The crustose brown algae of New Zealand: A taxonomic study

Diplura sp., Pt. Elsdon, Wellington.

Joseph Buchanan

A thesis submitted as part
fulfilment for the degree of Master
of Science

School of Biological Sciences
Victoria University of Wellington
Te Whare Wananga o te Upoko o te ika a Maui

August 2005

Acknowledgements

I would like to express thanks to the many people who have supported this work. Firstly to Joe Zuccarello and Phil Garnock-Jones for supervision, advice and support; to Anna Chappell for support and extensive help in the laboratory; to Maria McMillan for proofreading, enthusiasm and unwavering support; to Wendy Nelson for advice and for suggesting the project; and to Catriona Hurd for setting me on the path of phycology. Thanks also to Dr. Florence Rousseau who made her alignment of LSU available and Cameron Jack who helped with photomicroscopy. The School of Biological Sciences plant group listened and provided feedback. The Victoria University School of Biological Sciences supported this work with a study assistance grant. Finally, thanks to the many friends, family and people in the Wellington community who showed interest, gave support and helped in many ways.

Abstract

Nine species of crustose brown algae are described from New Zealand’s coast. Three species are microthalli of species of Scytosiphonaceae: *Colpomenia bullosa* Yamada, *Scytosiphon lomentaria* (Lyngbye) Link and *Petalonia binghamia*e (J. Agardh) Vinogradova. One species of Lithodermataceae, *Pseudolithoderma roscoffense* Loiseaux is described from Northland. Four species are Ralfsiaceae, *Ralfsia expansa* (J. Agardh) J. Agardh, *Ralfsia confusa* Hollenberg, a new species, *Ralfisa sp*. “smooth”, and *Hapalospongidion gelatinosum* Saunders. *H. saxigenum* Lindauer is identical to *Hapalospongidion gelatinosum* Saunders. One new species of *Diplura,* currently placed in the Ralfsiaceae, is described. *Ralfsia verrucosa* (Areschoug) Areschoug, previously reported from New Zealand, was not found.

ITS-2 sequences show that *Ralfsia expansa, Ralfsia confusa* and *Ralfsia sp*. “smooth” are closely related. *Ralfsia expansa* is more distantly related. These relationships are consistent with morphological differences.

LSU nrDNA sequences show *Diplura sp.* and *Pseudolithoderma roscoffense* are not closely related to other Ralfsiaceae. These algae form a weakly supported group with members of the Sphacelariales. *Hapalospongidion* and three *Ralfsia* species form a well supported group, but this group’s relationship to other phaeophycean orders is not resolved. These results are discussed in relation to plastid number and the status of the order Ralfsiales.

Contents

Chapter One: General introduction

Chapter Two: Materials and methods

Chapter Three: Crustose brown algae in New Zealand

Chapter Four: Molecular phylogenetics

List of Figures

List of Plates

List of Tables

Chapter One:
General introduction

1.0 The crustose brown algae

THE brown algae form the morphologically diverse class Phaeophyceae of the Heterokontophyta. Phaeophycean thalli range from simple filaments, such as *Ectocarpus*, through relatively undifferentiated tubes, blades, or sacs, to species with complex thalli with differentiated blades, stipes, pneumatocysts, and specialized tissues for translocation (*Macrocystis* and other Laminariales). Most species are benthic and marine, a few are freshwater and some, such as *Sargassum natans* (Linnaeus) Gaillon, are pelagic. The class Phaeophyceae contains over 250 genera and over 1500 species (Lee & Wilcox 2000).

All macroalgal groups contain crustose species, usually considered to be prostrate thalli firmly attached to the substrate and composed of closely appressed assurgent or vertical filaments. A few parenchymatous brown algae have prostrate thalli resembling crusts (*Sphacelaria mirabilis* (Reinke *ex* Batters) Prud'homme van Reine, the "*Aglaozonia*" phase of some Cutleriacaeae) but these are usually excluded from a strict definition of crustose algae, which only includes pseudoparenchymatous species (Fletcher 1978, Dethier 1987). There are a few species of crustose Chlorophyta (e.g., *Pseudulvella consociata* Setchell et

Gardner) (Boney 1982, Abbott & Hollenberg 1976), many crustose Rhodophytes, including fleshy species (*Hildenbrandia*, *Peyssonnelia*, the "*Petrocelis*" phase of *Mastocarpus* (Dethier 1987, Sussman & DeWreede 2001), and the calcified non-geniculate coralline algae (Harvey *et al*. 2005). Some Cyanobacteria, such as *Oscillatoria,* also have crustose thalli, as do some marine lichens, such as *Verrucaria,* usually with a green algal photobiont and the lichenised form of *Petroderma maculiforme*, with a brown algal photobiont (Sanders *et al*. 2004).

The crustose brown algae are a polyphyletic group of largely marine Phaeophyta. The crustose thallus consists of a basal disc of prostrate filaments that give rise to either loosely or firmly adherent erect filaments that are relatively short and close packed, forming a crust spreading over the substrate, usually less than 1–2 millimeters thick (Fletcher 1978). These algae are little studied, especially in the Southern Hemisphere, and New Zealand species have not been systematically investigated (Hurd *et al.* 2004). Species are difficult to identify, the thalli are not especially attractive and they have no obvious utilitarian value. Apart from a series of studies by Dethier in the North-West United States (Dethier 1981, 1984, 1987, 1994, Dethier & Steneck 2001) their ecological function is largely unstudied, despite some species being the dominant flora of some habitats.

The paucity of reliable morphological characters, morphological plasticity, and conflicting studies of their life histories have confounded simple classification schemes for the crustose brown algae. The majority of species have been placed in the Ralfsiaceae, Lithodermataceae or the Scytosiphonaceae. The Ralfsiaceae and Lithodermataceae are often combined, and these algae are morphologically similar to crustose Scytosiphonacean thalli, but have different life histories and phylogenies (Wynne 1969). Two other families have been established for crustose genera, the Nemodermataceae for *Nemoderma* by Feldmann (1937), and the Mesosporaceae for *Mesospora*, *Hapalospongidion* and *Basispora* by Tanaka & Chihara (1982), but neither family has been widely accepted.

The Ralfsiaceae and Lithodermataceae have isomorphic life histories, whereas several species of the Scytosiphonaceae have a crustose microthallus[1] as one phase of a heteromorphic life history, with the other phase a bladed, saccate or tubular macrothallus. Culture experiments have shown that several algae originally placed in the Ralfsiaceae are actually crustose microthalli of scytosiphonacean species (Wynne 1969).

---

[1] The microthalli of heteromorphic species are referred to by different workers as the adelophycean, prostrate or sporangiophytic stage. I use the terms microthallus and macrothallus following Christensen (1980), distinguishing the two by the organisation of the thallus, with macrothallus referring to the more differentiated thallus.

The Scytosiphonaceae are currently placed in a wide circumscription of the Ectocarpales, a large order of simple brown algae recently revised by molecular phylogenetic studies (Siemer *et al*. 1998). The family appears to be monophyletic, although many genera are not, and the relationships between species and between the family and other Ectocarpalean families are becoming increasingly well resolved (Rousseau & de Reviers 1999, Kogame *et al.* 1999, Cho *et al*. 2005). In contrast, there have been few molecular phylogenetic studies of the Ralfsiaceae and Lithodermataceae, monophyly of these groups has not been established and the ordinal placement and relationships with other phaeophycean families is unclear.

1.1 Ordinal and Familial relationships

The Lithodermataceae and the Ralfsiaceae have been referred to several different orders (Table 1.1). Most workers have followed some variation of five main schemes:

1. *Family(ies)of the Ectocarpales*. Fritsch (1945) and Parke (1953) placed both the Lithodermataceae and the Ralfsiaceae in the Ectocarpales based on the alga possessing simple pseudoparenchymatous thalli and having “ectocarpalean” life histories (that is, an alternation of generations between isomorphic sporophyte and gametophyte). Other workers followed this scheme but merged the Lithodermataceae into the Ralfsiaceae (Parke & Dixon 1976, Wynne 1982, Bold & Wynne 1985)

2. *Family(ies) of the Chordariales*. Early studies placed *Ralfsia* in the Chordariales (e.g., Agardh 1848 as Chordarieæ). Some workers have maintained this scheme. Kylin (1947) placed the Lithodermataceae and the Ralfsiaceae in the Chordariales. Lindauer *et al.* (1961), Abbott & Hollenberg (1976) and Womersley (1987) followed this scheme but merged the Lithodermataceae into the Ralfsiaceae.

3. *Placing* Ralfsia *and other genera in the Scytosiphonaceae*. Pedersen (1976) retained the Lithodermataceae in the Ectocarpales, but moved *Ralfsia* into the Scytosiphonaceae of the Scytosiphonales, based on life history studies that demonstrate a “ralfsioid” microthallus in *Scytosiphon* and *Petalonia*. This placement has been questioned as diagnostic characters for the Scytosiphonales include a plastid with a pyrenoid and a life history stage without unangia (Feldmann 1949). These characters are absent or inconsistent in the Ralfsiaceae (Nelson 1982). None-the-less, this scheme was followed by Christensen (1980) who included *Nemoderma* and *Heribaudiella* in the Lithodermataceae and *Analipus* in the Scytosiphonaceae, and by Fletcher (1987) who also included *Stragularia* in the Scytosiphonaceae (including *S. spongiocarpa*, a species with an isomorphic life history).

4. *Placing in the Myrionemataceae*. Skottsberg (1921) placed some crustose brown algal genera in the Myrionemataceae, a family of small, largely epiphytic algae with a direct life cycle and thalli of prostrate radiating filaments and short erect filaments (although usually with less coherent filaments than *Ralfsia*). Hamel (1931–39) considered the Ralfsiées a “tribe” of the Myrionemataceae. This scheme was followed by Loiseaux (1967, 1968).

None of the above schemes has been supported by molecular studies, which do not show a close relationship between the Scytosiphonaceae or Ectocarpales and *Ralfsia* (Tan & Druehl 1994) or *Analipus* (Tan & Druehl 1994, Cho *et al.* 2003) or *Nemoderma* (Rousseau *et al.* 2001).

5. *As a separate order*: Nakamura (1972) proposed a new order, the Ralfsiales, with three diagnostic characters. (1) an isomorphic life history; (2) a single parietal plate-shaped chloroplast without a pyrenoid and (3) a discal-type early development of the thalli. Nakamura distinguished the Ralfsiales from the filamentous Ectocarpales, with a branched, prostrate prothallus, and the Scytosiphonales and Chordariales with heteromorphic life histories. This proposed order contained three families, the Ralfsiaceae, the Lithodermataceae and the Nemodermataceae. The Ralfsiaceae are characterized by thalli of curved assurgent filaments and laterally attached sporangia; the Lithodermataceae by filaments emerging vertically from the basal layer and terminal plurangia. The Nemodermataceae is monotypic, containing the genus *Nemoderma* and characterized by intercalary unangia and lateral plurangia. Nakamura did not include a Latin description and the order Ralfsiales is regarded as invalid by some authors, but valid by common usage by others (Silva & de Reviers 2000). The order has not been generally accepted but was followed by Tanaka & Chihara (1980a), who later added a fourth family, the Mesosporaceae, containing *Hapalospongidion*, *Mesospora* and *Basispora*. Tanaka & Chihara do not regard plastid number as a diagnostic character for the Ralfsiales and included *Diplura* and *Endoplura*, genera with several plastids per cell, in the Ralfsiaceae (Tanaka & Chihara 1981b). They also include *Basispora* in the proposed Mesosporaceae, a genus described by John & Lawson (1974) as possessing several discoid plastids per cell. Hardy & Guiry (2003) accepted the Ralfsiales, but placed *Sorapion*, *Stragularia* and *Symphyocarpus* in the Scytosiphonaceae of the Ectocarpales. Costello *et al.* (2004) placed the Lithodermataceae in the Ectocarpales and accepted the Ralfsiales as a separate order, but placed *Nemoderma* and *Symphyocarpus* in the Scytosiphonaceae. Phillips & Price (1997) recognised the Mesosporaceae but placed this family and the Ralfsiaceae in the Chordariales.

Wynne & Loiseaux (1976) questioned the reliability of the three diagnostic characters proposed by Nakamura. Nelson (1982b) found qualifications or exceptions to all three characters. She concluded that the order was unwarranted and referred the Ralfsiaceae to the Ectocarpales. However a molecular study by Tan & Dreuhl (1994) determined that the order Ectocarpales is polyphyletic and the Ralfsiales *sensu* Nakamura are not closely related to other Ectocarpales or any existing Phaeophycean order. Their study only included *Ralfsia fungiformis* (Gunnerus) Setchell & Gardner (the type species of *Ralfsia*) and *Analipus japonicus* (Harvey) Wynne as representatives of the Ralfsiales. Their data, based on 18S nrDNA sequences, did not resolve the relationship between *Analipus* and *Ralfsia* and they did not propose a new order.

In this study I will treat the heteromorphic Scytosiphonaceae and the isomorphic Ralfsiaceae as separate families. The relationship between the Ralfsiaceae *sensu stricto* and the Lithodermataceae has not been resolved and there is no previous molecular data for the Lithodermataceae. For the present I will treat these as separate families, but with the caveat that the position of several genera (*Petroderma, Porterinema, Jonsonnia, Sorapion, Symphyocarpus*) remains unclear.

Table 1.1. Familial and ordinal placement of genera of crustose brown algae. Genera that are unambiguous microthalli of the Scytosiphonaceae are not included.

Author	**Hamel 1931–39**	**Fritsch 1945**		**Kylin 1947**		**Papenfuss 1951**	**Pedersen 1976**	
Order	Ectocarpales	Ectocarpales		Chordariales		Ectocarpales	Ectocarpales	Scytosiphonales
Family	MYRIONEMATACEES (including “Tribu de Ralfsiées”)	MYRIONEMATACEAE	MESOGLOACEAE	RALFSIACEAE	LITHODERMATACEAE	RALFSIACEAE	LITHODERMATACEAE	SCYTOSIPHONACEAE
Genera	*Heribaudiella* *Lithoderma* *Mesospora* *Nemoderma* *Ralfsia* *Sorapion* *Symphyocarpus*	*Heribaudiella* *Lithoderma* *Mesospora* *Nemoderma* *Petroderma* *Ralfsia* *Stragularia* *Symphyocarpus*	*Analipus* *Heterochordaria*	*Ralfsia*	*Lithoderma*	*Acrospongium* *Hapalospongidion* *Heribaudiella* *Lithoderma* (including *Pseudolithoderma*) *Mesospora* *Nemoderma* *Petroderma* *Pseudolithoderma* *Ralfsia* (including *Stragularia*) *Sorapion* *Symphyocarpus*	*Petroderma* *Porterinema* *Pseudolithoderma* *Symphyocarpus* *Sorapion*	*Ralfsia*

Table 1.1. (Continued)

Author	**Wynne 1982**	**Womersley 1987**	**Fletcher 1987**			**Costello *et al*. 2004**	
Order	Ectocarpales	Chordariales	Ectocarpales	Scytosiphonales	Ralfsiales	Ectocarpales	Ectocarpales
Family	RALFSIACEAE	RALFSIACEAE	LITHODERMATACEAE	SCYTOSIPHONACEAE	RALFSIACEAE	SCYTOSIPHONACEAE	LITHODERMATACEAE
Genera	*Acrospongium*	*Hapalospongidion*	*Petroderma*	*Ralfsia*	*Hapalospongidion*	*Nemoderma*	*Jonsonnia*
	Analipus	*Pseudolithoderma*	*Pseudolithoderma*	*Stragularia*	*Lithoderma*	*Symphyocarpus*	*Sorapion*
	Basispora	*Ralfsia*	*Sorapion*		*Porterinema*		*Petroderma*
	Diplura		*Symphyocarpus*		*Pseudolithoderma*		
	Endoplura				*Stragularia*		
	Hapalospongidion				*Ralfsia*		
	Hapterophycus						
	Jonsonnia						
	Lithoderma						
	Mesospora						
	Nemoderma						
	Petroderma						
	Porterinema						
	Pseudolithoderma						
	Ralfsia						
	Sorapion						
	Symphyocarpus						

1.2 The Ralfsiaceae Farlow 1881

The family Ralfsiaceae was established by Farlow (1881, as Ralfsieæ) based on *Ralfsia* Berkeley, for crustose brown algae with discrete unangial sori and multicellular, clavate paraphyses. Later treatments regarded a single plastid and intercalary plurangia as diagnostic characters for the Ralfsiaceae (e.g., Nakamura 1972).

Most species have been placed in one of five genera: *Ralfsia*, *Hapalospongidion*, *Lithoderma*, *Pseudolithoderma* or *Stragularia*. One subtidal genus, *Zeacarpa* (Anderson *et al.*1988) and one freshwater genus, *Heribaudiella* (recently discussed by Wehr 2002), have been described.

Detailed studies of the Ralfsiaceae are limited, but have been carried out in Great Britain (Fletcher 1978), the west coast of the North America (Hollenberg 1969), Japan (Tanaka & Chihara 1980a–c, 1981a–c) and the west coast of Mexico (Léon-Alvarez & González-González 1993).

