TAXON 33(1): 53–63. FEBRUARY 1984

# REINSTATEMENT OF THE GENUS *MASTOCARPUS* KÜTZING (RHODOPHYTA)[1]

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*Summary*

Morphological, life history and biochemical characters are used to show why the genus *Mastocarpus* should be reinstated for four widely distributed species of *Gigartina* (Gigartinaceae). *Mastocarpus* species have channelled thalli on which the female reproductive structures and carposporophytes are formed on specially formed papillate structures, have heteromorphic-type (and associated direct-type) life histories involving an alternation with tetrasporophytes previously referred to the genus *Petrocelis,* and tetrasporangia are formed singly. *Gigartina* species do not have specially formed papillae, have isomorphic gametophytes and sporophytes, and tetrasporangia are produced in branched or unbranched chains. *Mastocarpus* species share many features in common with the Phyllophoraceae and Gigartinaceae but it is proposed that the Petrocelidaceae Denizot be adopted for this genus on the basis of the character of the formation of tetrasporangia singly rather than in chains.

*Introduction*

*Gigartina* Stackhouse (Gigartinales; Gigartinaceae) is a widely distributed genus of marine red algae; the 90 or so species are major constituents of intertidal marine algal floras in many geographic areas and are of some commercial importance as sources of carrageenan, a hydrocolloid widely used in the food industry and other industries as an emulsifier-stabilizer. Kim (1976), in a study of the morphology, structure and reproduction of the Gigartinaceae, concluded that only two genera could be distinguished within this family; *Gigartina* (in which he included *Iridaea* Bory and *Rhodoglossum* J. Agardh) and *Chondrus* Stackhouse. His inclusion of *Iridaea* and *Rhodoglossum* in *Gigartina* did not gain general acceptance (cf. Silva, 1979). Kim (1976) also stated that species of *Gigartina* referred by Setchell and Gardner (1933, 1934) to the subgenus *Mastocarpus* (Kützing) Setchell et Gardner should, with the exception of *G. alveata* (Turner) J. Agardh and *G. ancistroclada* Montagne, be removed from the family Gigartinaceae. He made no formal nomenclatural combinations at that time.

In the course of our cooperative studies on the structure, life histories, reproduction and interfertility of *Gigartina* species referable to the subgenus *Mastocarpus* (West, 1972; Polanshek and West, 1975, 1977; Masuda and Uchida, 1976; West, Polanshek and Guiry, 1977; West, Polanshek and Shevlin, 1978; Masuda and Kurogi, 1981; West, Masuda and

[1] Supported partially by U.S. Dept. of Commerce, National Oceanic Atmospheric Sea Grant NOAA 04-6-158-44021 (1975–76) and 04-8-M01-189 (1977–79) to JAW; North Atlantic Treaty Organization Grant no. 1130 (1977–79) to JAW and MDG; U.S. National Science Foundation Grants GB-40550 (1974–75) to JAW, INT-7916892 (1980–82) to JAW; PCM 7917342 (1980–82) to JAW; and National Board of Science and Technology (Ireland) SRG 14-1979 (1979–82) to MDG. We are grateful to G. Blunden and E. L. McCandless for their comments, and to the British Museum (Natural History) for facilities.

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Guiry, 1981; Guiry and West, in press) from the Pacific coast of North America, the North Atlantic, Japan and Chile we conclude, in agreement with Kim (1976), that the subgenus *Mastocarpus* should be separated from the genus *Gigartina.*

Gigartina.—This genus was created by Stackhouse (1809: 55, 74) with only one species, *Gigartina pistillata* (S. G. Gmelin) Stackhouse [=*Fucus pistillatus* S. G. Gmelin (1768: 159), =*F. gigartinus* L. (1759: 1344)]. At the same time Stackhouse created the genus *Mammillaria* Stackhouse (1809: 55, 74) with two species: *M. expansa* Stackhouse and *M. echinata* (Stackhouse) Stackhouse, both of which are synonymous with *Gigartina stellata* (Stackhouse in Withering) Batters (the currently accepted name for *Fucus mammillosus* Goodenough et Woodward; the specific epithet of which was used in coining the generic name *Mammillaria*). Although a type species was not selected, *Mammillaria* Stackhouse has been placed in synonymy with *Gigartina* Stackhouse. *Mammillaria* Haworth 1812 (Cactaceae) has been conserved and it is thus not available for use.

