992) recently studied this species, and in the course of the study observed the type material of *C. cimbricum* and *C. fastigiatum*, as well as the *C. fastigiatum* species concept of Boo & Lee (1985). At that time he pointed out that '...the name *fastigiatum* is illegitimate as a latter homonym of *C. fastigiatum* (Linnaeus) Wiggers (=*Polysiphonia lanosa*)'. In trying to come up with a legitimate synonym for *C. fastigiatum*, Rueness listed two likely species, *C. codii* and *C. cimbricum*, and said further work would be necessary to chose the correct one. Since then, Maggs & Hommersand (1993) have reduced *C. codii* to *C. cimbricum*, and it seems likely from Rueness' evidence that *C. fastigiatum* should also be reduced to *C. cimbricum*.

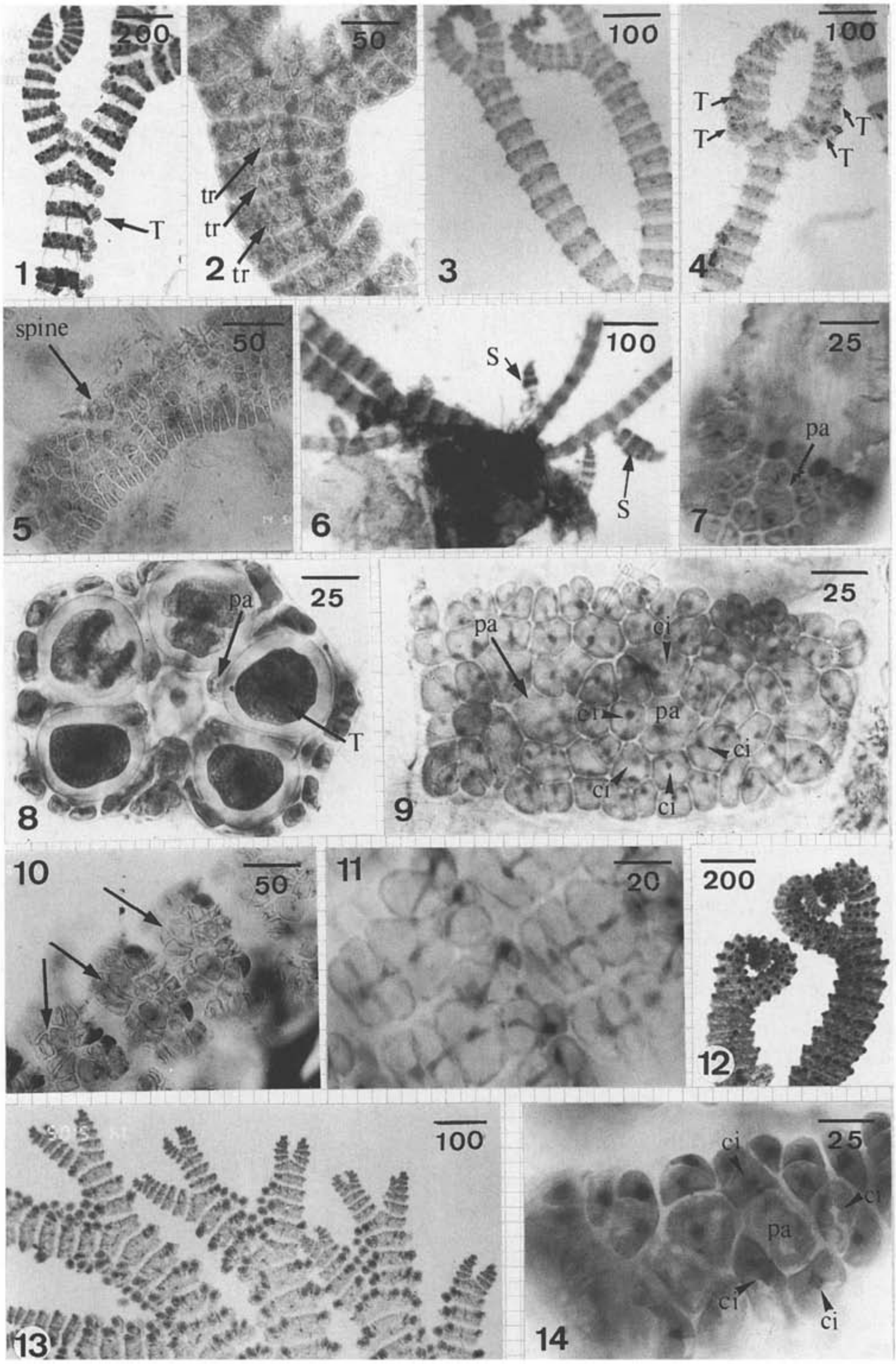
Another curious distribution of records is found with *C. cliftonianum*. In the tropical western Pacific it is only recorded in this study and for northern Australia. The probable explanation comes from this species' size and growth habit. Thalli up to 0.5 cm in length were sometimes found, but 0.1–0.2 cm was the typical size. The species also epiphytizes very small and cryptic hosts, usually *Jania* or juvenile *Padina* spp. The species is likely to be simply overlooked when collecting or sorting due to its small size.