The Ralfsiaceae are generally considered to have isomorphic or direct life histories. Kuckuck reported anisogamy and sexuality in the life history of *Nemoderma* (Fritsch 1949, pp. 124–5), and Loiseaux (1968) reported sexual fusion of isomorphic zoospores from unangia in *Ralfsia clavata* (Harvey) Crouan. Other studies of the Ralfsiaceae have reported neither isogamy nor sexuality (e.g., Wynne 1969). Loiseaux (1968) showed a direct life cycle in *Ralfsia verrucosa* (Areschoug) J. Agardh, with spores from unangia developing into thalli with unangia and spores from plurangia producing plurangia-bearing thalli.

1.2.1 Ralfsia Berkeley

The genus *Ralfsia* was established by Berkeley in 1843 based on *Ralfsia deusta* (currently *Ralfsia fungiformis* (Gunnerus) Setchell & N. L. Gardner). Systematic treatments of the genus have been confused by the morphological congruence between *Ralfsia* and the microthalli of the Scytosiphonaceae.

Before the role of microthalli in the life history of the Scytosiphonaceae was understood, Batters (1890) divided *Ralfsia* into two sub-genera: *Eu-Ralfsia* for species with laterally adherent filaments that curved assurgently to vertical and discrete unangial sori, and *Stragularia,* a genus established by Strömfelt (1886), based on *Stragularia adhaerens,* with strictly vertical erect filaments and expansive or confluent unangial sori. These sub-genera were formally named by De Toni (1895). Some workers now regard *Stragularia* as a separate genus that represents Scytosiphonacean microthalli (Wynne 1969, Fletcher 1987), while others maintain these species in *Ralfsia* and regard them as independent of the Scytosiphonaceae (Loiseaux 1968, Hollenberg 1969).

Batters (1890) placed *Ralfsia verrucosa* (Areschoug) Areschoug in *Eu-Ralfsia* and transferred *Ralfsia clavata* (Harvey) Crouan and *Ralfsia spongiocarpa* Batters to *Stragularia*. In culture experiments, Loiseaux (1968) showed an isomorphic direct life history for *Ralfsia clavata* (Harvey) Crouan from France. Similar results were obtained by Kristiansen & Pedersen (1979) culturing Danish material. Conversely, Fletcher (1978), Edelstein *et al.* (1970a) and Yoneshigue-Valentin & Pupo (1994) culturing British, eastern Canadian and Brazilian material respectively, found *Ralfsia clavata* (Harvey) Crouan was the microthalli of *Petalonia fascia* (O.F. Müller) Kuntze.

With the removal of the Ralfsiaceae from the Ectocarpales (Tan & Druehl 1994) and the proposal of a separate order the Ralfsiales (Nakamura 1972), *Ralfsia clavata* can be placed in either of two orders: the Ectocarpales where it represents a stage in the life cycle of a member of the Scytosiphonaceae; or the Ralfsiales where it is shown to have an isomorphic life history. Obviously this is unsatisfactory and molecular studies could show whether more than one species is present or whether differences represent variable life history pathways.

To add to the confusion, Wynne (1969) found *Ralfsia californica* Setchell et Gardner, an alga that is morphologically distinct from *Ralfsia clavata*, was also a stage of the life history of *Petalonia fascia*. He referred to the microthalli of the Scytosiphonaceae as the "*Stragularia*" stage and stated that "anatomical features seem sufficient to distinguish species of *Ralfsia* from *Stragularia*," but acknowledged that Loiseaux's (1968) work showed that "even *Stragularia* may be a heterogenous group of species." Morphological separation of *Ralfsia* and scytosiphonacean microthalli was further blurred by Hollenberg's (1969) descriptions of two species: *Ralfsia confusa* Hollenberg, which resembles *Stragularia* in having strictly vertical filaments and expansive unangial sori; and *Ralfsia pacifica* Hollenberg (*in* Smith 1944), with curved, assurgent filaments but with expansive unangial sori. Both species have plurangia typical of *Ralfsia* with uniseriate or biseriate locules terminated by a sterile cap cell.

The continued usage of the epithet *Stragularia* is confusing. Fletcher (1987) recognized *Stragularia* as a separate genus, with two British species *S. clavata* (Harvey *in* Hooker) Hamel and *S. spongiocarpa* (Batters) Hamel. He regarded the former as the microthallus of *Petalonia fascia* and the latter as an isomorphic species, but placed these two genera and

Ralfsia in the Scytosiphonaceae. Rueness *et al.* (2001) listed two species of *Stragularia* (apparently misspelt) from Europe, *Strangularia* (sic) *clavata* (Harvey) Hamel (with *Ralfsia tenuis* and *Ralfsia bornetii* as synonyms) and *Strangularia pusilla* Strömfelt whereas Wynne (1998) maintained *Ralfsia bornetii* Kuckuck as a separate species. The relationships of species within *Ralfsia* and the circumscription of the Ralfsiaceae and Scytosiphonaceae could be resolved through molecular studies, but this work has not been undertaken.

Circumscription of species within *Ralfsia* has been confounded by the paucity of morphological variation and by morphological plasticity. Over thirty species of *Ralfsia,* the most speciose genus, have been described, but many of these are synonyms or of uncertain status. *Ralfsia verrucosa* (Areschoug) J. Agardh and *Ralfsia expansa* (J. Agardh) J. Agardh are widely reported, the former from temperate seas in both the northern and southern hemispheres, and the latter from the tropics and warm temperate regions (Fig. 1.1). However many of these reports lack taxonomic detail and the distribution of these species is uncertain. Thorough studies by Léon-Alvarez & González-González (1995, 2003) on environmental variation in *Ralfsia hancockii* Dawson and on the separation of this species from *Ralfsia expansa* (J. Agardh) J. Agardh show how progress can be made in this area.

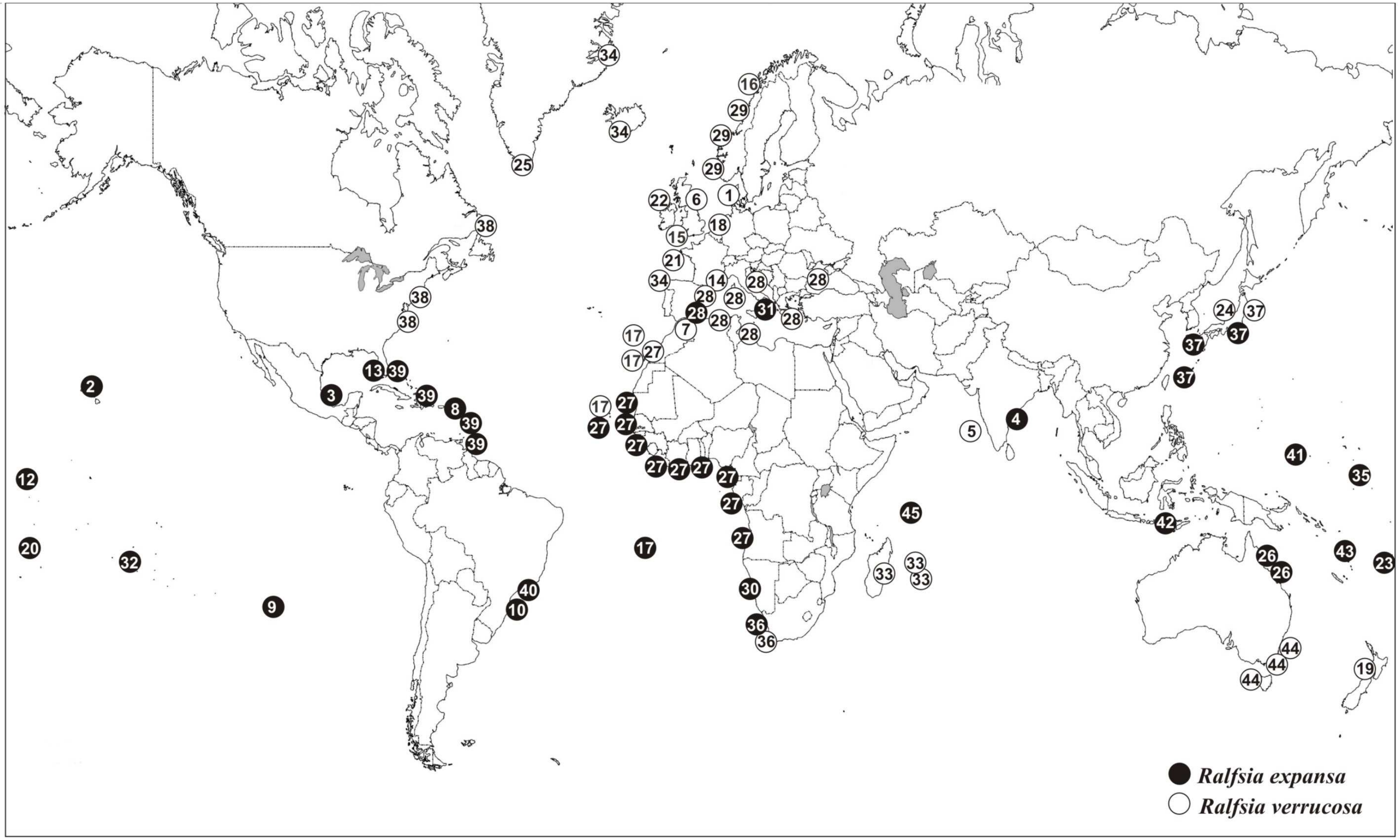

Fig. 1.1. Selected reports of *Ralfsia expansa* (J. Agardh) J. Agardh and *Ralfsia verrucosa* (Areschoug) J. Agardh.

Sources: 1. Athanasiadis 1996; 2. Abbott & Huisman 2004; 3. Agardh 1848; 4. Balakrishnan & Kinkar 1981; 5. Barton 1903; 6. Batters, 1890; 7. Benhissoune *et al.* 2002; 8. Børgesen 1914; 9. Børgesen 1924; 10. Brito *et al.* 2002; 11. Dangeard 1949; 12. Dawson 1956; 13. Earle 1969; 14. Feldmann 1937; 15. Fletcher 1987; 16. Jaasund 1964; 17. John *et al* 2004; 18. Kornmann & Sahling 1977; 19. Lindauer *et al*. 1961; 20. Littler & Littler 2003; 21. Loiseaux 1968; 22. Morton 1994; 23. N'Yeurt *et al.* 1996; 24. Noda 1987; 25. Pedersen 1976; 26. Phillips & Price 1997; 27. Price *et al.* 1978; 28. Ribera *et al* 1992; 29. Rueness *et al*. 2001; 30. Rull Lluch 2002; 31. Sartoni & Boddi 1989; 32. Setchell 1926; 33. Silva *et al.* 1996; 34. South & Tittley 1986; 35. South *et al.* 2001; 36. Stegenga *et al.* 1997; 37. Tanaka & Chihara 1980b; 38. Taylor 1957; 39. Taylor 1960; 40. Tórgo 1963; 41. Trono 1969; 42. Weber-van Bosse 1913; 43. Womersley & Bailey 1970; 44. Womersley 1987; 45. Wynne 1995.

1.3 The Lithodermataceae Hauck 1883–85

Genera placed in the Lithodermataceae are mostly relatively small, thin crusts, often with loosely adherent filaments. The genera are usually separated from the Ralfsiaceae on the basis of possessing several plastids per cell and having terminal unangia and plurangia. However, *Petroderma* and *Porterinema*, genera often placed in the Lithodermataceae, have a single plastid in each cell (Wilce *et al.* 1970), and *Lithoderma*, the type genus of the family, is based on *Lithoderma fatiscens* Areschoug, a species with laterally attached sporangia. Lund (1959) transferred species with terminal sporangia to a new genus, *Pseudolithoderma*. Other genera are partly filamentous (*Porterinema*) or parenchymatous (*Jonsonnia*, according to Lund 1959).

Papenfuss (1951) transferred all species of Lithodermataceae to the Ralfsiaceae. Fletcher (1987) transferred *Ralfsia* to the Scytosiphonaceae, and retained the Lithodermataceae with four British genera, *Pseudolithoderma*, *Petroderma*, *Sorapion* and *Symphyocarpus*. Hardy & Guiry (2003) split the family, placing *Petroderma* and *Pseudolithoderma*, along with *Ralfsia* in the Ralfsiaceae of the Ralfsiales and *Sorapion* and *Symphyocarpus*, along with *Stragularia*, in the Scytosiphonaceae of the Ectocarpales. The transfer of *Sorapion* and *Symphyocarpus* to the Scytosiphonaceae is presumably based on these algae possessing a single plastid with a pyrenoid in each cell (Sears 2002), a diagnostic character of the Scytosiphonales, but I am unaware of studies showing a heteromorphic life history in these species. Costello *et al.* (2004) placed *Lithoderma, Porterinema* and *Pseudolithoderma* in the Ralfsiacae, with *Jonsonnia, Sorapion* and *Petroderma* in the Lithodermataceae and *Symphyocarpus* in the Scytosiphonaceae.

The problems of morphological plasticity and the lack of useful taxonomic characters in these algae are demonstrated by a study by Ravanko (1970). In culture experiments with Finnish crustose species she found characters previously regarded as diagnostic for species and genera (including plastid number, cohesion of filaments and position of the reproductive structures) varied with the age and growth environment of the alga. She considered *Lithoderma fatiscens* Areschoug, *L. rosenvingii* Waern, *L. subextensum* Waern, *Pseudolithoderma extensum* (Crouan *et* Crouan) S. Lund, *Sorapion kjellmani* (Wille) Rosenvinge, *S. simulans* Kuckuck, *Ralfsia ovata* Rosenvinge and *Petroderma maculiforme* (Wollny) Kuckuck to be a single species, probably conspecific with the freshwater species *Heribaudiella fluvatilis* (Areschoug) Svedelius. In a second study Ravanko (1975) also regarded *Porterinema fluviatile* (Porter) Waern as conspecific with these algae. This result is problematic and again shows the need for molecular studies to resolve species circumscriptions.

1.4 The Scytosiphonaceae Farlow 1881 emend. G. Y. Cho et Boo *in* Cho *et al.* 2003

The Scytosiphonaceae develop as either parenchymatous (saccate, tubular or bladed) macrothalli or as pseudoparenchymatous or filamentous microthalli. The crustose microthalli of the Scytosiphonaceae were unknown until the mid-1960s. Prior to this the genera were placed in various families, usually within the Ectocarpales, with their life history assumed to be isomorphic. Kjellmann (1893) placed most genera in the Encoeliaceae, Kylin (1947) placed the same genera in the Punctariaceae. Fritsch (1945) placed *Petalonia* and *Scytosiphon* in the Asperococcaceae of the Ectocarpales and *Colpomenia* and *Hydroclathrus* in the Encoeliaceae of the same order. Feldmann (1949) elevated the family to ordinal status for phaeophytes with a single plastid with a pyrenoid in each cell, plurangia on the macrothallus and unangia absent.

The order Scytosiphonales was considered to contain nine genera and in two families (Kogame *et al.*1999). The Scytosiphonales have since been reduced to a family of the Ectocarpales *sensu lato,* based on molecular data (Peters & Ramírez 2001). The demarcation of some genera is unclear, and molecular phylogenetic studies (Kogame *et al.* 1999, Cho *et al.* 2003) show a revision of the family is needed. Kogame *et al.* showed species of *Colpomenia*, *Scytosiphon* and *Petalonia* are intermixed over several clades, and divided the Scytosiphonaceae into a warm temperate group and a cold temperate group, along lines that do not reflect previous taxonomic divisions of the group.

Prior to culture studies, macrothalli and microthalli of Scytosiphonaceae were often identified as separate species. The microthalli of *Scytosiphon gracilis* and *Petalonia zosterifolia* was identified as the filamentous *Compsonema saxicolum* (Kuckuck) Kuckuck. *Scytosiphon lomentaria* microthalli were identified as the crustose *Microspongium gelatinosum* Reinke, and *Petalonia fascia* microthalli were identified as *Stragularia clavata* (Harvey in Hooker) Hamel (Kogame *et al.* 1999). Some authors retain these names, or use them to describe types of microthalli, as in “*Microspongium gelatinosum* phase” or “*Microspongium gelatinosum*-type microthalli” (e.g., Fletcher 1987).

In the 1960s, culture experiments began to elucidate the relationships between microthalli and macrothalli. Dangeard (1963) found microthalli with unangia in cultures of *Petalonia zosterifolia*, and Nakamura (1965) cultured macrothalli of *Scytosiphon lomentaria* and *Petalonia fascia* from zoospores from unangia of crustose algae. Lund (1966) and Tatewaki (1966) separately reported microthalli in the life history of *Scytosiphon lomentaria* from

Scandinavia and Japan respectively, Tatewaki completing the entire life history in culture. Since then culture studies have attempted to determine the relationship between microthalli and macrothalli for different species of Scytosiphonales, in the United States by Wynne (1969), in Australia by Clayton (1976, 1978, 1981, 1988), and in Japan by Nakamura & Tatewaki (1975) and Kogame and co-workers (1996, 1997a, 1997b, 1998).