*Gigartina* as currently conceived is a heterogeneous assemblage of species. *G. pistillata,* the holotype species, has a slightly flattened frond which is dichotomously branched to the third order. The ultimate branches are often irregularly pinnate, particularly in female plants. The procarp of this species consists of a supporting cell and a 3-celled carpogonial branch which does not bear a sterile cell branch (Guiry, unpublished data). A compact but well-developed pericarp is formed around the carposporophyte. Young cystocarps are often sunken in the tissue of the female plant, but as they mature they become protuberant. When borne on the short ultimate branches the cystocarps may appear stalked (Kim, 1976; Guiry, unpublished). Tetrasporangia are formed on plants similar in morphology to the gametangial plants. Tetrasporangial initials are formed from accessory filaments derived from medullary cells resulting in branched chains of 3–4 cruciately divided tetrasporangia. Guiry (unpublished) observed that carpospores of field-collected plants from England and France give rise in culture to plants which were similar in morphology to the gametangial plants and which formed tetrasporangia.

Mastocarpus.—This genus was created by Kützing, apparently in ignorance of Stackhouse's (1809) *Mammillaria* (the publication in which the latter appeared had a very restricted distribution); he included four species: *Mastocarpus mammillosus* (Goodenough et Woodward) Kützing (=*Fucus mammillosus* Goodenough et Woodward); *M. radula* (Esper) Kützing (=*Fucus radula* Esper); *M. stiriatus* (Turner) Kützing (=*Fucus stiriatus* Turner); and *M. papillatus* (C. Agardh) Kützing (=*Sphaerococcus papillatus* C. Agardh). Kützing (1843) did not indicate a type species, but Setchell and Gardner (1933: 258), in choosing *Gigartina mammillosa* (Goodenough et Woodward) J. Agardh as the 'typical species' of their subgenus *Mastocarpus* (Kützing) Setchell et Gardner, effectively lectotypified the genus.

Setchell and Gardner (1933: 281–282) described the subgenus *Mastocarpus* as follows:

"The species of *Mastocarpus,* as subgenus, have in common the repeated dichotomy that, in its best development, gives rise to a palmate frond. The margins are usually described as swollen, but this seems rather exaggerated. The margin is rounded and often slightly enlarged. It has a tendency to curl, so as to make one surface concave, the other convex. This is always to be seen toward the base of the blade and even throughout in the forms with narrow divisions, but is less conspicuous in the forms with very broad divisions. The margins also are free from outgrowths, or very nearly so, except in a few species, where they may occur, and even plentifully. In most plants, even where marginal papillae may seem to occur, careful examination will show that, while close to, they are not actually on the margin. Careful search has failed to reveal any tetrasporic plants of the species of this section. It may be that this type of reproduction is absent and the failure to find them, or to find descriptions of them in the literature, seems to support such a hypothesis. Individuals of both cystocarpic and antheridial plants occur in such abundance and so generally distributed, that, even if the season for tetraspore reproduction were much more limited than seems probable, it certainly is remarkable that not a single tetrasporic individual is recorded or has rewarded the careful search made for them."

They included in the subgenus some 17 species, many of which they considered to be "microspecies."