Conclusion

This research was undertaken to document species richness of *Ceramium* in the Taiwan flora. In this regard, it was successful insofar as it increased the number of species recognized from 8 to 13, and increased the individual records from 31 to 153. As a result of this study, clear photo documentation and descriptions are available to ease the identification task of future *Ceramium* investigations in the region, whether theoretical or applied. This study can also be used as a model for documenting other genera in the flora.

We consider it unsuccessful, however, in accurately characterizing the actual richness of the *Ceramium* flora. The primary reason for this was the unexpectedly poor preservation of *Ceramium* in 5% formalin. A large amount of material was unable to be sorted due to dissociation of the specimens when sorting was attempted. Other preservation techniques should be tested.

Not all of our sorted material has been reported here because many specimens could not be clearly characterized, primarily because they were partial specimens lacking critical features. It is possible that continued



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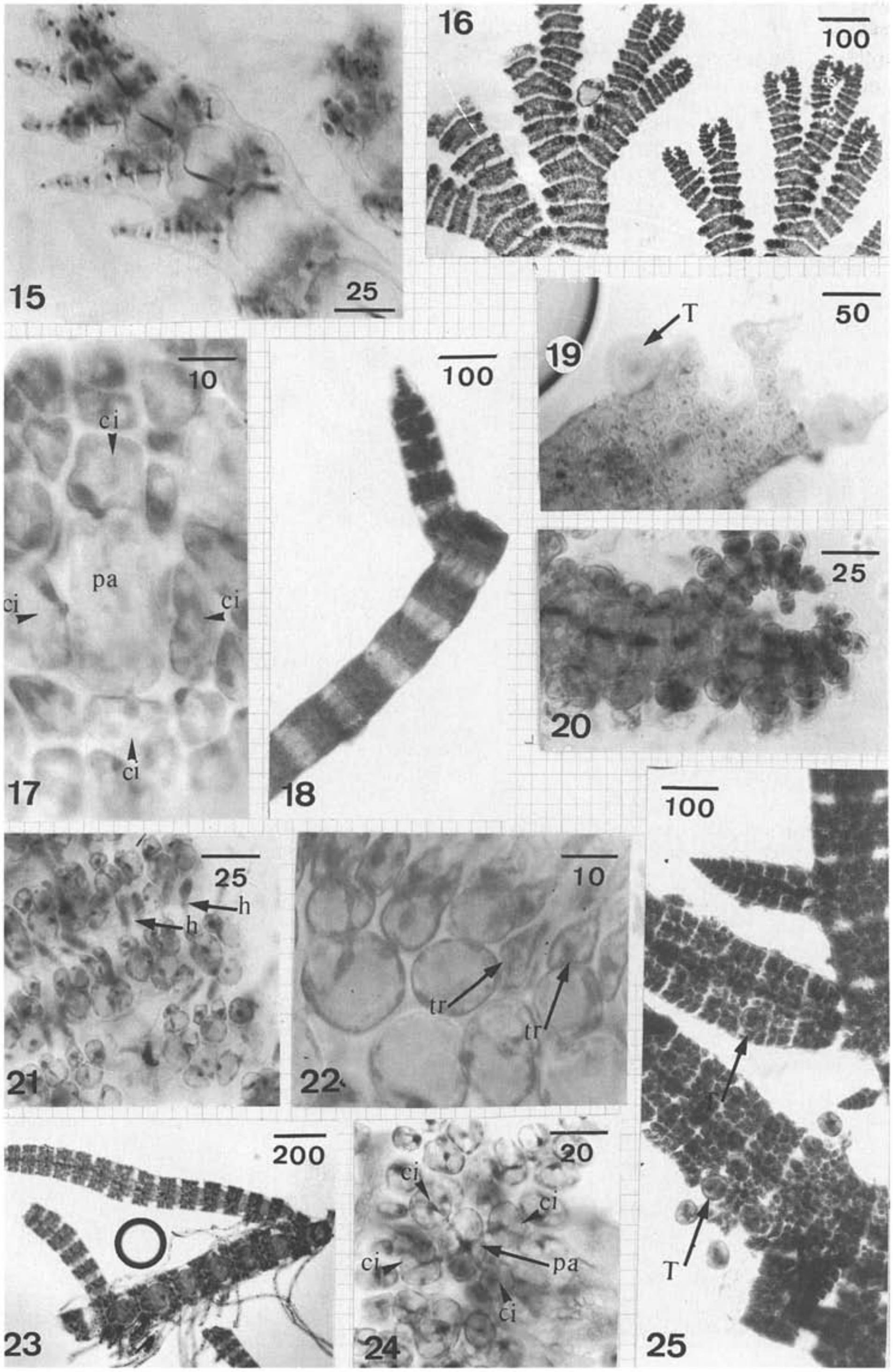
Figures 1–14.



Figures 15–25.

careful study of these difficult-to-sort Taiwan collections could reveal up to five additional species. Furthermore, still other species may exist around Taiwan at depths greater than 10 m, in specialized habitats, as opportunistic species, or as seasonal ephemerals. Further research might also involve culture of species under a range of environmental conditions to document variation in taxonomic characters. For unknown species 1 and 3, complete life history stages need to be obtained either through culture or by increasing the number of samples.

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