While earlier workers (Nakamura 1965, Tatewaki 1966) regarded the scytosiphonacean life history as an alternation between a crustose sporophyte and an erect gametophyte, later work showed sexual fusion was rare and there was no obligate alternation of generations. Rather, the type of thallus produced varies with environmental conditions (Wynne 1969, Lüning & Dring 1973).

Confusion has arisen as some studies have associated macrothalli of different species of scytosiphonacean algae with morphologically similar microthalli while other studies have associated similar macrothalli with different types of microthalli. A number of explanations exist: (1) Variations in microthalli might be artifacts of culture conditions; (2) field collected microthalli have been poorly and inconsistently described, resulting in misidentifications; (3) macrothalli might have been separated or lumped on the basis of morphological characters that are environmentally variable. A number of factors can alter morphological expression in the Scytosiphonaceae. Lüning & Dring (1973) showed variation in morphology based on light conditions in *Scytosiphon* and Hsaio (1969) showed variation based on iodine nutrition in *Petalonia*. Molecular identification of field collected microthalli is a useful tool for overcoming some of these problems (e.g., Kogame & Masuda (2001) for *Colpomenia bullosa*).

Studies by Kogame (1996, 1997a, 1997b, 1998) and Kogame *et al.* (1999) and by Cho and co-workers (2002, 2003, 2005) have begun to resolve some of the relationships within the Scytosiphonaceae, and to correlate them with the morphology of the microthalli, by combining culture experiments with molecular phylogenetics. A molecular phylogeny of the family by Kogame *et al*. (1999) based on *rbc*L, *rbc*S and LSU rDNA showed that several genera of the Scytosiphonaceae are not monophyletic, and identified morphological characters of the microthalli that are congruent with the molecular phylogeny. For example *Scytosiphon lomentaria* (Lyngbye) Link and *Scytosiphon canaliculatus* (Setchell & Gardner) Kogame, despite having very similar macrothalli, are not closely related. These species have very different microthalli and form clades with species with similar microthalli. Conversely *Petalonia fascia* (O.F. Müller) Kuntze, *P. binghamiae* (J. Agardh) Vinogradova and

Scytosiphon tenellus Kogame form a clade of species with "*Stragularia*-type" microthalli (i.e., relatively coherent crusts).

1.5 Molecular systematics and phylogeny of the Phaeophyta

Draisma *et al.* (2001) wrote: "the perennial reshuffling of taxa within and among brown algal orders signal the difficulties of circumscription due to morphological convergence." The difficulties in ordinal placement of the crustose brown algae are a part of this larger problem which is beginning to be resolved by molecular studies.

Early schemes for ordinal division of the Phaeophyta are reviewed by Scagel (1966), Clayton (1984) and de Reviers & Rousseau (1999). Molecular phylogenies have overturned previous concepts of evolution of the Phaeophyta with the Ectocarpales, characterised by simple thallus construction and regarded as ancestral to all the Phaeophyceae except the Fucales (Fritsch 1945, Papenfuss 1953), now regarded as one of the most derived groups.

In the 1990s Ian Tan and Louis Druehl undertook a series of molecular phylogenetic studies of the brown algae based on nuclear ribosomal DNA sequences. Their first study (Tan & Druehl 1993) produced a preliminary phylogeny of the Phaeophyta based on 18S (Small Sub-Unit, SSU nrDNA) sequences from species representing nine phaeophycean orders from the North-east Pacific. The second study (Tan & Druehl 1994) investigated the relationship of two Ralfsiaceae with the Ectocarpales, and the third (Tan & Druehl 1996) investigated the relationship between the Sporochnales, Desmarestiales and Laminariales.

Tan & Druehl's first (1993) phylogeny of the Phaeophyta grouped the Ectocarpales, Chordariales, Dictyosiphonales and Scytosiphonales in a well supported clade, with other orders in a separate poorly resolved group. This result supported the scheme of Fritsch (1945) who regarded these taxa as families in a large order, the Ectocarpales, containing a number of families that have been raised to ordinal status by other workers.

In a further analysis Tan & Druehl (1994) added SSU rDNA sequences from *Analipus japonicus* (Harvey) Wynne and *Ralfsia fungiformis* (Gunnerus) Setchell et Gardner. Nakamura (1972) included *Analipus japonicus* in his proposed order Ralfsiales. However this placement of *Analipus* is uncertain. Nelson (1982b) found several anatomical differences between *Analipus* and the Ralfsiaceae, and placed *Analipus* in the Heterochordariaceae of the Ectocarpales. *Analipus* has also been placed in the Scytosiphonales (Christensen 1980). Tan & Druehl's study placed *Analipus japonicus* outside the Ectocarpales but did not show a close relationship with *Ralfsia fungiformis*. Their analysis supported the division of the Phaeophyta into two major clades, adding the Punctariaceae, Leathesiaceae and Elachistaceae to a broad circumscription of the Ectocarpales.

Other studies also used SSU nrDNA sequences to investigate relationships among the Laminariales (Saunders & Druehl 1992, Druehl & Saunders 1992) and Fucales (Saunders & Kraft 1995). They concluded that the 18S gene is too conserved to resolve more than the major branches among the Phaeophyta. Adding SSU sequences from other taxa to alignments did not improve resolution (Peters 1998). Further resolution of relationships within the Phaeophyta required other sources of information.

A number of workers combined information from 18S sequences with information from the more conserved regions of the Internal Transcribed Spacer regions of the nrDNA. Phaeophycean ITS regions vary greatly in length and sequences are conserved between taxa in some groups and are very variable in others. Burkhardt & Peters (1998) reported the length of the ITS-1 region from various Phaeophyta as varying between 206 and 789 nucleotides. ITS-2 is generally less variable. Alignment of the whole spacer regions is only possible with closely related species (Burkhardt & Peters 1998, Müller *et al.* 1998, Peters & Clayton 1998).

Burkhardt & Peters (1998) investigated relationships of the Ectocarpalean kelp endophyte genus *Laminariocolax* using combined SSU alignments and alignments of “conserved ITS motifs” which made up 293 positions of 1640 total ITS positions, and could be aligned over a wide range of phaeophycean species. Peters also used SSU and ITS data to resolve relationships among the Laminariales (Peters 1998) and as evidence for establishing the order Scytothamnales (Peters & Clayton 1998).

Other studies combined SSU and 28S[2] (Large Sub-Unit or LSU) nrDNA. Several studies used 600–1000 positions from the 5′ end of the LSU gene. This area includes two variable regions, the D1 and D2 regions, which provide phylogenetically useful information. Müller *et al.* (1998) used these regions of the LSU gene and SSU data as evidence that *Asterocladon* does not belong to either the Ectocarpales or Scytothamnales.

Draisma *et al.* (2001) compared phylogenetic information from ribosomal DNA with those from plastid encoded *rbc*L sequences. Their extensive analysis included rbcL sequences from 58 species and nrDNA sequences from 59 species. They were able to align 95% of the rbcL

---

[2] This gene is referred to as 28S or 26S by different authors. For consistency I refer to it as the LSU gene or LSU nrDNA.

gene and ribosomal DNA including partial SSU and about 25% of the LSU gene (552–600bp). The latter included the D1 and D2 regions of the LSU, source of most of the phylogenetically useful information. The two data sets produced trees that were broadly in agreement, but *rbc*L data produced better resolved trees. Draisma *et al.* suggest there may be problems in aligning the D1 and D2 regions of LSU nrDNA over widely diverged species as Partition Homogeneity Testing showed LSU alignments that excluded the D1 and D2 regions were incongruent with LSU alignments that included these regions, a result the authors find difficult to interpret. Rousseau *et al.* (2001) produced another broad phylogeny of the Phaeophyta, using SSU and LSU data from 67 species. Cho *et al*. (2004) produced a comprehensive phylogeny of the Phaeophyta by combining *rbc*L data with a new set of sequences of *psa*A and *psa*B genes. These three studies have produced the most complete overall phylogenies of the Phaeophyta. Unfortunately, Draisma *et al.* did not include any representatives of the Ralfsiales, and Rousseau *et al.* only included *Nemoderma tingitanum*, a species limited to southern Europe and the Mediterranean and the sole member of the Nemodermataceae Feldmann. *Nemoderma tingitanum* is also morphologically distinct from most Ralfsiaceae, in having intercalary sporangia and developing erect axes (Parente *et al.* 2000). The Nemodermataceae were placed in the Ralfsiales by Nakamura (1972), but *Nemoderma* has also been placed in the Scytosiphonaceae (Costello *et al.* 2004). The only representative of the Ralfsiales included in the study by Cho *et al.* was *Analipus japonicus*.

Rousseau *et al.* (2001) found no clear affinity between *Nemoderma* any other group (their phylogeny shows *Nemoderma* as a sister taxon to the Fucales). Cho *et al.* (2004) resolved *Analipus japonicus* as a sister taxon to a clade containing the Fucales, Cutleriales and Phyllariaceae. Only Tan & Dreuhl's early (1994) molecular study used an unambiguous member of the Ralfsiaceae, *Ralfsia fungiformis*. This study placed *Ralfsia fungiformis* outside the Ectocarpales and among a number of morphologically complex phaeophycean orders, but with no clear affinity to any particular group, nor to *Analipus japonicus.*

1.6 ITS sequences in the Phaeophyta

The Internal Transcribed Spacer Regions (ITS) of the nuclear ribosomal DNA separate the short sub-unit, the 5.8S gene and the large sub-unit (Fig.1.1). This whole region is highly repeated and separated by the Inter-Genic Spacer (IGS) (Hillis & Dixon 1991). ITS sequences have been employed to separate groups at the level of families, genera and subpopulations.

Variation between ITS regions is not consistent in the Phaeophyta. Saunders & Druehl (1993a) compared the ITS sequences from two morphologically divergent Laminariales,

ETS SSU (18S) ITS-1 ITS-2 LSU (28S)

Alaria and *Postelsia palmaeformis* and found most regions of both ITS-1 and ITS-2 were conserved. In their study ITS-1 and ITS-2 each had two short variable regions, varying between 17 and 55 nucleotides, separating longer regions that were between 78% and 94% conserved. Van Oppen *et al*. (1993) found ITS sequences of *Desmarestia viridis/confervoides* from the northern and southern hemisphere populations were nearly identical. In contrast, Burkhardt & Peters (1998) found large parts of the ITS regions were too variable to be phylogenetically useful above the generic level in a study of the phylogenetic relationships of *Laminariocolox,* a genus of endophytic brown algae found in Laminariales. Serrão *et al.* (1999) found a high degree of variability of ITS sequences in *Fucus*, but were able to align sequences from the Fucaceae, again with numerous gaps. Pairwise divergences varied greatly between different genera, different species and within individuals.

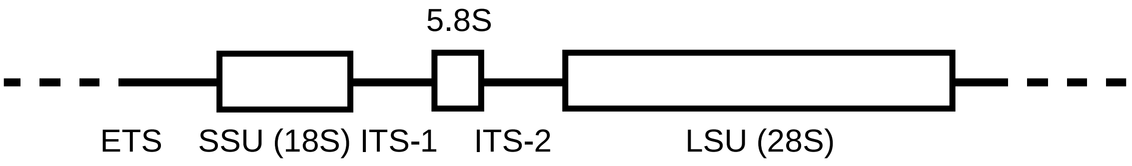

Fig. 1.2. Regions of the nuclear ribosomal DNA.

Stiger *et al.* (2000) used ITS-2 sequences from *Sargassum* and were able to align sequences with the insertion of numerous gaps. Leclerc *et al.* (1998) used ITS sequences to investigate relationships within the northern hemisphere genus *Fucus* and Saunders & Druehl (1993b) and a further analysis by Druehl *et al.* (1997) used ITS sequences to investigate taxonomic division within the *Alariaceae-Laminariaceae-Lessoniaceae* complex of the Laminariales.

1.7 Outline and scope of this study

The crustose brown algae of New Zealand have received little attention (Hurd *et al.* 2004). In this study I have attempted to describe the New Zealand species of the Ralfsiaceae, and the more prominent microthalli of the Scytosiphonaceae. Epiphytic species have not been investigated. I have attempted to overcome some of the problems presented by morphological convergence by using ITS nrDNA sequences to separate species and infer relationships between them. I also attempt to elucidate the ordinal relationships of the Ralfsiaceae by comparing LSU nrDNA sequences from New Zealand species with published sequences for *Nemoderma tingitanum* and other Phaeophyta.

This study supports the requirement under Objective 3.1 (Improving our knowledge of coastal and marine ecosystems) of the New Zealand Biodiversity Strategy (New Zealand Department of Conservation/Ministry for the Environment 1998) to “improve our knowledge of marine species, including taxonomy, distribution, habitat requirements, and the threats to species.”

Chapter Two:

Materials and methods

2.1 Morphological descriptions

Algae were collected from various locations around the North and South islands of New Zealand (Fig. 2.1) between September 2003 and June 2005. Specimens were returned to the laboratory in chillers or fixed in 4% formaldehyde/seawater buffered with sodium bicarbonate. Specimens were examined under a dissecting microscope and radial longitudinal sections cut by hand and mounted in seawater or glycerol. Drawings were made using a *camera lucida* on a Carl Zeiss light microscope and measurements were made using an eyepiece micrometer. Micrographs were taken on an Olympus Provis AX70 microscope with an Olympus DP70 digital imaging system.

Morphological characters were recorded following the terminology used by Hollenberg (1969), Tanaka & Chihara (1980a–c, 1981a–c) and León-Alvarez & Norris (2005).

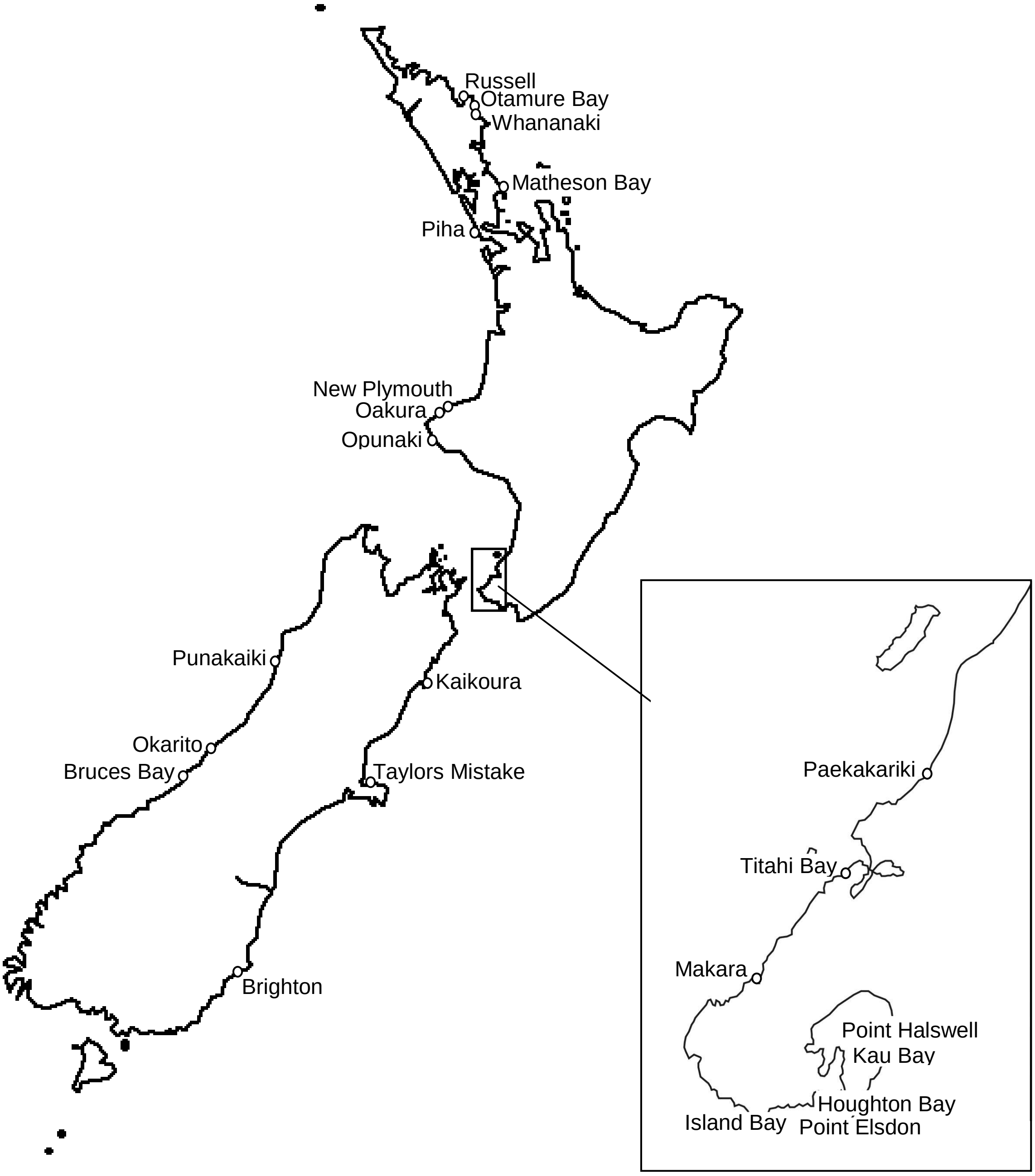

Fig.2.1. Collection sites.