*Gigartina stellata,* the type of the subgenus *Mastocarpus,* has a flattened, dichotomously to palmately branched frond, the blade margins of which are inrolled giving a channelled appearance. The procarp consists of a supporting cell and a 3-celled carpogonial branch, the second or third cell of which bears a sterile cell branch. Procarps and cystocarps are only formed on specially-produced outgrowths ("papillae") which develop from the concave surface of the blades, or, more rarely, from the margins or apices. A pericarp is not formed around the carposporophyte. Tetrasporangia are formed on *Petrocelis*-like crustose plants dissimilar in morphology to the gametangial plants, the sporangial initials being formed directly from vegetative cells in an intercalary position and giving rise to cruciately divided tetrasporangia only one of which is always formed on each erect filament. West, Polanshek and Guiry (1977) showed that tetraspores from plants of *Petrocelis cruenta* J. Agardh [the holotype species of *Petrocelis* J. Agardh (1851: 489)] from Ireland gave rise in culture to dioecious plants similar in morphology, structure, and reproduction to *Gigartina stellata.* Chen, Edelstein and McLachlan (1974) previously reported "apogamous"* recycling in culture of cystocarpic plants of *G. stellata* from Nova Scotia. Rueness (1978) later reported a similar "apogamic"* life history in plants of this species from Norway, and Dion and Delépine (1979) found both types of life history at Roscoff, northern France. Guiry and West (in press) show that *Gigartina stellata* in the North Atlantic exhibited two basic types of life history: a heteromorphic-type* in which dioecious plants alternate with crustose plants bearing tetrasporangia; and a direct-type* in which carpospores give rise to foliose plants (which are, on occasion, monoecious; Guiry and Coleman, 1982) and tetrasporangia are not formed. Using laboratory hybridization techniques, Guiry and West (in press) also demonstrated that plants of *Gigartina stellata* from the British Isles and northern France are interfertile with *Petrocelis cruenta*-derived gametophytes from the type locality of *Petrocelis cruenta* J. Agardh [Dixon and Irvine (1977b: 138): Brest] and consequently reduced *P. cruenta* to a synonym of *Gigartina stellata.*

*Relationship of* Mastocarpus *to other genera of Gigartinaceae.*—Setchell and Gardner (1933) in their review of the genus *Gigartina* (which was primarily in relation to the species occurring on the Pacific coast of North America) repeatedly commented that the subgenus *Mastocarpus* might represent a genus separate from the genus *Gigartina.* Kim (1976) showed that species referable to the Gigartinaceae, with the exception of species of *Chondrus* and *Gigartina* subgenus *Mastocarpus,* have at least some pericarpial filaments enveloping the carposporophyte although the degree of development of this layer is variable. All *Chondrus* species lack a sterile branch on the carpogonial branch and most have isomorphic gametophytes and tetrasporophytes known from field material and laboratory culture. *Chondrus* has little affinity with *Mastocarpus* because the tetrasporangia are formed in branched chains from accessory filaments produced by medullary cells in a manner rather similar to those of *Gigartina pistillata.*

In the course of our investigations of the morphology, life history and reproduction of *Gigartina* species referable to the subgenus *Mastocarpus,* i.e., *G. stellata, G. pacifica* Kjellman, *G. jardinii* J. Agardh (=*G. agardhii* Setchell et Gardner) and *G. papillata* (C. Agardh) J. Agardh, we have found that these species have the following features in common: the thallus is flattened and dichotomously to palmately branched, often with inrolled margins

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* The term "heteromorphic-type" is used to refer to life histories in which the carpospore germinates to produce a *Petrocelis*-like tetrasporophyte and "direct-type" to designate life histories in which the carpospore germinates to give another foliose gametangial thallus. Neither apogamy nor apomixis has yet been demonstrated in the latter type.

giving a channelled appearance; proliferations are often formed from the margins; the carpogonial branch always bears a sterile cell branch; procarps and cystocarps are only formed in specially-produced papillate outgrowths from the surface or the margins of the thallus; the outwardly developing carposporophyte lacks enveloping pericarpial filaments; and tetrasporangia are formed singly in an intercalary position on upright filaments aggregated to form crustose plants previously known as *Petrocelis* species.

The following species should be included in the genus *Mastocarpus*:

1. **Mastocarpus stellatus** (Stackhouse in Withering) Guiry comb. nov.
Basionym: *Fucus stellatus* Stackhouse in Withering (1796: 99).
Synonyms: *Fucus mammillosus* Goodenough et Woodward (1797: 174). *Fucus echinatus* Stackhouse (1797: 65). *Mammillaria expansa* Stackhouse (1809: 74). *Mammillaria echinata* (Stackhouse) Stackhouse (1809: 74). *Gigartina mammillosa* (Goodenough et Woodward) J. Agardh (1842: 104). *Mastocarpus mammillosus* (Goodenough et Woodward) Kützing (1843: 398). *Petrocelis cruenta* J. Agardh (1851: xi adnot., 489). *Gigartina turneri* Setchell et Gardner (1933: 287).

Silva (1952: 264) proposed the name *Gigartina coronopifolia* (Zoega) P. Silva for *Fucus coronopifolius* Zoega (1772: 19) which was described from material collected in Iceland, probably by Koenig. Zoega's description of *F. coronopifolius* could conceivably apply to the entity currently known as *Gigartina stellata* [see also Lyngbye (1819: 15, 57) and Strömfelt (1886: 72)] but no specimens appear to have been preserved. Zoega (1772: 19) cited *Fucus Coronopi facie* of Ray (1724: 45) as a synonym. Ray's description [or indeed Dillenius's; see Henrey (1975: 266)] is somewhat ambiguous; however, examination of the specimen cited (D. Stevens Buddle H.S. Vol. I, fol. 12, no. 23) which is preserved in the Sloane Herbarium (BM) and annotated in Dillenius's handwriting (fide J. H. Price) as the specimen used in the description, showed that *Fucus Coronopi facie* is representative of the species now known as *Sphaerococcus coronopifolius* Stackhouse. Stackhouse (1801: 82) cited Ray's polynomial in his description of this latter species. *Sphaerococcus coronopifolius* is however unknown in Icelandic waters, reaching its northern limit in the British Isles (Dixon and Irvine, 1977a), however, as the protologue of *Fucus coronopifolius* Zoega encompasses two quite disparate entities and in the absence of a type specimen, we propose that *Fucus coronopifolius* Zoega be rejected as a *nomen dubium*. Silva's (1952) proposal, although quite correct nomenclaturally, has not been adopted in the intervening thirty years. We also consider that a change in the specific epithet would, at this time, serve little purpose.

A plethora of early names has been applied to the entity now passing under the name *Gigartina stellata*. The latter name has been used since Batters (1902: 64) showed that *Fucus stellatus* Stackhouse in Withering (1796: 99) had nomenclatural priority over *Fucus mammillosus* Goodenough et Woodward (1797: 174). Batters stated that he had examined material (LINN) of *Fucus stellatus* but Dixon and Irvine (1977a: 241) could not find this material and thus lectotypified *Fucus stellatus* with the description in Withering. Stackhouse (1801, pl. 12) later illustrated a specimen of *Fucus stellatus* which clearly respesents the entity currently known as *Gigartina stellata*.

Results from extensive life history and hybridization studies of *Gigartina stellata* (Guiry and West, in press) indicate that three entities may be passing under this name. One entity has a direct-type life history and may be monoecious. The other two entities have heteromorphic-type life histories and are dioecious. The latter two entities are 98.8% incompatible and are geographically separated; one is widely distributed in the British Isles and on the north coast of France, whilst the other is found on the Atlantic coasts of Portugal and Spain and on the north coast of France. Although there are morphological differences between these entities (Guiry and West, in press), it is not possible at present to distinguish them with certainty.

Given the nomenclatural and taxonomic ambiguity which currently surrounds this species

complex, it seems best to propose that the *status quo* be maintained and that the name *Mastocarpus stellatus* be used for the present.