2.2 DNA Extraction

Algal thalli were collected from the field and brushed with a stiff nylon stencil brush to remove diatoms and any fragile epiphytes. Scrapings of young parts of the thallus were obtained with a small wood-carving gouge, either in the field where substrata were not easily removable, or from field collected thalli under a dissecting microscope. Samples were air dried or dried with silica gel. Thalli of *Hapalospongidion* break down into slime soon after removal from rock so samples were taken from thalli that were air dried while still attached to pieces of rock.

Dried samples were frozen in liquid nitrogen and ground to a fine powder. DNA was extracted using a slightly modified version of the procedure of Phillips *et al*. (2001). 20–50 mg of powdered tissue was incubated in 500 μl CTAB-PVPP extraction buffer for 60–120 mins at 55ºC. The extraction buffer contained 1000 μl 2% hexadecyltrimethylammonium bromide (CTAB) w/vol, 10 μl 10% w/vol sodium dodecyl sulfate (SDS), 5 mg polyvinylpolypyrrolidone (PVPP), 10 μl β-mercaptoethanol, and 40 μl EDTA. Following incubation, 400 μl SEVAG (chloroform:isoamyl alcohol 24:1 vol/vol) was added to each sample, mixed by inversion and incubated at room temperature for 10 minutes.

Samples were centrifuged at 13000 rpm for 30 mins at 4ºC for 30 mins. The supernatant was transferred to a clean tube and polysaccharides were precipitated following the procedure of Kraan & Guiry (1998). 0.1 volumes NaOAc and 0.25 volumes EtOH were added to each sample. One volume SEVAG was added and the samples incubated for a further 10 minutes. Samples were centrifuged for 10 mins at 13 000 rpm and the supernatant transferred to a clean tube. A second precipitation step was carried out where samples contained large amounts of polysaccharide.

Samples were incubated for 30 minutes with 5 μl RNase at 37ºC. 0.1 volume NaOAc and one volume isopropanol was added and the samples incubated at -20ºC overnight to precipitate DNA. DNA was pelleted by centrifuging and the pellet washed with 1 ml 70% EtOH, dried and resuspended in 40 μl ddH_2O.

Material recovered was often stained with phenolic compounds and/or retained significant amounts of polysaccharides. DNA was further purified by gel electrophoresis (Saunders 1993).

DNA was separated by running for 1–2 hours through a 1% low melting point agarose gel and stained with ethidium bromide. Bands with intact DNA were excised and DNA recovered using a Quiagen Gel Extraction kit following the manufacturer's instructions. In some samples DNA was still bound in large amounts of polysaccharide which prevented DNA from separating under electrophoresis. Good purification was obtained by resuspending DNA in ddH_2O overnight at 4 ºC then removing the aqueous phase from the sample and purifying this by gel electrophoresis.

2.3 PCR amplification

DNA amplifications were performed in a GeneAmp PCR System 2700 thermocycler (Applied Biosystems). Each 50 μl reaction volume contained 2 μl template, either undiluted or diluted to 10% or 2% with distilled water, 2 μl dNTP, 4 μl each primer (10 µM), 5 μl PCR buffer (100 mM Tris-HCl, 500 mM KCl (Roche Diagnostics)), 3 μl 25 mM $MgCl_2$, 0.2 μl Taq DNA polymerase (5 000 U/mol New England Biolabs), and 2.5 μl DMSO. An initial denaturation step of 94° for 2 mins was followed by 20 cycles at a higher annealing temperature (1 min at 94° C, 1 min at 55° C, and 2 mins at 72° C), followed by 15 cycles at a lower annealing temperature (1 min 94° C, 1 min at 45° C, 2 mins at 72°), with a final extension step of 15 mins at 72° C.

PCR products were checked for length and yield on 1% agarose gels. Bands were excised and DNA extracted using a Qiagen Gel Extraction kit. Sequencing reactions were performed with the ABI Prism BigDye Terminator v 3.1 Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems), and forward and reverse sequences for all taxa used in the analysis were determined by capillary sequencing using an ABI3730 Genetic Analyzer by the Allan Wilson Centre Genome Service, Massey University.

2.4 Primers

The internal transcribed spacer (ITS) regions of the nrDNA were amplified with primer pairs ITS2 and ITS5 (ITS-1) and ITS3 and ITS28 (ITS-2). ITS primers are shown in Table 2.1. Attempts to amplify the entire ITS-1–5.8S–ITS-2 region failed repeatedly so ITS-1 and ITS-2 regions were amplified separately.

Table 2.1. ITS primers

Primer	Sequence (5′–3′)	Reference
ITS5 (F)	GGAAGTAAAAGTCGTAACAAGG	White *et al.* 1990
ITS2 (R)	GCTGCGTTCTTCATCGATGC	White *et al.* 1990
ITS3 (F)	GCATCGATGAAGAACGCAGC	White *et al.* 1990
ITS28cc (R)	CGCCGTTACTAGGGGAATCCTTGTAAG	Hillis & Dixon 1991

The 5′ end of the LSU nrDNA region was amplified with primer pair LSU-16 and LSU1046. Three additional internal primers were used for sequencing. LSU primers are shown in Table 2.2. LSU 410F is complementary to the primer published as LSU 410(F) in Müller *et al.* (1998) as a primer based on the published sequence was found to amplify in the 3′–5′ direction.

Table 2.2. LSU primers

Primer	Sequence (5′–3′)	Reference
LSU-16 (F)	CCGATCAAGCAAGAGGACC	Müller *et al.* 1998
LSU-1046 (R)	TGGCCCACTAGCAACCTTC	Müller *et al.* 1998
LSU602 (R)	ACTCCTTGGTCCGTGTTTCA	Müller *et al.* 1998
LSU410 (R)	TCCTTCGCTTCCCTTTCAG	Müller *et al.* 1998
LSU410F (F)	GCTGAAAGGGAAGCGAAGG	Müller *et al.* 1998

2.5 Sequence alignment and phylogenetic analysis

Electropherogram outputs for each sample were checked using SeqMan 5.08 (DNA Star Inc.). Consensus sequences were aligned in MEGA 3.0 (Kumar *et al.* 2004). The ITS-2 data set was aligned using the ClustalX algorithm. Sources of sequences obtained in this study that were included in the analysis are shown in Table 2.3.

Alignments of LSU DNA were based on the alignment of Rousseau *et al.* (2001), which included 66 other phaeophycean taxa and *Tribonema aequale* (Xanthophyceae) as an outgroup. Taxa are shown in Table 2.4.

Distance, parsimony and likelihood analyses of ITS and LSU data sets was carried out in PAUP* (version 4, Swofford 2002). For the maximum likelihood analysis the nucleotide substitution model was first determined using MODELTEST version 3.7 (Posada & Crandall 1998). The model and parameters selected are shown in Table 2.5.

Bootstrapping (Felsenstein 1985) was performed in PAUP* using 10 random sequence additions and 1000 resamplings. In the maximum likelihood analysis of the LSU data set the maximum number of trees sampled at each step was limited to 100000 trees and bootstrapping of this analysis was not possible. Bayesian posterior probabilities for the ITS data set were estimated in MrBayes (Huelsenbeck & Ronquist 2001) from 1 million generations sampled every 100 generations, with a 1000 generation burn-in.

Table 2.3. Location of specimens sequenced in this study and included in phylogenetic analyses[1].

Species	**Location**	**Latitude, Longitude**	**Field Number**	**Sequences analysed**
Diplura sp.	Pt Elsdon, Wellington	41° 20′ 30″S 174° 47′ 00″E	RV16	LSU[2]
Hapalospongidion gelatinosum Saunders	Pt Elsdon, Wellington	41° 20′ 30″S 174° 47′ 00″E	HP4	LSU
Pseudolithoderma roscoffense Loiseaux	Matheson Bay, Northland	36° 17′ 30″S 174° 48′ 30″E	PS5	LSU
Ralfsia confusa Hollenberg	Whananaki, Northland	35° 30′ 30″S 174° 28′ 30″E	TH12	ITS 2
Ralfsia confusa Hollenberg	Kau Bay, Wellington	41° 17′ 00″S 174° 50′ 00″E	TH7	ITS 2
Ralfsia confusa Hollenberg	Pt Halswell, Wellington	41° 16′ 45″S 174° 49′ 45″E	TH16	ITS 2
Ralfsia confusa Hollenberg	Russell, Northland	35° 16′ 30″S 174° 08′ 30″E	TH11	ITS 2
Ralfsia confusa Hollenberg	Island Bay, Wellington	41° 20′ 15″S 174° 46′ 30″E	TH21	LSU
Ralfsia expansa (J. Agardh) J.Agardh	Pt Elsdon, Wellington	41° 20′ 30″S 174° 47′ 00″E	CCB21	ITS 2
Ralfsia expansa (J. Agardh) J.Agardh	Otamure Bay, Northland	35° 29′ 30″S 174° 27′ 45″E	PS6	ITS 2, LSU
Ralfsia sp. “smooth”	Pt Halswell, Wellington	41° 16′ 45″S 174° 49′ 45″E	SR1	ITS 2
Ralfsia sp. “smooth”	Island Bay, Wellington	41° 20′ 15″S 174° 46′ 30″E	SR10c	ITS 2
Ralfsia sp. “smooth”	Pt Elsdon, Wellington	41° 20′ 30″S 174° 47′ 00″E	SR6	ITS 2, LSU

---

[1] These samples are being deposited in the Museum of New Zealand herbarium (WELT).

[2] Identical sequences were obtained from Kaikoura specimens.

Table 2.4 Taxa used in LSU analyses.

Order, Species, Taxonomic Authority	**GenBank Accession Number for LSU sequence**
Xanthophyceae	
Tribonema aequale Pascher	[YO7979]
Phaeophyceae	
Ascoseirales	
Ascoseira mirabilis Skottsberg	[AJ229141]
Cutleriales	
Cutleria multifida (J. E. Smith) Greville	[AF053119]
Desmarestiales	
Arthrocladia villosa (Hudson) Duby	[AJ229142]
Desmarestia aculeata (Linnaeus) Lamaroux	[AJ229143]
Desmarestia ligulata (Lightfoot) Lamaroux	[AJ229144]
Himantothallus grandifolius (A. & E. S. Gepp) Zinova	[AJ229145]
Phaeurus antarcticus Skottsberg	[AJ229146]
Dictyotales	
Dictyopteris polypodioides (De Candolle) Lamaroux	[AF130716]
Dictyota dichotoma (Hudson) Lamaroux	[AF130715]
Taonia atomaria (Woodward) J. Agardh	[AF130714]
Ectocarpales	
Adenocystis utricularis (Bory) Skottsberg	[AF071778]
Chordaria flagelliformis (Müller) C. Agardh	[AJ229129]
Dictyosiphon foeniculaceus (Hudson) Greville	[AJ229137]
Hincksia granulosa (J. E. Smith) P. C. Silva *in* P. C. Silva *et al.*1987	[AF071783]
Myriotrichia clavaeformis Harvey *in* Hooker	[AJ229138]
Petalonia fascia (O. F. Müller) Kuntze	[AF071158]
Punctaria latifolia Greville	[AF115429]
Pylaiella littoralis (Linnaeus) Kjellman	[AF071782]
Scytosiphon lomentaria (Lyngbye) Link	[AF071159]
Streblonema maculans (Hamel) South & Tittley	[AF071784]
Striaria attenuata (C. Agardh) Greville	[AJ229139]
Utriculidium durvillei (Bory) Skottsberg	[AF071157]
Fucales	
Anthophycus longifolius (Turner) Kützing	[AF091273]
Ascophyllum nodosum (Linnaeus) Le Jolis	[AF053106]
Axillariella constricta (J. Agardh) Silva	[AF091273]
Bifurcaria bifurcata Ross	[AF053113]
Bifurcaria brassicaeformis (Kützing) Barton	[AF091280]
Bifurcariopsis capensis (Areschoug) Papenfuss	[AF130717]
Caulocystis cephalornithos (Labillardière) Areschoug	[AF091279]
Cystoseira nodicaulis (Withering) M. Roberts	[AF053111]
Cystosphaerae jacquinotii (Montagne) Skottsberg	[AF130718]
Durvillaea antarctica (Chamisso) Hariot	[AF130719]
Durvillaea potatorum (Labillardière) Areschoug	[AF091283]
Fucus vesiculosus Linnaeus	[AF053105]

Himanthallia elongata (Linnaeus) S. F. Gray	[AF053108]
Hormosira banksii (Turner) Descaisne	[AF091270]
Pelvetia canaliculata (Linnaeus) Descaisne & Thuret	[AF053107]
Phyllospora comosa (Labillardière) C. Agardh	[AF130720]
Sargassum muticum (Yendo) Fensholt	[AF053109]
Seirococcus axillaris (R. Brown *ex* Turner) Greville	[AF091284]
Turbinaria turbinata (Linnaeus) O. Kuntze	[AF091272]
Xiphophora chondrophylla (R. Brown ex Turner) Montagne *ex* Harvey	[AF091271]
Notheia anomala Harvey & Bailey	[AF091270]

Laminariales

Alaria esculenta (Linnaeus) Greville	[AF071151]
Chorda filum (Linnaeus) Stackhouse	[AF053117]
Halosiphon tomentosus (Lyngbye) Jassund	[AF071156]
Laminaria digitata (Linnaeus) Lamaroux	[AF071153]
Laminaria ochroleuca Bachelot de La Pylaie	[AF071154]
Macrocystis pyrifera (Linnaeus) C. Agardh	[AF053116]
Saccorhiza polyschides (Lightfoot) Batters	[AF053118]

Ralfsiales?

Nemoderma tingitanum Schousboe *in* Bornet	[AF130722]

Scytothamnales

Scytothamnus australis (J. Agardh) Hooker & Harvey	[AF071780]
Splachnidium rugosum (Linnaeus) Greville	[AF071781]
Stereocladon rugulosus (Bory de Saint-Vincent) Hariot	[AJ229132]

Sporochnales

Sporochnus pedunculatus (Hudson) C. Agardh	[AF130723]

Sphacelariales

Cladostephus spongiosus (Hudson) C. Agardh	[AF053115]
Halopteris scoparia (Linnaeus) Sauvageau	[AF091285]
Sphacelaria cirrosa (Roth) C. Agardh	[AF071150]

Syringodermatales

Syringoderma phinneyi Henry & Müller	[AJ243782]

Tilopteridales

Haplospora globosa Kjellman	[AF130724]
Phaeosiphoniella cryophila Hooper, Henry & Kuhlenkamp	[AF130725]
Tilopteris mertensii (Turner *in* Smith) Kützing	[AF130726]

Incertae sedis

Asteronema ferruginea (Harvey) Delépine & Asensi	[AJ229134]
Asterocladon lobatum D.G. Müller, E.R. Parodi & A.F. Peters	[AJ229136]
Asteronema rhodochortonoides (Børgeson) Müller & Parodi	[AJ229135]
Bachelotia antillarum (Grunow) Gerloff	[AF130721]

Table 2.5. Model and parameters selected by MODELTEST for Maximum Likelihood analysis of ITS and LSU data sets.

Data set	**Model selected**	**-ln likelihood**	**Base Frequencies**				**Substitution model**						**Proportion of invariable sites**	**Variable sites**
			A	C	G	T	A–C	A–G	A–T	C–G	C–T	G–T		
LSU	GTR + I +Γ[3]	8159.1030	0.1909	0.2542	0.3327	0.2222	0.6074	1.4536	0.8272	0.5450	3.2969	1.0000	0.3049	Gamma distribution shape parameter: 0.5121
ITS	F81[4]	1066.2351	0.1877	0.2971	0.2902	0.2249	All rates equal						0	Equal rates for all sites

---

[3] Tavaré 1986

[4] Felsenstein 1981

Chapter Three:

Crustose brown algae in New Zealand

THE crustose brown algae were not represented in the early algal collections made in New Zealand (e.g. Laing 1926). Most of these collections consisted of herbarium specimens mounted on paper and identified by taxonomists abroad, and many crusts are not easily separated from substrata and attached specimens are heavy. Although some species are widely distributed and locally abundant, the first collections were made by Lindauer in the 1940s. In 1947, Lindauer wrote:

> "Numerous species belonging to the subgenera *Strangularia* [sic] and *Euralfsia* are abundant along the coasts, but have, so far, not been systematically investigated. They appear as yellowish to dark brown and almost black, circular or irregular, smooth soft and lubricious, or hard, corrugated crusts on stones in the intertidal belt and beyond."
>
> (Lindauer 1947)

Ralfsia verrucosa was included in Lindauer's *Algae Nova-Zelandicae Exsiccatae* (Fascicle 13, issued October 1948, species number 310 (Nelson & Phillips 1996)) and Lindauer (1949) published a description of *Hapalospongidion saxigenum*. Both species were included in Lindauer *et al*. *Marine Algae of New Zealand* (1961). Since then no further crustose algae have been identified to species level in New Zealand, although two unnamed species of *Ralfsia* were reported from Kaikoura in South & Adams (1976) as well as *Ralfsia verrucosa*, and Adams (1994) noted that several species of Scytosiphonales probably had alternate crustose forms. A crustose alga identified to the genus *Pseudolithoderma* has been the subject of ecological studies in the northern North Island (Jeffs 1985, Williamson 1992).