*Mastocarpus stellatus* is found from northern Russia south to Portugal and from Morocco south possibly to Rio de Oro, Mauritania. In the western Atlantic it occurs from southern Newfoundland south to Rhode Island. Its occurrence in the Pacific is doubtful.

2. *Mastocarpus pacificus* (Kjellman) Perestenko (1980: 72).
Basionym: *Gigartina pacifica* Kjellman (1889: 31).
Synonyms: *Chondrus mammillosus* var. *ochotensis* Ruprecht (1850: 126 [318]). *Chondrus mammillosus* var. *unalaschcensis* Ruprecht (1850: 126 [318]). *Gigartina unalaschcensis* (Ruprecht) J. Agardh (1899: 11). *Gigartina ochotensis* (Ruprecht) Ruprecht ex Yendo (1916: 57).

Polanshek and West (1975) showed that gametophytes derived from field-collected plants of *Petrocelis middendorffii* (Ruprecht) Kjellman (*Cruoria middendorffii* Ruprecht, 1850: 137 [329]) from the Aleutian Islands (Amchitka I.) were interfertile with field-collected plants of *Gigartina pacifica* from the same locality. They also found that these *Petrocelis*-derived gametophytes were interfertile with some strains of gametophytes derived from plants of *Petrocelis franciscana* Setchell et Gardner from California. As they could find no morphological features to distinguish between these two *Petrocelis* species, they proposed that *P. franciscana* be reduced to a synonym of *P. middendorffii.* The type locality of *P. middendorffii* is the Ochotsk Sea and it may be that this species represents the tetrasporophyte of *Gigartina pacifica,* which was described from Bering I. However, no data are available on the life history and interfertility of plants from this area.

Polanshek and West (1975) described a direct-type life history for some plants of *Gigartina pacifica* from Amchitka which was also found in Japanese plants of *G. ochotensis* (Masuda and Uchida, 1976). Masuda and Kurogi (1981) described a heteromorphic-type life history for other *G. ochotensis* populations in Japan, commenting that *G. pacifica* and *G. ochotensis* were not distinguishable (Masuda and Kurogi, 1981: 165 adnot.). Perestenko (1980: 72) had earlier placed *G. ochotensis* in synonymy with *G. pacifica.*

Makienko and Klochkova (1978: 22) listed the combination "*Mastocarpus unalaschcensis* (Post. et Rupr.) Makienko" without citing the basionym thus rendering it invalid under Art. 33.2, ICBN (Stafleu et al., 1978).

*Mastocarpus pacificus* is found from the Aleutian Islands south to Hokkaido, Japan on the west and southeastern Alaska on the east (Lindstrom, 1977). The status of this species further south on the North American mainland needs further study (Polanshek and West, 1975).

3. **Mastocarpus jardinii** (J. Agardh) J. A. West comb. nov.
Basionym: *Gigartina jardinii* J. Agardh (1876: 200).
Synonym: *Gigartina agardhii* Setchell et Gardner (1933: 290).

West, Polanshek and Shevlin (1978) further discuss the nomenclature of this species. Two types of life history were reported by West et al. (1978) for this species from California: a direct-type life history and a heteromorphic-type life history involving a *Petrocelis*-like crust which has not yet been found in nature. These life history types parallel the situation in *Mastocarpus stellatus* and *M. pacificus.* Only heteromorphic-type life histories have been found in populations of *M. jardinii* from Oregon, Washington and British Columbia.

*Mastocarpus jardinii* occurs from British Columbia south to southern California (West et al., 1978).

4. *Mastocarpus papillatus* (C. Agardh) Kützing.
Basionym: *Sphaerococcus papillatus* C. Agardh (1821: pl. 19).
Synonyms: *Gigartina papillata* (C. Agardh) J. Agardh (1846: pl. 19). *Chondrus mammillosus* var. *sitchensis* Ruprecht (1850: 126 [318]). *Gigartina sitchensis* (Ruprecht) Kjellman (1889: 31). *Gigartina latissima* Eaton ex J. Agardh (1899: 32). *Gigartina obovata* J. Agardh (1899: 25). *Petrocelis fran-*

*ciscana* Setchell et Gardner in Gardner (1917: 391). *Gigartina dichotoma* Gardner (1927: 333). *Gigartina cristata* Setchell et Gardner (1933: 289).

Setchell and Gardner (1933: 259 et seq.) pointed out that *Mastocarpus papillatus* sensu Kützing represented a plant from South Africa. However, although Kützing (1843: 298) mentioned only having seen a plant from South Africa, he cited C. Agardh's (1821: pl. 19) *Sphaerococcus papillatus* as a synonym. Accordingly, the binomial *Mastocarpus papillatus* applied to C. Agardh's material rather than to Kützing's specimen. Setchell and Gardner (1933: 259, 295) proposed the new name *Gigartina kuetzingii* for Kützing's South African plant (Kützing, 1867: pl. 45, Figs. a, b). *Sphaerococcus papillatus* C. Agardh is listed by C. Agardh (1821: plate descriptions) to have been collected by Chamisso at "Owahiee." A considerable amount of confusion has arisen over specimens of algae collected by Adelbert von Chamisso on the voyage of the *Rurik* (Papenfuss, 1976: 25); Setchell and Gardner (1933: 288) considered it likely that the type specimen of *Sphaerococcus papillatus* (Herb. Agardh no. 23883 (LD)—inscribed "e mari atlantico. Chamisso"!) was collected at Golden Gate, San Francisco where Chamisso spent a month in 1816. Coincidentally, *Petrocelis franciscana* Setchell et Gardner, which represents the crustose tetrasporophyte of *Gigartina papillata,* was also collected originally at Golden Gate. As pointed out earlier, however, *Petrocelis*-phases of *Mastocarpus* species are not distinguishable on morphological characters (Polanshek and West, 1975).

Yendo (1916: 57) illustrated original material of *Chondrus mammillosus* var. *sitchensis* Ruprecht (as "*Gigartina sitchensis* Rupr.") from Ruprecht's herbarium (LE) which he considered to be representative of *Gigartina papillata.*

In common with the previous three *Mastocarpus* species, *M. papillatus* has been shown (Polanshek and West, 1975) to have both a direct-type and a heteromorphic-type life history. Populations from California, Oregon, Washington and British Columbia may have either type, but populations from Mexico (Baja California) only have heteromorphic-type life histories.

*Mastocarpus papillatus* is known from Alaska south to Baja California. The status of this species in the western Pacific is rather more confused. Yendo (1916: 57) considered that *Gigartina sitchensis* (Ruprecht) Kjellman (as "*Gigartina sitchensis* Rupr."), originally described from the Ochotsk Sea, represented *Mastocarpus papillatus* but thought that this species did not occur in Japan. Abbott and Hollenberg (1976: 525), however, listed *Gigartina papillata* from Japan although the species is not reported by Mikami (1965).

*Other species of* Mastocarpus.—For the present it seems desirable that only these four species be referred to the genus *Mastocarpus.* However, a species referable to the genus *Mastocarpus* also occurs in Chile (West, unpublished data). It is very similar morphologically to *M. papillatus* from California, with which it crosses successfully in culture. The plant known as *Gigartina mammillosa* in Japan (Yendo, 1916; Mikami, 1965) probably represents a further species of *Mastocarpus* (Masuda and West, unpublished). Although it may be possible in the future to describe as separate species those plants with direct-type life histories and those with heteromorphic-type life histories, we refrain from doing so at present because field collected plants are not distinguishable without culture investigations.

*Familial status of* Mastocarpus *Kützing.*—Kim (1976: 3, 26–29, 37) suggested that species referred to *Gigartina* subgenus *Mastocarpus* as delimited by Setchell and Gardner (1933), except for *Gigartina alveata* (Turner) J. Agardh and *G. ancistroclada* Montagne, be removed from the Gigartinaceae Bory (1828: 149) to a new monotypic family, the Mastocarpaceae, but he did not provide a valid description of this family. The genus *Petrocelis* J. Agardh is clearly synonymous with the genus *Mastocarpus*; thus the family name Petrocelidaceae Denizot (1968: 173, 307) becomes an available name for a family which would include *Mastocarpus* Kützing (Silva, 1980: 80–81).