No descriptions of microthalli of the Scytosiphonaceae from New Zealand have been published. Parsons (1982) studied the New Zealand species of *Colpomenia* but did not include descriptions of microthalli.

3.1 Morphological characters of crustose brown algae

Thallus organisation and construction

All of the crustose brown algae considered here are pseudoparenchymatous. The thallus is constructed of one or more layers of branched, radiating filaments that form a basal layer. From this layer filaments branch off, either at right angles, or at acute angles and curving to vertical. The vertical filaments are variously referred to as assimilatory filaments, dorsal filaments, perithallial filaments, or upright filaments. Following terminology devised for non-geniculate coralline rhodophytes (Woelkerling *in* Womersley 1996) thalli with vertical filaments at right angles to the basal layer are termed dimerous, while those with filaments curving to vertical are termed monomerous.

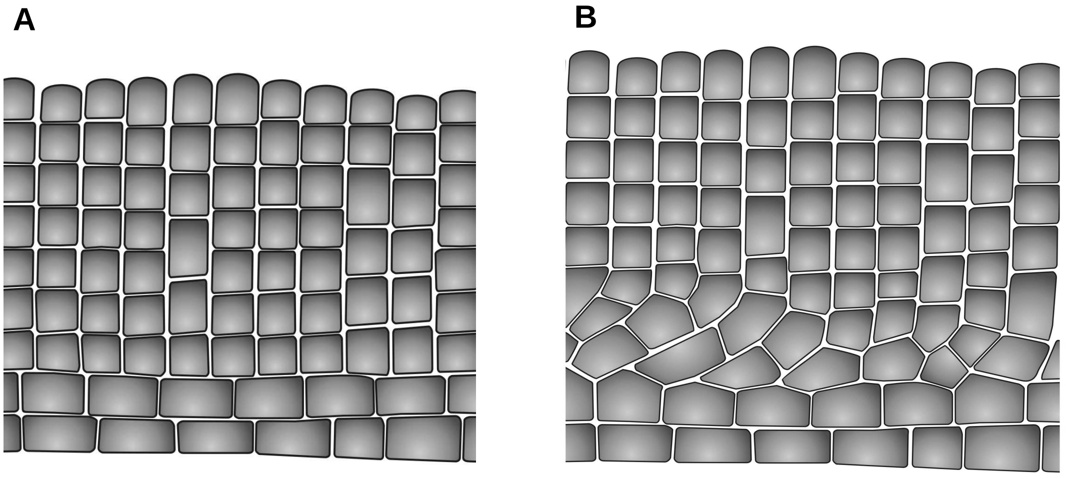

Fig. 3.1. Thallus structure A. Dimerous thallus. B. Monomerous thallus.

In some crusts the basal layer is not clearly distinguished. Instead a central region of several layers of horizontal filaments forms what Woelkerling refers to as a central core, with filaments curving both upward and downward. This construction is termed bilateral. Sartoni & Boddi (1989) refer to a multiaxial growing region in *Ralfsia expansa*, where the edge of the thallus has a bilateral construction, with the central core also giving rise to filaments that extend the thallus laterally.

The erect filaments show varying degrees of lateral adherence. In some species the filaments are tightly adherent, and will not separate without considerable pressure, in others the filaments are free from one another and only loosely held together by a gelatinous matrix, in an intermediate form the filaments are weakly adherent and readily separate under slight pressure.

I also follow Woelkerling in referring to a vertical section through the radius of an orbicular thallus as a longitudinal radial section. Other workers have termed this a transverse section.

Reproductive anatomy

León-Alvarez & Norris (2005) attempted to clarify the terminology used to describe reproductive structures, especially unangia, in the Phaeophyta. Firstly they distinguish the origin of reproductive structures from the position of the structure, as terminology for these characters has been used interchangeably and leads to confusion. They reserve the term position to describe the relationship of reproductive structures relative to the surrounding filaments or to the whole thallus. In the first case either basal, mid-level, sub-superficial or superficial, in the second case central, intermedial, marginal or irregular. Origin refers to the attachment of the structure to the thallus: terminal, lateral or intercalary. Secondly they point out that different definitions have been applied to the terms “paraphyses” and “stalks.” They do not attempt to define these terms but suggest descriptions state whether or not these structures are morphologically differentiated from other filaments.

Following León-Alvarez & Norris the term lateral is only applied to a reproductive structure that is sessile (i.e. lacking a stalk or pedicel) on a reproductive filament (Fig 3.2B), whether or not this filament is differentiated into an erect or assimilatory filament and a paraphysis. All other structures are either intercalary (Fig. 3.2D) or terminal on a filament (Fig.3.2A), even if that filament is only one-cell long (Fig. 3.2B). A single celled filament is termed a pedicel by Tanaka & Chihara 1980a).

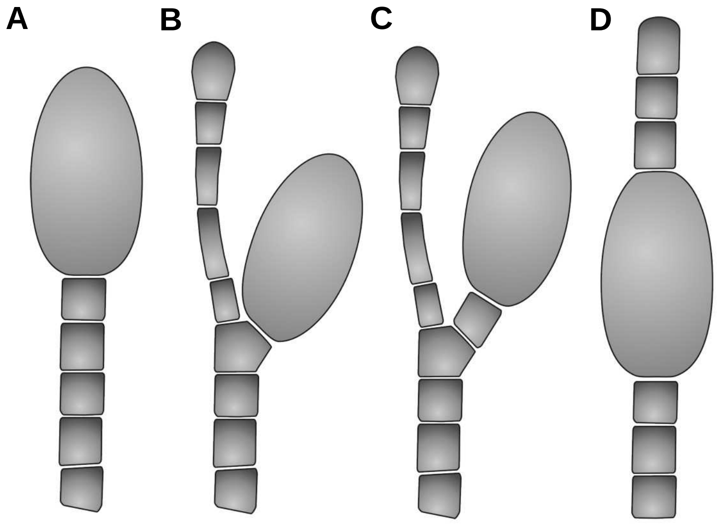

Fig. 3.2. Origin of unangia, based on León-Alvarez & Norris (2005): **A**. Terminal. **B**. Lateral and sessile. **C**. Terminal. **D**. Intercalary.

I concur with Tanaka & Chihara’s (1980a–c and 1981a, b) use of the arrangement of the plurangia as a diagnostic character for species delineation in the Ralfsiaceae. Their use of presence and number of pedicels or stalk cells of the unangia as diagnostic characters is problematic as these characters are variable within some species, including *Ralfsia verrucosa* (Fletcher 1987) and *Ralfsia expansa* (Børgeson 1924).

Typical vegetative thalli can be identified to the species level by the practiced eye by vegetative habit alone, but identification of older, eroded or very young thalli requires microscopic examination, preferably of fertile tissue. Most Scytosiphonaceae microthalli are smaller and distinct from the Ralfsiaceae, but the microthallus of *Colpomenia bullosa* is similar in outward appearance to *Ralfsia* and *Diplura*, but has thin-walled, elongate cells. Older thalli of *C. bullosa* also develop overlapping lobes that are not found in any New Zealand Ralfsiaceae.

3.2 Key to families of crustose brown algae in New Zealand

1. Plurangia absent; single discoid plastid per cell……………………….…Scytosiphonaceae
1. Plurangia terminal or intercalary; plastid single parietal or several discoid……..……….2

2. Several discoid plastids per cell; plurangia terminal; thallus dimerous…..Lithodermataceae
2. Single plastid per cell; plurangia intercalary; thallus monomerous or dimerous…………………………………………………………………..Ralfsiaceae

3.3 Scytosiphonaceae Farlow 1881 emend. G. Y. Cho & Boo *in* Cho *et al.* 2003

The family Scytosiphonaceae was established by Farlow (1881), and elevated to ordinal status by Feldmann (1949) for Phaeophyta with simple unbranched thalli, only plurangial reproductive structures and cells with a single plastid with a pyrenoid. Microthalli as part of a heteromorphic life history were discovered in the 1960s (Dangeard 1963, Tatewaki 1966, Lund 1966). The order was reduced to a family of the Ectocarpales by Peters & Ramírez (2001). The diagnosis of the family was emended by G. Y. Cho et Boo (Cho *et al.* 2003) to include *Myelophycus*, a genera with an isomorphic life history, after Cho *et al.* found *rbc*L and Rubisco spacer sequences indicated *Myelophycus* and the Scytosiphonaceae were monophyletic.

The microthalli of the Scytosiphonales vary in structure, from simple filamentous thalli ("*Compsonema saxicolum*-type"), through gelatinous, loosely adherent tufts or crusts ("*Microspongium gelatinosum*-type") to pseudoparenchymatous crusts with laterally adherent filaments ("Ralfsioid" or "*Stragularia clavata*-type"). Kogame *et al*. (1999) found that differences in morphology of the microthallus were correlated with phylogenetic distance and in some cases the morphology of the microthallus was a more useful taxonomic character than that of the macrothallus. Unfortunately descriptions of the microthalli are inconsistent, usually from culture and microthallus morphology is known to vary with culture conditions (Lüning & Dring 1973).

Four genera are found in New Zealand: *Hydroclathrus* Bory, *Petalonia* Derbès et Solier (including *Endarachne* (J. Agardh) Vinogradova), *Scytosiphon* C. Agardh, and *Colpomenia* (Endlicher) Derbès et Solier. This study reports macrothalli of three species. Other microthalli are no doubt present, but are probably small, epiphytic or cryptic.

3.4 ***Scytosiphon*** C. Agardh 1820

Scytosiphon is a genus characterised by a simple erect thallus of tubular or flattened axes arising from a common base. The upright phase alternates with a prostrate microthallus, usually considered the sporophyte, which may be crustose or filamentous.

Only *Scytosiphon lomentaria* (Lyngbye) Link has been reported from New Zealand (Adams 1994), but macrothalli vary considerably in size and other species might be present. According to Womersley (1987) only *Scytosiphon lomentaria* is found in Australia, but in two forms. The first form has hollow tubular axes, with constrictions, the second has flattened axes with the sides adjacent but not united. This second form includes Australian specimens previously identified as *Petalonia zosterifolia* (Reinke) Hamel.

3.4.1 Scytosiphon lomentaria (Lyngbye) Link

Microthallus (=”*Microspongium gelatinosum*” phase)

Plate 1; Fig. 3.3

A thin, fragile crust on rock or shells, firmly attached to substrate without rhizoids. Crust up to 15 mm diameter, but confluent crusts indistinguishable and individual thalli probably smaller. Colour mid–dark brown, surface soft and spongy..

Thallus: Outline irregular, 250–450 μm thick. Structure pseudoparenchymatous, organisation dorsiventral, construction dimerous. Basal layer of branched radiating filaments, 2–4 cells thick, giving rise to erect filaments branching at right angles to the basal filaments. Erect filaments of 4–16 laterally adherent cells, then filaments becoming free from one another. Rhizoids absent.

Basal cells elongate, rectangular, 4–6.5 μm in diameter, 1.5–3 diameters long. Cells of lower, laterally adherent, part of erect filaments rectangular, 6–9 μm diameter, and 0.75–1.7 diameters long. Cells with single, parietal plastid in upper part of cell.

Multicellular hyaline hairs single or in groups issuing from the mid thallus and extending 150–175 μm above the surface of the paraphyses. Hair cells 4–5 μm diameter, 22–35 μm long.

Reproduction: Unangia terminal on filaments, sessile on cell from which issues a single paraphysis. Unangia clavate, or elongate obovate, 12.5–25 μm diameter, 75–105 μm long.

Paraphyses clavate, 90–110 µm long, of 8–12 cells: lower cells elongate, 4–5 µm diameter, 12–26 µm long; upper cells becoming shorter and widening; apical cells dome-shaped and slightly swollen, 8–10 µm diameter, 10–14 µm long.

A similar crust growing on limpets from Raoul Island in the Kermadec group is in the Museum of New Zealand herbarium (WELT A12662).

Discussion

Microsporangium gelatinosum with unangia was described by Reinke (1889) from the Baltic, this alga is now recognized as a different species from an alga bearing plurangia that was described by under the same name by Reinke in 1888. *M. gelatinosum* was later recognized as the microthallus of *Scytosiphon lomentaria* following culture experiments (Lund 1966, Tatewaki 1966, McLachlan *et al*. 1971).

Other culture experiments have identified various species of crustose brown algae as the microthalli of *Scytosiphon lomentaria*, including *Ralfsia californica* (Wynne 1969) and *Streblonema* (Dangeard 1963). Microthalli do not develop consistent morphologies in culture.

Fletcher (1987) acknowledges the wide variety of morphologies reported from culture and field studies of the crustose stage of *Scytosiphon lomentaria*, with *Ralfsia*-like crusts and *Microspongium gelatinosum*-like crusts reported. He favours the view that the crustose stage is identifiable with *Microspongium gelatinosum* Reinke, and that crustose stages reported as "*Ralfsia*-like" are often more similar to *M. gelatinosum*. Womersley (1987) describes the crustose stage as being "ralfsioid", with erect filaments monostromatic at the edges of the thallus. His illustration (Fig. 108D, p.299) shows unangia with a two or three-celled stalk.

According to Fletcher (1987), only Wynne's (1969) study shows cultures of crustose, unangia-bearing sporophytes of *Scytosiphon lomentaria* that are truly ralfsioid (i.e. with assurgent, coherent filaments). Other studies show either filaments or crusts with non-coherent erect filaments similar to *Microsporangium gelatinosum*.

According to Kogame (1996, 1998) and Kogame *et al.* (1999), the macrothallus of *Scytosiphon lomentaria* (Lyngbye) Link has tubular, constricted axes, bearing loosely arranged plurilocular sori (the plurangia separate under gentle pressure), without a cuticle, and with a microthallus of the *Microspongium gelatinosum* type. The macrothallus of *Scytosiphon gracilis* Kogame has coherent plurangial sori without ascocysts (globose, single-celled paraphyses) and a *Compsonema*-like microthallus of loosely arranged filaments. *Scytosiphon tenellus* Kogame has a macrothallus with coherent plurangial sori with ascocysts and a *Stragularia*-type microthallus. A fourth Japanese species, *Scytosiphon canaliculatus*, has a crustose microthallus previously identified as *Hapterophycus canaliculatus*.

I was unable to amplify DNA extracted from this species, despite several attempts. The morphology of the alga is identical to the "*Microspongium gelatinosum*" phase of *Scytosiphon lomentaria* described by Fletcher (1987) and Fletcher *et al.* (1988).

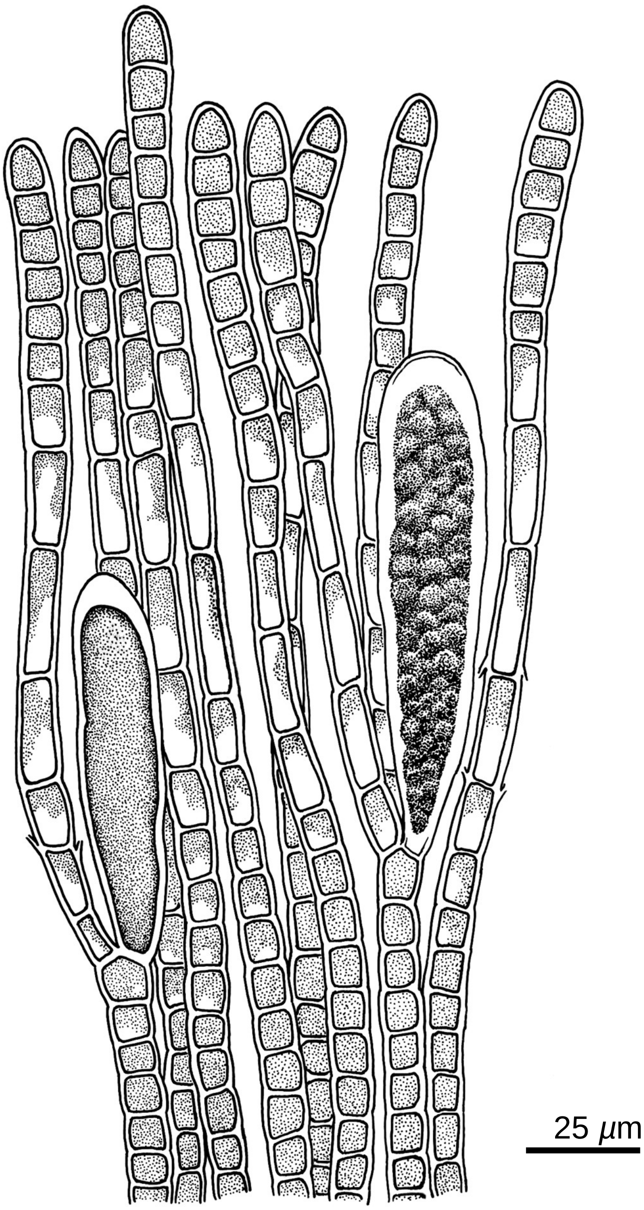

Fig. 3.3. *Scytosiphon lomentaria*, upper part of crustose microthallus with unangia.