The familial distinctions among multiaxial representatives of the Gigartinales in which the supporting cell functions as an auxiliary cell and in which cruciately divided tetra-

sporangia form are not clear. A comparison of the features of some of these families (except for the Gracilariaceae) is given in Table 1. The Petrocelidaceae has certain features in common with both the Phyllophoraceae and the Gigartinaceae (3-celled carpogonial branch, cruciately divided tetrasporangia, etc.), some features in common with the Phyllophoraceae only (life history type, non-accessory origin of tetrasporangia, elongate cylindrical spermatia, sterile cell branch on the carpogonial branch, complete absence of enveloping tissue, both inwards and outwards development of the primary gonimoblast and presence of hordenine), and some features in common with the Gigartinaceae only (filamentous appearance of the medullary filaments of the gametophytes and similarities in carrageenan chemistry). The character of the formation of tetrasporangia singly instead of in chains distinguishes the Petrocelidaceae from the Phyllophoraceae and the Gigartinaceae. Some species of *Gymnogongrus* (Phyllophoraceae) have been reported to form only 1–2 tetrasporangia in a chain (Masuda, DeCew and West, 1979: 64, Fig. 2D) but these may not have been mature, having only a single transverse division. Most species of Phyllophoraceae appear to have 4–10 mature tetrasporangia in a row at the time of discharge.

Spermatia of the Phyllophoraceae and Petrocelidaceae are cylindrical (3–4 $\mu$m diam. × 10–12 $\mu$m long) whereas those of the Gigartinaceae are spherical (4–6 $\mu$m diam.). A sterile cell branch is found on the carpogonial branch of some species of Phyllophoraceae (species of *Gymnogongrus, Ahnfeltia* and *Stenogramme*: Doubt, 1935; Kylin, 1956; Mikami, 1965; Masuda, 1981) whereas such a branch appears to be absent in the Gigartinaceae sensu stricto. The occurrence of the amine hordenine (N,N-trimethyltyramine) in *Mastocarpus stellatus* and in some members of the Phyllophoraceae (Barwell, 1981; Barwell and Blunden, 1981; Barwell, Farnham and Fletcher, 1982) suggests a further link between the Petrocelidaceae and the Phyllophoraceae, particularly in the light of its absence in species of Gigartinaceae examined to date. However, the occurrence of stachydrine and *trans*-4-hydroxystachydrine in all *Mastocarpus* species examined to date and their absence in species of Phyllophoraceae and Gigartinaceae is of considerable taxonomic significance at the generic (Blunden et al., 1982) and perhaps also at the familial level.

A major feature which has been used to distinguish the Phyllophoraceae and Gigartinaceae is the appearance of the medullary filaments—compact and pseudoparenchymatous in the former and filamentous in the latter. However, some problems have arisen with regard to the genus *Besa* Setchell (1912: 236) which was originally placed by Setchell in the Gigartinaceae as it has elongated cells in the medullary areas of the frond. Abbott and Hollenberg (1976: 515) place *Besa* in the Phyllophoraceae despite its medulla of "... somewhat elongate cells." McCandless, West and Guiry (1982), after an examination of isotype material of the type species, *Besa papillaeformis* Setchell, concluded that as it contained $\iota$ (iota)-carrageenan, the genus was best referred to the Phyllophoraceae. Accordingly, the structure of the medulla cannot be used with absolute certainly to distinguish members of these two families. As *Mastocarpus* species have gametophytes with filamentous medullary cells the Petrocelidaceae is, in this regard, more closely related to the Gigartinaceae.