3.5 Colpomenia (Endlicher) Derbès et Solier

According to Parsons (1982) there are four species of *Colpomenia* in New Zealand. *Colpomenia sinuosa* (F. C. Mertens ex Roth) Derbès et Solier, an epilithic species[1] found in warmer waters; *Colpomenia peregrina* (Sauvageau) Hamel, which is epilithic or epiphytic and found in cooler waters and *Colpomenia ecuticulata* Parsons, an epiphytic species known only from the Three Kings Islands and Northland. The fourth species, *Colpomenia bullosa* (Saunders) Yamada was first collected from Leigh in 1980. This alga has since been found on East Cape in the North Island and Wellington harbour (Nelson & Adams 1991, Adams 1994).

According to Kogame *et al.* (1999), *C. peregrina*, *C. sinuosa* and *C. bullosa* have crustose life history stages, but as far as I am aware only crusts of *C. bullosa* and *C. peregrina* have been described from field material (by Kogame & Masuda 2001 and Kogame & Yamagishi 1997 respectively). *Colpomenia sinuosa* crusts are only known from culture (Kogame 1997b, Toste *et al.* 2003).

3.5.1 Colpomenia bullosa (Saunders) Yamada 1948

Microthallus

Plates 2 & 3; Fig. 3.4

Microthallus crustose, on rock and shells, young thalli can often be peeled from substrate intact, older thalli loosely attached with numerous long rhizoids. Often covering large areas in rock pools. Older thalli easily recognized by distinctive imbricate lobes. 3–40 mm diameter, often becoming confluent and overgrowing other conspecific individuals or *R. confusa*. Colour dark brown, edges pale. Young thalli smooth or with some low concentric and radial ridges; older lobed thalli with many pale edges resulting in a golden-brown appearance. Drying dark brown.

Thallus: Outline orbicular in young thalli; irregular in older thalli. Up to 500 μm thick or thicker when multistratose. Structure pseudoparenchymatous, organisation dorsiventral or bilateral, construction monomerous. Basal layer of branched radiating filaments firmly laterally adherent, branching at acute angles and giving rise to laterally adherent assurgent filaments slowly curving to vertical or running horizontal and forming a central core then curving upward and downward to form a bilateral thallus. Downward curving filaments

---

[1] Adams (1994) describes this as an epiphytic species, but Parsons says that the species is not known to be epiphytic.

giving rise to numerous straight or sinuous rhizoids, up to 450 μm long and 5–7.5(–15) μm diameter.

Cells of basal layer elongate rectangles or polyhedrons 10–35 μm diameter and 0.9–4(–7) diameters long. Medullary cells thin-walled, rectangular, elongate 7.5–14(–17) μm diameter and 1.2–5 diameters long, Epithallial cells dome shaped 6–12.5(–15) μm diameter and 0.6–4 diameters long covered by a thin cuticle. Cells with a single usually discoid plastid 4–7 μm diameter.

Thallus with few to many multicellular hyaline hairs, single or in tufts arising from medulla, 5–7.5 um diameter and up to 350 μm long. Hair cells elongate 20–35 μm long.

Reproduction: Unangia usually in young thalli, in irregular groups accompanied by loose filaments or paraphyses little differentiated from vegetative filaments but extending above surrounding thallus surface, not laterally adherent and without a cuticle. Unangia clavate, 9–17.5 μm diameter at widest part and 25–150 μm long, attached laterally to filaments (Plate 3C, Fig. 3.4B).

In warm rock pools, low intertidal and shallow sub tidal. Small crusts appearing late summer and dying off over following summer. Dominant in some rock pools, growing quickly to cover large areas. In the field *Colpomenia bullosa* can be distinguished from other crustose algae by the combination of dark thallus which can be peeled from the substrate, numerous rhizoids and by the lobed appearance of older thalli.

Discussion

Parsons (1982) describes *C. bullosa* as arising from a crustose base, but this is probably confusion resulting from macrothalli settling on microthalli. Specimens of the upright macrothallus clearly have a saccate base sessile on rock without an adherent crust. The monomerous construction of the crust resembles Batters’ (1890) *Eu-Ralfsia* rather than *Stragularia*. Fletcher (1987) regarded monomerous thalli as a diagnostic character that distinguished *Ralfsia* from microthalli of the Scytosiphonaceae. This character might be reliable in *Scytosiphon*, but does not appear to be consistent across the Scytosiphonaceae.

It might be possible to distinguish *Colpomenia bullosa* macrothalli in the field by vegetative morphology alone: the thallus develops upright, finger-like saccate projections that emerge from a common base. However three names have been applied to species of *Colpomenia* that share this character: *Colpomenia bullosa* (Saunders) Yamada, *Colpomenia phaeodactyla* Wynne & Norris, and *Colpomenia durvillei*[2] (Bory) Ramírez. The circumscription of these species is unclear (Table 3.1).

Colpomenia bullosa was first collected by Saunders from Pacific Grove, California in 1896 and described under the name *Scytosiphon bullosus* (Saunders 1898). Yamada (1948) described the same species from Japan and transferred it to *Colpomenia* because of the lack of a basal meristematic zone characteristic of *Scytosiphon*. Wynne (1972) maintained that this alga cannot be separated from *C. peregrina* (Sauvageau) Hamel, a species first described from France, but Parsons (1982) separated the two species on the basis of differences in the plurilocular tissue. Setchell & Gardner (1925) considered *C. bullosa* a form of *C. sinuosa: C. sinuosa* f. *deformans* Setchell & Gardner.

Vandermuelen *et al.* (1984) reviewed the type material of *C. sinuosa* (F. C. Mertens ex Roth) Derbès et Solier, *C. peregrina* (Sauvageau) Hamel and *C. bullosa* (Saunders) Yamada. They found *Colpomenia sinuosa* has punctate sori with a cuticle covering the plurangia – a structure that is absent in the two other species. *C. peregrina* and *C. bullosa* can be separated by the morphology of the plurangia: in *C. bullosa* these are long and thin, and frequently uniseriate, whereas *C. peregrina* has shorter plurangia with locules in multiseriate rows.

Wynne & Norris (1976) described a new species, *Colpomenia phaeodactyla* from the Gulf of California. This species has clusters of long (usually 8–15cm) hollow sacs and extensive plurilocular sori with long uniseriate or biseriate plurangia. Paraphyses and hairs are rare. They regard this species as synonymous with *C. sinuosa* f. *deformans* Setchell & Gardner and *Colpomenia bullosa* of Norris (1972) but not *C. bullosa* (Saunders) Yamada 1948. The latter species is firmer and usually has only single sacs (see also Wynne 1972). Probably two species are found in Japanese waters. According to Wynne & Norris, the alga described by Okamura (1936) is *C. bullosa* but the species recorded by Chihara (1970) is closer to *C. phaeodactyla*. They refer to a communication from Mitsuo Chihara who thinks that *C. bullosa* is found in northern Japan – Hokkaido, Sanriku and the Kurile islands, while *C. phaeodactyla* is found in central Japan.

Ramírez & Rojas (1991) published the new combination *Colpomenia durvillei* based on material from Chile and Peru that had previously described as either *Colpomenia bullosa*

---

[2] Wynne (1999) employs the spelling *Colpomenia durvillei*, while Ramírez & Rojas (1991) and Adams (1994) use "*durvillaei*." I follow Wynne in using "*durvillei*", the correct termination according to Garnock-Jones (*in* Connor

(Saunders) Yamada, *Colpomenia phaeodactyla* Wynne & Norris, or *Utriculidium durvillei* (Bory) Skottsberg. The name is derived from *Asperococcus durvillei* applied by Bory to the original material collected from Concepción, Peru in 1826 by D'Urville. Ramírez & Rojas recognise the similarity between *C. phaeodactyla*, *C. bullosa* and *C. durvillei* all of which can have erect finger-like axes. They distinguished *C. durvillei* from *C. phaeodactyla* by the absence of hairs and paraphyses in the plurilocular sori in *C. durvillei*, and agreed that some forms of *C. durvillei* were indistinguishable from *C. bullosa* (Saunders) Yamada.

Kogame *et al*. (1999) published a molecular phylogenetic study of Japanese Scytosiphonales, using *rbc*L, partial *rbc*S and partial large sub-unit nrDNA. The taxa formed two major clades. In the first clade *Colpomenia sinuosa* grouped with *Chnoospora implexa*, *Hydroclathrus clathratus* and *Rosenvingea intricata*. In the second major clade *Colpomenia bullosa* and *Colpomenia phaeodactyla* formed a sub-clade, which grouped with species of *Petalonia* and *Scytosiphon*. The position of *Colpomenia peregrina* was not resolved within either major clade. These results suggest that (1) *Colpomenia* is polyphyletic, and (2) vegetative morphology and growth patterns of the macrothalli do not distinguish genera within the Scytosiphonales. However some morphological characters of the prostrate phase did correlate with the molecular data. Unfortunately this study only used Japanese material so did not clarify the relationship of *C. durvillei* (Bory) Ramírez with *C. bullosa* (Saunders) Yamada.

ITS-2 sequences from crustose stages from the south coast of Wellington and Matheson Bay, Northland are identical to those of *C. bullosa* collected from Muroran in southern Hokkaido (Kogame & Masuda 2001). This suggests that the New Zealand species is synonymous with *C. bullosa* (Saunders) Yamada, in agreement with Parsons (1982) who described an alga from Leigh in northern New Zealand as *C. bullosa*. Parsons illustrated a section through a plurilocular sorus with several paraphyses, whereas Ramírez & Rojas found paraphyses only occasionally on South American material, but frequently in the type material of *C. phaeodactyla*. While the name *C. bullosa* (Saunders) Yamada has been applied to Chilean specimens, it is not clear whether *C. durvillei* (Bory) Ramírez and *C. bullosa* (Saunders) Yamada are a single species (Cho *et al.* 2005). Kogame & Masuda (2001) retain the name *C. bullosa* (Saunders) Yamada for the northern Japanese species. Adams (1994) uses the name *C. durvillaei* but illustrates an alga with a single erect sac. This is closer to Wynne's (1972) conception of *C. bullosa*, but not to Ramírez & Rojas' (1991) description of a thallus of "1–22 proyecciones erectas en forma de finos dedos sacados." Ramírez & Rojas state that the three

---

& Edgar 1987). According to the Article 60 of the International Code of Botanical Nomenclature (Greuter *et al.* 2000) such an incorrect termination is treated as an orthographic error to be corrected.

species may be synonymous but in the absence of a major study they prefer to maintain the taxa as independent species.

The crustose microthallus of *Colpomenia bullosa* was first reported by Nakamura & Tatewaki (1966). It has only been described from Japanese material. Kogame & Masuda (2001) described microthalli from cultured material and small crusts (up to 10 mm diameter) found in the field. The crustose phase in New Zealand is larger and distinctive, with older crusts developing small ridges on the surface that develop into large overlapping lobes (Plate 3A, 3B). In section the microthalli cells (Fig. 3.4A, Plate 2A-B) resemble those of *Scytosiphon canaliculatus* (Kogame 1996, Fig.20, p.89), which has a microthallus that develops lobed branches and resembles the haptera of some phaeophytes.

Table 3.1: Characters from descriptions of *Colpomenia* species (n.s=not specified).

		Author			
		Santelices *et al.* 1989	Wynne & Norris 1976	Ramírez & Rojas 1991	Parsons 1982
Name		*Colpomenia phaeodactyla*	*Colpomenia phaeodactyla*	*Colpomenia durvillei*	*Colpomenia bullosa*
Location		Central Chile	Gulf of California	Chile	Leigh, New Zealand
Plurangia	Length	25 μm	28–38 μm	30–35–40 μm	60 μm
	Width	4–5 μm	n.s.	4–5 μm	4 μm
	Locules	5–8 μm	9–12 (in Fig. 5b, p.7)	14–18 (in Fig. 9, p.18)	11–16 (Fig. 5, p.294)
	Arrangement	n.s.	Uni or biseriate	Uni or biseriate	Uni or biseriate
	Paraphyses	n.s.	Rare	Rare	common
	Hairs	n.s.	Rare	Rare	common
Thallus		Up to 60 digitate projections, 3–5 mm long, a few (up to 6) up to 50 mm long	6–12–(30) long hollow sacs, 80–150 mm long, 8–15 mm wide, rarely up to 55 mm wide	1–22 erect projections, 20–130 mm long, 10 mm diameter	1–3 hollow sacs, 120 mm long, 35 mm wide

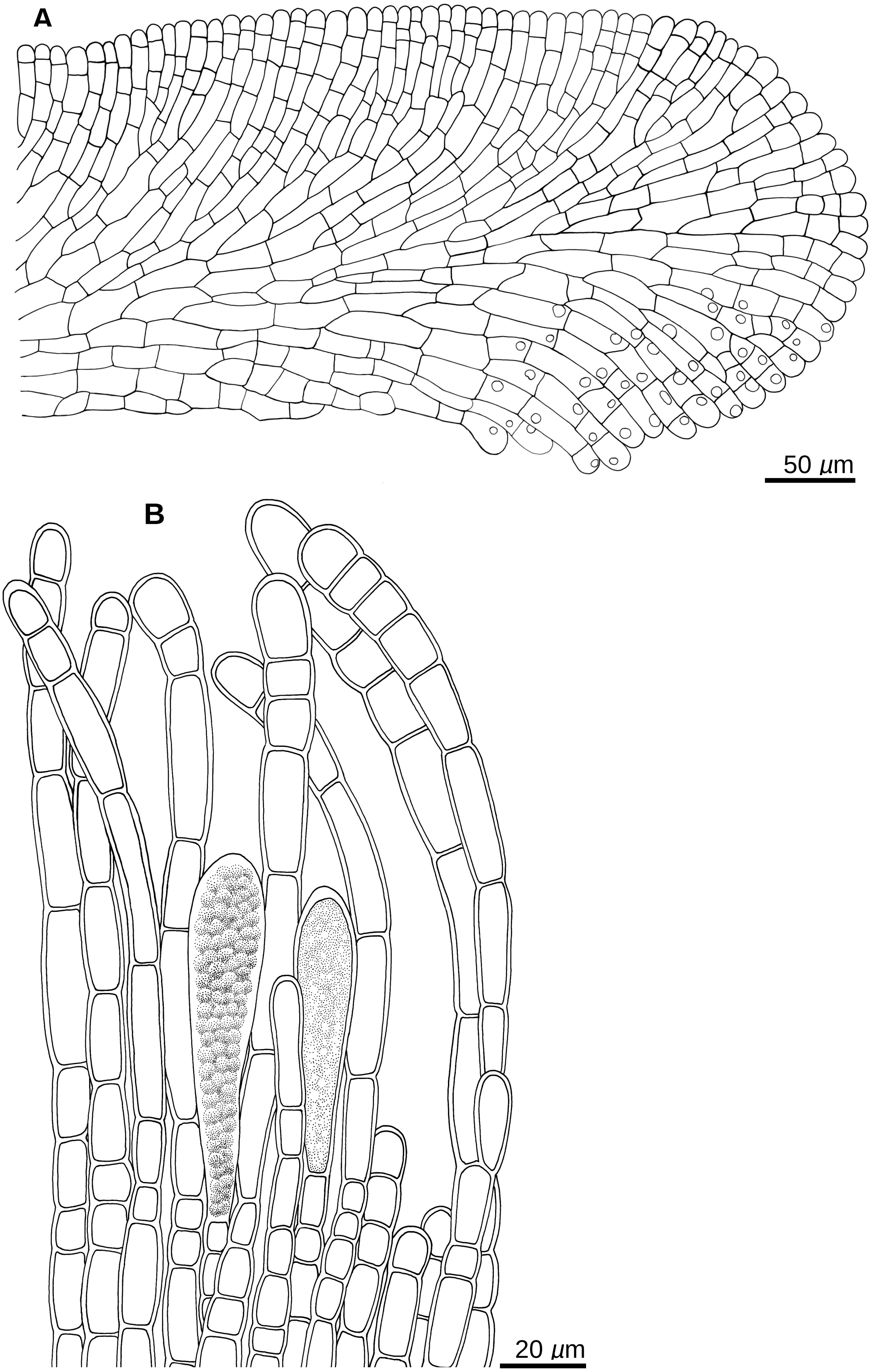

Fig. 3.4. *Colpomenia bullosa*, microthallus. **A.** Radial longitudinal section of edge of thallus, plastids shown in selected cells only. **B.** Unangia among paraphyses.

3.6 Petalonia Derbès et Solier

A genus with four species. *Petalonia binghamiae* was previously placed in a monotypic genus *Endarachne* J Agardh. Vinogradova (1973 *fide* Silva *et al.* 1996) merged *Endarachne* with *Petalonia*, and the combination *Petalonia binghamiae* (J. Agardh) Vinogradova is used by some authors (e.g. Kogame *et al.* 1999), but *E. binghamiae* J. Agardh is retained by others (e.g. Parente *et al*. 2003). Feldmann (1949) included *Endarachne* in his newly erected order Scytosiphonales, while Papenfuss (1951) placed it in the Punctariaceae. In the molecular phylogeny of Kogame *et al.* (1999), *Petalonia binghamiae* formed a clade with *Petalonia fascia* and *Scytosiphon tenellus*, and Cho *et al.* (2002) confirmed the close relationship and distinctness of *P. binghamiae* and *P. fascia* using ITS sequences from Korean material. *Petalonia fascia* has been reported from New Zealand (Adams 1994) but microthalli were not found in this study.

3.6.1 Petalonia binghamiae (J. Agardh) Vinogradova

Crustose thallus

Fig. 3.5

Crustose thalli thin and soft, up to 10 mm diameter. On rock, adhering tightly to substrate without rhizoids. Confluent crusts are indistinguishable from one another. Colour mid brown, drying dark brown. On intertidal rocks and in rock pools, usually on exposed beaches.

Thallus: Outline orbicular or irregular, up to 140 μm thick, becoming thicker when forming the basal part of upright thalli. Structure pseudoparenchymatous, organisation dorsiventral, construction dimerous. Distromatic basal layer of branched radiating filaments, laterally adherent, giving rise to straight or slightly curved vertical filaments of 6–10 cells. Vertical filaments loosely adherent and separate easily under pressure.

Cells of basal layer elongate, rectangular or polyhedral 8–12.5 μm diameter and 1–2 diameters long. Cells of vertical filaments rectangular 8–12 μm diameter and 0.6–1.5 diameters long. Epithallial cells domed, sometimes swollen, 8–12 μm long and 1–2 diameters long. Thallus with multicellular hyaline hairs, singly or in groups of 2–4, up to 600 μm long, cells 6–7.5 diameter and 30–70 μm long.

Upright blades develop directly from crustose thalli or small discoid holdfasts, the crust then thickening and forming a holdfast. The crust resembles sterile thalli of *Ralfsia confusa*, but can be separated by the soft thalli and easily separated vertical filaments. Crustose thalli were usually found alongside other thalli with upright blades, often on rocks on exposed beaches near sand.

Type material from Santa Barbara, California.

Discussion

The erect thallus of *Petalonia binghamiae* (J. Agardh) Vinogradova consists one or several unbranched blades, narrowing to a stipe and connected to a common base. The species is reasonably common on exposed coasts of New Zealand. Blades of *P. binghamiae* have a medulla of intertwining filaments, and this character is used to separate the species from *P. fascia*, which has a medulla of isodiametric cells (Adams 1994). However according to Vinogradova (1973 *fide* Silva, Basson & Moe 1996) intermediate forms exist and some specimens of *P. fascia* can have medullary cells that are elongate or filamentous.

The erect thallus was described in detail by Nizamuddin & Farooqui (1968) from material from the Karachi Coast and Arabian Sea.

I observed crustose thalli over several months in shallow pools at Island Bay, Wellington. In some cases erect blades grew from small holdfasts, without the formation of an expansive crust. In other cases blades developed from crusts several millimetres across. These observations are consistent with studies of *Petalonia*/*Endarachne binghamiae* by Parente *et al.* (2003) from the Azores and Brophy & Murray (1989) and Wynne (1969) from California, in that the crustose phase is not separate from the erect phase. ITS-2 sequences obtained from material from the south coast of Wellington are identical to those published by Cho *et al*. (2002) from Korea.

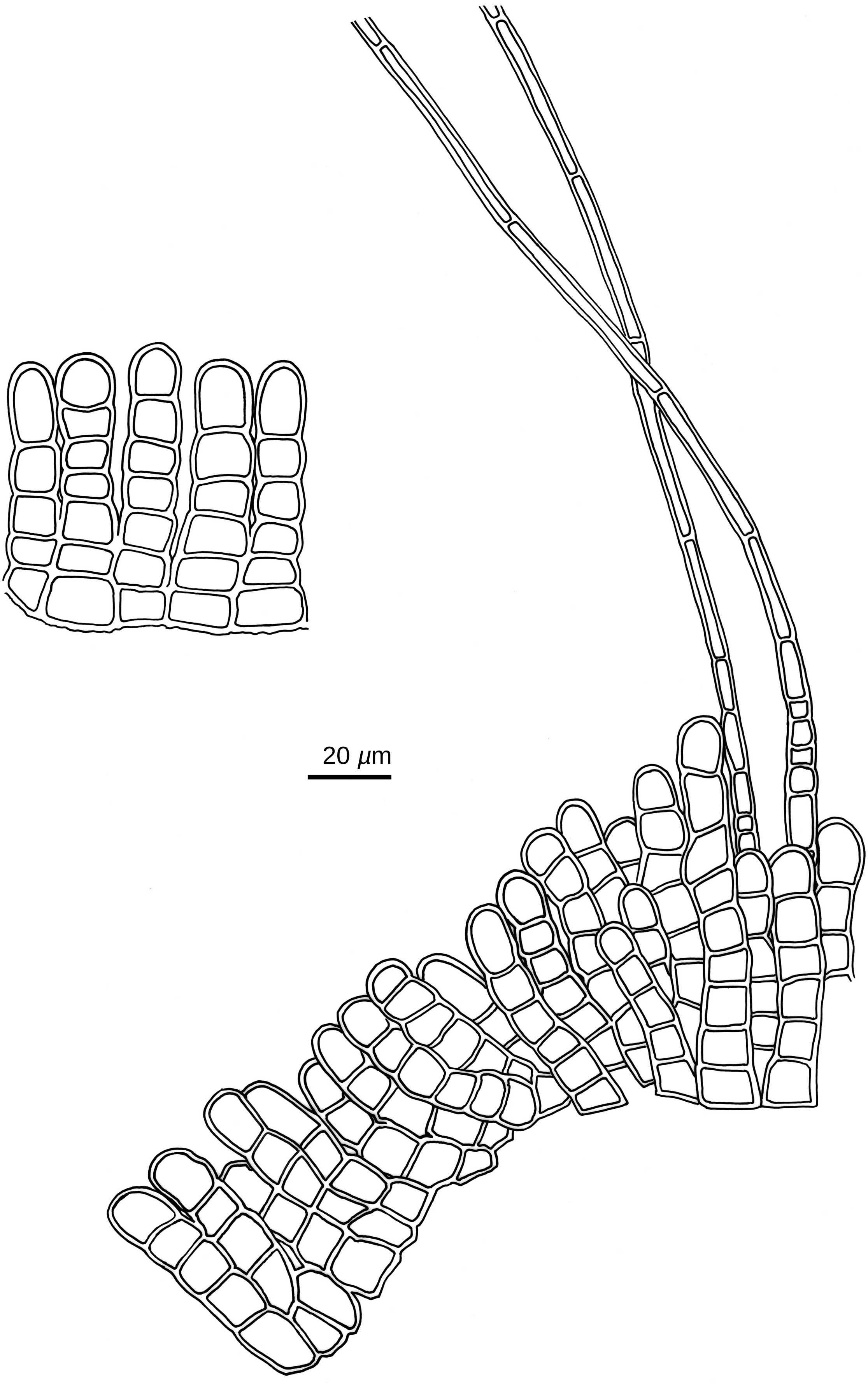

Fig.3.5. *Endarachne binghamiae*. Two radial longitudinal sections of crustose thalli.

3.7 Lithodermataceae Hauck 1883–85 (as Lithodermaceae)

Thallus: Crustose, relatively thin, firm or soft, surface smooth. On rock, basal layer adhering tightly to the substrate with or without rhizoids. Structure pseudoparenchymatous, organization dorsiventral, construction dimerous. Basal layer monostromatic or distromatic of laterally adherent, branched, radiating filaments, giving rise to vertical or slightly curved erect filaments branching at right angles from basal filaments. Hairs present or absent. Plastids one plate-like or several discoid per cell, with or without pyrenoids.

Reproduction: Plurangia and unangia lateral or terminal on erect filaments. Plurangia uniseriate to multiseriate with transverse or oblique cross walls. With or without ascocyst-like paraphyses.

Early treatments of the crustose brown algae included the Lithodermataceae for crustose brown algae with relatively thin thalli, usually terminal plurangia and unangia and several plastids per cell. Later authors (e.g. Hollenberg 1969, Parke & Dixon 1976) included the Lithodermataceae within the Ralfsiaceae. Fletcher (1987) followed Pedersen (1976) in placing the genus *Ralfsia* within the Scytosiphonaceae, and placed crustose brown algae with terminal unangia and plurangia in the Lithodermataceae. He included the genera *Petroderma, Pseudolithoderma, Sorapion* and *Symphocarpus* in the family.

Molecular studies (Tan & Druehl 1993, this study) do not show a close relationship between *Ralfsia* and the Scytosiphonaceae, and the separation of the Ralfsiaceae and the Lithodermataceae appears to be warranted (see Chapter Four).

Pseudolithoderma Svedelius ex Kjellman & Svedelius, 1910: 175

Thallus: Crustose, often confluent, relatively thin, surface smooth, gelatinous or not. Structure pseudoparenchymatous, organization dorsiventral, construction dimerous. Basal layer monostromatic or distromatic of laterally adherent, branched, radiating filaments, giving rise to lateral coherent vertical or slightly curved erect filaments branching at right angles from basal filaments. Basal layer adhering tightly to the substrate without rhizoids. Hairs present or absent. Plastids discoid, several per cell, without pyrenoids.

Reproduction: Plurangia and unangia terminal on erect filaments. Plurangia uniseriate to multiseriate with transverse or oblique cross walls. With or without ascosyst-like paraphyses.

Type species: *Pseudolithoderma extensum* (Crouan *frat*.) S. Lund 1959

Pseudolithoderma was established by Kjellman & Svedelius (1910) based on *Lithoderma fatiscens sensu* Kuckuck (1894). Areschoug (1875) had described *Lithoderma fatiscens*, a species with laterally attached plurangia, whereas Kuckuck's alga had terminal plurangia. Lund (1959) retained this species in *Lithoderma*, while Waern (1949) regards this alga as a species of *Sorapion*. Several species of *Lithoderma* or *Pseudolithoderma* grow on the Swedish coast and there has been a great deal of taxonomic confusion. Ravanko (1970) merged several species on the basis of culture studies, but other authors have continued to recognize these algae as separate species (see Table 3.3).

This genus has seldom been reported outside of the North Atlantic and Mediterranean. Tanaka & Chihara (1981c) reported *Pseudolithoderma subextensum* from Japan and Hollenberg (1969) described *Pseudolithoderma nigra* from California. In the southern hemisphere Womersley (1987) described *Pseudolithoderma australis* from southern Australia and Skottsberg (1921) described a new species, *Lithoderma piliferum*, from the Falkland Islands. This species has terminal plurangia and is consistent with *Pseudolithoderma*.

Within the genus species have been separated by differences in the structure of the plurangia and unangia and by different degrees of lateral adherence of the erect filaments. These characters are summarized in Table 3.3.

One species in New Zealand.

3.7.1 Pseudolithoderma roscoffense Loiseaux 1968

Plate 4; Fig. 3.6

A relatively localized species forming dark patches of thin, confluent crusts among barnacles on the east coast of Northland.

Thallus: Outline irregular, usually confluent. On rock, adhering firmly to substrate without rhizoids. Vegetative crust up to 120 μm thick; soral areas slightly raised up to 140 μm thick. Colour dark brown or nearly black, drying mid-brown. Surface smooth or undulating. structure pseudoparenchymatous, organisation dorsiventral, construction dimerous. Basal layer monostromatic or distromatic of branched, radiating filaments, giving rise to lateral coherent vertical or slightly curved erect filaments branching at right angles from basal filaments. Erect filaments of 6–20 cells.

Basal cells isodiametric or elongate, 5–12.5 µm diameter and 0.7–2.4 diameters long. Cells of vertical filaments isodiametric or flattened, 5–14 µm diameter and 0.5–1.7 diameters long. Epithallial cells covered by a comparatively thick cuticle, 5–10 µm thick.

Hairs absent in specimens examined.

Reproduction: Plurangia grouped in superficial sori without paraphyses, terminal on erect filaments, 6–10 µm diameter and 28–37(–55) µm long, composed of 8–10 locules arranged in 2–4 tiers per filament. Unangia not seen.

Discussion

This alga forms dark patches among barnacles in the low intertidal on low rocky flats in Northland. The species was reported as *Pseudolithoderma sp.* by Williamson (1994) and as *Ralfsia verrucosa* by Jeffs (1985) in ecological studies carried out at Matheson Bay and Echinoderm Reef near Leigh. Williamson (1994) and Williamson & Creese (1996a and 1996b) described the nutritional relationships between the alga and barnacles, the growth of patches of the alga, and the invertebrate fauna associated with the alga.

Williamson (1992) identified the alga as *Pseudolithoderma sp.*, possibly an undescribed species, with its closest affinities to *Pseudolithoderma australis* Womersley 1987. Williamson described phaeophycean hairs originating from the basal layer, but singly rather than in clusters as described by Womersley, and noted that the erect filaments were longer than those of *P. australis* Womersley.

Jeffs (1985) studied the grazing of *Siphonaria*, a pulmonate limpet, on algae in the same area, which he identifies as *Ralfsia verrucosa*. He found that *Siphonaria* ingested large amounts of the alga, but did not digest them and filaments egested by *Siphonaria* regrew in culture. *Siphonaria* avoided areas of high barnacle density, which became refugia for the alga. In the absence of *Siphonaria* the alga was overgrown by diatoms, *Oscillatoria* and other cyanobacteria.

Jeffs' description of the alga is not consistent with *Pseudolithoderma*. He describes a thallus up to 2 mm thick, with a monomerous structure. His micrograph of a section of the alga (Plate 4i) also shows a monomerous thallus, with filaments curving from horizontal to vertical with a wide radius.

I visited Matheson Bay in July 2004. I found patches of brown crustose algae growing among barnacles on low intertidal mudstone flats, as described in studies by Jeffs and Williamson. These patches were composed of two species, a thicker crust consistent with *Ralfsia expansa*, described above, and a thinner crust consistent with *Pseudolithoderma*. Patches of the filamentous cyanobacterium *Oscillatoria* were also interspersed among the crust. *Ralfsia expansa* was distinguishable by the thicker thallus, by a monomerous structure and, in a few specimens, by plurangia with a prominent sterile apical cell. This species appeared to be more common on or among barnacles, whereas *Pseudolithoderma* was usually on mudstone between patches of barnacles. *Pseudolithoderma* was identified by its thin, dimerous thallus and in some areas, by terminal plurangia which lacked a sterile apical cell.

Confusion has arisen due to the intermixing of these two species. It is not easy to distinguish thalli of the two species in the field. Crusts of both species are irregular, patchy and subject to heavy grazing. The basal structures of the crusts were difficult to section from samples taken from the soft mudstone due to overgrowing of different individuals and because of intermeshing of filaments with sand grains. Plate 4(i) in Jeffs (1985) is *Ralfsia expansa,* and references to long erect filaments in Williamson (1992) are probably also *Ralfsia expansa*. The presence of hairs is variable in *R. expansa* and hairs reported by Williamson could belong to either species.

The New Zealand species differs from *P. paradoxum* Sears & Wilce, *P. rosenvingii* (Waern) Lund and *P. australis* Womersley, in having firmly adjoined erect filaments. It resembles *P. subextensum* as described by Tanaka & Chihara (1981c) but they do not state how locules are arranged in the plurangia of their alga. Their illustration (Fig. 2A p. 14) shows plurangia with transverse walls, while *P. subextensum* Waern (1949) has oblique walls.

Pseudolithoderma nigra Hollenberg, *P. adriaticum* (Hauck) Verlaque, and *P. roscoffense* Loiseaux have four tiered plurangia and firmly adjoined filaments, as does the New Zealand species (Fig. 3.6, Plate 4B). The current alga differs from *P. nigra* in having a thinner thallus and lacking ascocysts among the plurangia. I can find no morphological differences between the current alga and *P. roscoffense* Loiseaux, so I refer the alga to this species. Fletcher (1987) regards *P. roscoffense* as possibly conspecific with *P. adriaticum*.

Table 3.2: Characters of species of *Pseudolithoderma*

Species	**Author**	**Location**	**Thallus size and appearance**	**Gelatinous cuticle**	**Filament adherence**	**Unangia**	**Plurangia**	**Paraphyses**
Pseudolithoderma subextensum (Waern) S Lund	Tanaka & Chihara 1981c	Japan	Chestnut brown, often growing amongst species of *Ralfsia* up to 250 μm thick	Present	Firmly adjoined	10 x 20–33 μm Cylindrical	Terminal, 10–14 x 20–40 μm	Ascocyst-like among unangia
Lithoderma subextensum Waern	Waern 1949	Öregrund, Sweden	Chestnut brown, nodulated, probably less than 1 cm diameter, about 100 μm thick	Present	Firmly adjoined	Cylindrical, elongated or with a waist. 20–30 x 8–14 μm	Oblique walled, often with side branches	
P. paradoxum Sears et Wilce	Sears & Wilce 1973	Cape Cod, Massachusetts	Irregular to orbicular dark brown patches, 5–150 mm diameter, hairs absent	Absent	Separable with slight pressure	Elongated cylinders, 10 x 30 μm, terminal	Unknown	absent
L. rosenvingii Waern	Waern 1949	Uppland, Gulf of Bothnia	Light yellow brown, several centimetres diameter, up to 100 μm thick	Present	Separating under light pressure	Elongate, terminal in groups of four surrounded by gelatinous outer wall		
P. nigra Hollenberg	Hollenberg 1969	Cape Cod, Massachusetts	2–10 cm diameter, 300–500(–800) μm thick, margins dark brown, mature thalli nearly black	Absent	Firmly adjoined	unknown	Terminal, 30–50(–70) μm x 8–14 μm. In tiers of four cells	Numerous, scattered among plurangia
L. extensum (Crouan) Hamel	Hamel 1931–39	France	Blackish brown, hairs absent	Present		Nearly spherical, terminal on filaments	Terminal, cylindrical, with 8 locules and oblique walls	

Table 3.2: Continued.