Carrageenan type can be used to distinguish the Phyllophoraceae from the Gigartinaceae (Table 1), but a certain amount of overlap is apparent. The gametophytes of species referred to the Phyllophoraceae generally have $\iota$ (iota) or $\iota$-$\kappa$ (iota-kappa)-carrageenan hybrids, and, with certain exceptions, $\lambda$ (lambda)-carrageenan in their tetrasporophytes (McCandless, West and Guiry, 1982). In species referred to the Gigartinaceae the gametophytes contain predominantly $\kappa$ (kappa)-carrageenan or $\kappa$-$\iota$ (kappa-iota) hybrids whereas the tetrasporophytes have $\xi$ (xi) or less commonly, $\pi$ (pi) and $\lambda$ (lambda)-carrageenans (McCandless, West and Guiry, in press). In *Mastocarpus* species it would appear that the gametophytes have largely $\kappa$ (kappa)-carrageenan but the sporophytes often have, in addition to $\lambda$ (lambda)-carageenan, $\pi$ (pi) and $\xi$ (xi)-carrageenan (DiNinno, McCandless and Bell, 1979; McCandless, West and Guiry, in press). The absence of $\iota$ (iota)-carrageenan in the Petrocelidaceae suggests a closer affinity with the Gigartinaceae. Carrageenan dimorphism as related

Table 1. Morphological, reproductive and biochemical features of three closely related families of the Gigartinales. The Chondriellaceae Levring (1941: 640) is also closely related but differs in that tetrasporangia are formed singly in a terminal position.

| | Gigartinaceae Bory (1828: 149) | Phyllophoraceae Rabenhorst (1863: 281) | Petrocelidaceae Denizot (1968: 173, 307) |
|---|---|---|---|
| Structure of medulla | Appearing filamentous | Usually appearing compact and pseudoparenchymatous | Appearing filamentous |
| Spermatia | Spherical | Cylindrical | Cylindrical |
| Carpogonial branch | 3-celled; procarpic | 3-celled; procarpic | 3-celled; procarpic |
| Position of auxillary cell | Supporting cell | Supporting cell | Supporting cell |
| Sterile branch on carpogonial branch | Absent | Present/absent | Present |
| Gonimoblast development | Inwards | Inwards/outwards | Inwards/outwards |
| Enveloping tissue | Present/absent | Absent | Absent |
| Tetrasporangial division | Cruciate | Cruciate[1] | Cruciate |
| Tetrasporangial initial origin | Accessory/non-accessory | Non-accessory | Non-accessory |
| Final arrangement of tetrasporangia | Unbranched or branched chains 4+ cells long | Unbranched chains 4+ cells long | Singly on each filament |
| Life history | Isomorphic gametophyte/tetrasporophyte | Isomorphic or heteromorphic gametophyte/tetrasporophyte or direct-type | Heteromorphic gametophyte/tetrasporophyte or direct-type |
| Carageenans | | | |
| Sporophyte | $\lambda$, $\pi$, $\xi$[3] | $\lambda$[2] | $\lambda$, $\pi$, $\xi$[3] |
| Gametophyte | $\kappa$, $\kappa$-$\iota$[3] | $\iota$, $\iota$-$\kappa$[2] | $\kappa$[3] |
| Hordenine | Absent | Present/absent | Present/absent |
| Stachydrine, *trans*-4-hydroxystachydrine | Absent | Absent | Present |

[1] Zonate tetrasporangia occur in *Ahnfeltia plicata* (Hudson) Fries, the type species of *Ahnfeltia* but this species is an agarophyte and does not belong in the Phyllophoraceae.

[2] See McCandless, West and Guiry (1982).

[3] See McCandless, West and Guiry (in press).

to reproductive phase is known only in the Gigartinaceae, Phyllophoraceae and Petrocelidaceae and confirms the close taxonomic linkage (as elucidated from reproductive features) of these three families.

For the present the Gigartinaceae, Petrocelidaceae and Phyllophoraceae should be regarded as separate families of the Gigartinales.

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