Species	**Author**	**Location**	**Thallus size and appearance**	**Gelatinous cuticle**	**Filament adherence**	**Unangia**	**Plurangia**	**Paraphyses**
P. australis Womersley	Womersley 1987	South Australia	Medium-dark brown	Absent	Separating moderately readily under pressure	Cylindrical to clavate 10–16 x 30–50 μm	Uniseriate, 5–8 loculi, oblong ovoid, 12–16 x 22–30 μm	none
P. roscoffensis (=roscoffense)	Loiseaux 1968	Roscoff, Finistère, France	1–3 cm diameter, yellow brown, clusters of hairs in pits	Present	Firmly adjoined	unknown	Terminal, 20–40 x 12–15 μm in four tiers of 3–10 locules	
P. roscoffensis	Fletcher 1987	Great Britain	200 μm thick, thin and light brown to moderately thick and black	Present	Firmly adjoined	Not seen	11–18 x 28–45 μm, transverse walled, usually four tiered	
P. adriaticum (Hauck) Verlaque	Verlaque 1988	Corsica		Present (Fig. 22, p. 190)	Firmly adjoined		12–16.5 (–18) μm diameter, 20–40 μm long, locules in tiers of four, divided transversely	

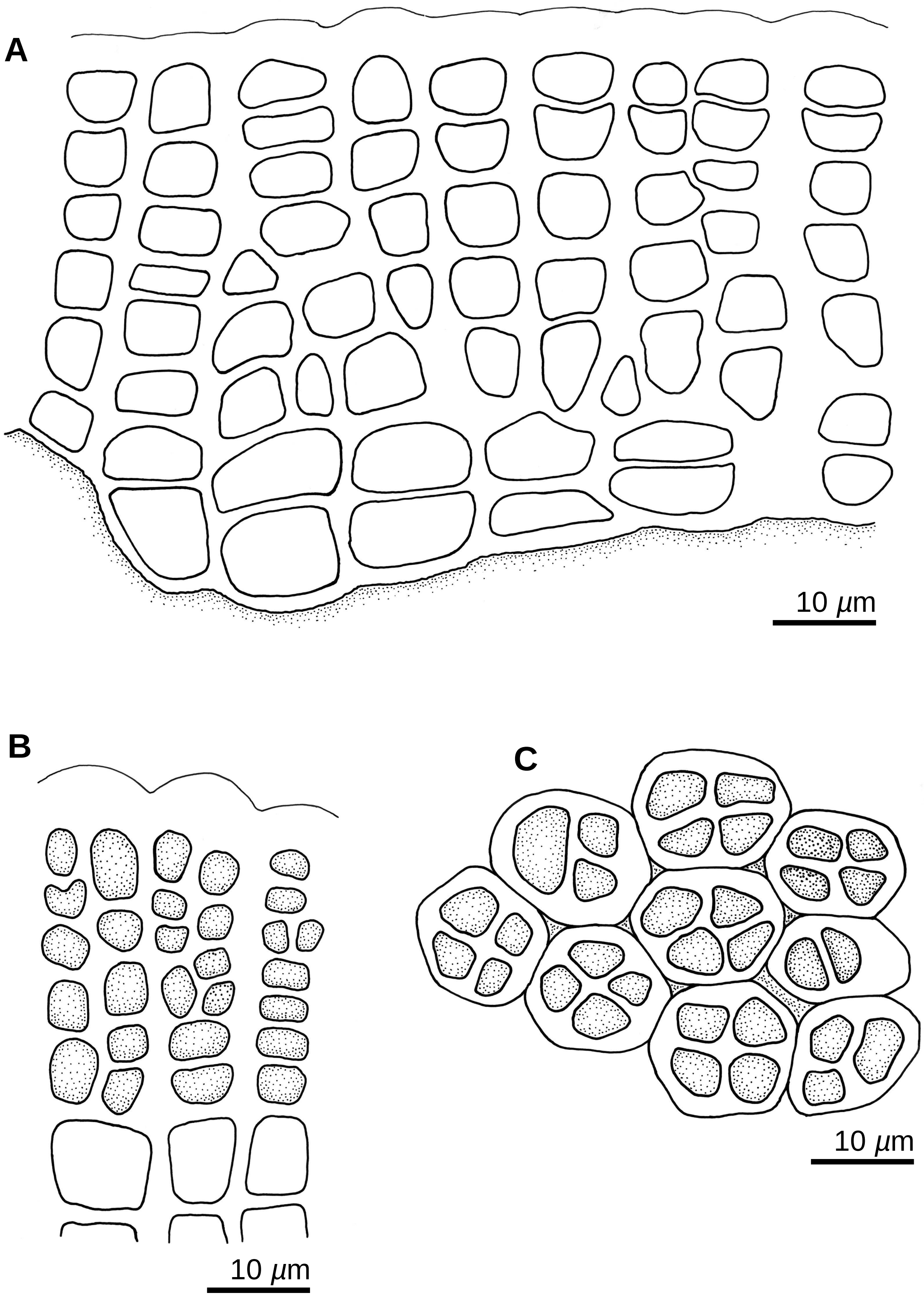

Fig. 3.6. *Pseudolithoderma roscoffense.* **A.** Vegetative thallus. **B.** Radial longitudinal section of plurangia. **C.** Quadripartite plurangia in surface view.

3.8 Diplura Hollenberg 1969 incertae sedis

Thallus: Crustose, outline orbicular or irregular. Young thalli firmly attached to substrate without rhizoids. Structure pseudoparenchymatous, organisation dorsiventral, construction monomerous or dimerous. Basal layer of laterally adherent branched radiating filaments giving rise to erect filaments. Erect filaments sparsely branched, more or less laterally adherent, gelatinous or not. Basal layer two or more cells thick. Cells with several small discoid plastids without obvious pyrenoids. Hairs present or absent.

Reproduction: Plurangia in expansive sori. Plurangia cylindrical, usually uniseriate in pairs terminal on erect filaments without paraphyses, with a single sterile terminal cell. Unangia unknown and probably lacking.

Type species: *Diplura simulans* from Orange County, California.

The genus was created by Hollenberg (1969) based on *Diplura simulans*[3]. A second species, *D. simplex,* was described from Japan by Tanaka & Chihara (1981b).

Diplura and *Endoplura* Hollenberg (1969) differ from other Ralfsiaceae in having several discoid plastids per cell. Hollenberg placed *Diplura* in the Ralfsiaceae based on the structure of the plurangia but rDNA sequences from this study do not support this relationship (see Chapter Four). The genus should possibly be placed in the Lithodermataceae, giving more weight to plastid number in the circumscription of families of crustose brown algae.

One species in New Zealand.

3.8.1 Diplura sp. "australis"

Plates 5 & 6; Fig. 3.7

A common species forming large confluent patches in the low to mid intertidal. Thalli usually 20–50 mm or more in diameter, individual thalli difficult to distinguish where confluent or overgrowing one another. Young thalli firmly attached to substrate without rhizoids, older thalli often loose, crumbly and detaching from substrate. Colour mid-brown to olive-brown or chestnut-brown, edges and young areas pale. Basal layer reddish to rust coloured. Drying to

---

[3] Hollenberg (1969) published his description under the name *Diplura similans*. This appears to be an orthographic error as he referred to the species as *Diplura simulans* in his captions and abstract. The epithet "*simulans*" is used by Abbott & Hollenberg (1976) and Tanaka & Chihara (1981b).

dark brown or reddish brown. Young thalli coriaceous with low radial or concentric ridges, older thalli wrinkled, verrucose and brittle.

Thallus: outline orbicular or irregular, 300–400(–800) μm thick, sori slightly raised. Structure pseudoparenchymatous, organization dorsiventral, construction monomerous. Basal layer of laterally adherent branched radiating filaments branching acutely to give rise to erect filaments. Erect filaments of 15–30(–36) cells, curving assurgently to vertical, laterally coherent, occasionally branching.

Basal layer of two or more filaments, cells either elongate and rectangular or irregular polyhedrons, 7–15 μm diameter and 1–3(–5.5) diameters long. Erect filaments of rectangular cells, 7–15(–18) μm diameter and 0.7–3 diameters long. Epithallial cells dome shaped 5–13 μm wide and 0.75–2 diameters long, with thin cuticle. Cells with refractive bodies, lower cells often filled with reddish substance. Several small discoid plastids without obvious pyrenoids. Plastids crowded in upper part of upper cells of erect filaments and obscured by physodes, scattered in lower cells. Hairs absent.

Reproduction: Plurangia in expansive sori in winter. Sori paler than underlying crust and extending over most of the thallus. Plurangia cylindrical, in pairs, terminal on erect filaments without paraphyses, 5–7.5 μm diameter and 25–50 μm long, without paraphyses. Arrangement of locules usually uniseriate, with 6–8 locules in each plurangium, and a single pale coloured, domed cap cell 10–15 μm long. Plurangia covered by a thin cuticle that peels away with cap cells during spore release. Unangia absent.

On rock in intertidal, usually on firmly attached rock, rarely on cobbles, on sheltered and moderately exposed coasts. North Island, South Island, covering large areas on the south coast of Wellington and at Kaikoura. Often with endophycotic ascomycete forming voids in upper thallus surrounded by thick walled cells filled with a reddish substance, visible as dark spots in the thallus.

Discussion

The New Zealand species is very similar in appearance to *Ralfsia verrucosa* (Areschoug) Agardh, a species described from New Zealand by Lindauer *et al.* (1961). *Diplura* differs from *Ralfsia* in having several discoid plastids in each cell (Plate 5B) and in the absence of unangia, whereas *Ralfsia* cells have a single plastid and bear unangia.

Diplura sp. “australis” resembles other species of *Diplura* in having paired plurangia terminal on each vegetative filament in expansive sori, several discoid plastids in each cell and lacking unangia (Fig. 3.7, Plate 6B). It differs in having upright filaments that are strongly laterally adherent, in lacking hair pits and in being less gelatinous.

Filaments of *Diplura sp. “australis”* separate only with considerable pressure, whereas *D. simulans* has filaments that are easily separated, and *D. simplex* has filaments that are “less easily separated” (Tanaka & Chihara 1981b). Tanaka & Chihara amended Hollenberg’s generic description to include species with laterally adherent filaments. Lateral coherence of filaments is variable in other genera of crustose brown algae, including *Pseudolithoderma* and *Ralfsia* and in microthalli of some genera of the Scytosiphonaceae, so this character should not preclude placing the New Zealand alga in *Diplura*.

The New Zealand species shares some characters with *Ralfsia australis*, described by Skottsberg (1921) from the Falkland Islands. Skottsberg rather tentatively distinguished the species from *Ralfsia verrucosa* by the lack of hairs. He was unable to find unangia and did not describe the plastids. It is not clear if this species has paired plurangia; Skottsberg did not describe the arrangement of plurangia on the filaments, but provided a small illustration of plurangia of *R. australis*, showing some filaments bearing single plurangia, and others with paired plurangia. *R. australis* is usually regarded as a morph of *R. verrucosa,* but the name has recently been applied to specimens from Macquarie Island by Ricker (1987) and from Antarctica by Wiencke & Clayton (2002). Ricker is cautious in placing his alga in *Ralfsia*. His alga is infertile with a thin thallus (up to 120 μm), pale brown or orange-brown with sometimes overlapping lobes and a mostly colourless basal layer. His micrographs show filaments of rather loosely packed, rounded cells, unlike those of *Ralfsia* or *Diplura*. Wiencke & Clayton reported this species from McMurdo Sound and the Antarctic Peninsula, but without descriptions.

This is the first description of *Diplura* from the southern hemisphere although Womersley (1987 p. 65) collected one specimen from South Australia that “may be referable to *Diplura*.”

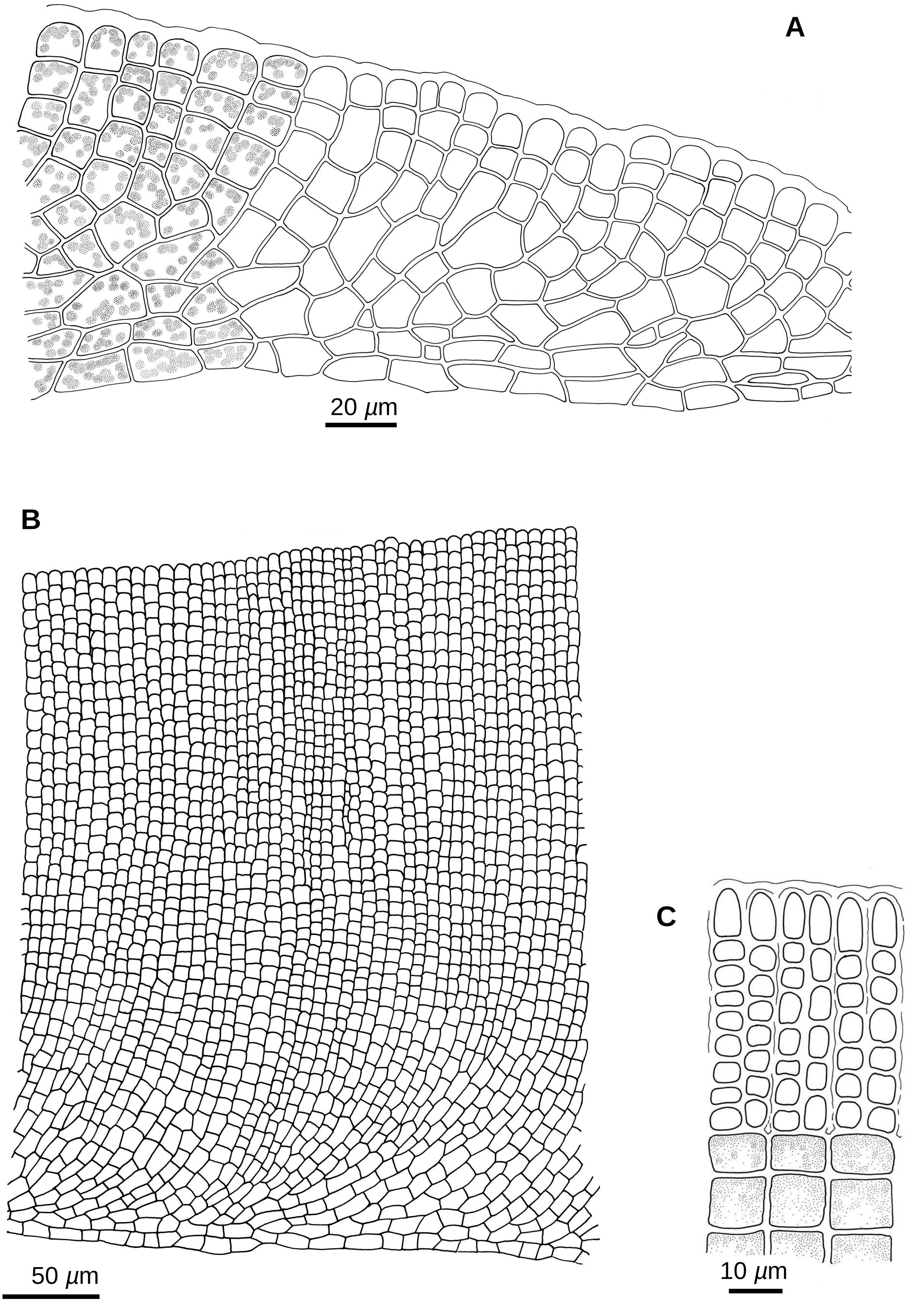

Fig. 3.7 *Diplura sp.* **A.** Radial longitudinal section of edge of thallus, plastids shown in some cells only. **B.** Radial longitudinal section of older thallus. **C.** Plurangia.

3.9 Ralfsiaceae Farlow 1881

Thallus: Crustose, orbicular when young, becoming irregular or confluent, surface smooth, bullate, verrucose or with concentric or radial ridges. Basal layer pseudoparenchymatous, erect filaments pseudoparenchymatous or free, branched or unbranched, organization dorsiventral or bilateral, construction monomerous or dimerous. Basal layer of branched radiating filaments. Attached to substrate with or without rhizoids. Plastids one per cell, plate-like without obvious pyrenoid. Hairs absent, single or in tufts.

Reproduction: Unangia and plurangia on the same or different thalli. Unangia in discrete or expansive sori. Unangia sessile and lateral to paraphysis or terminal on a stalk. Paraphysis differentiated from the vegetative filaments, multicellular, clavate. Plurangia terminal or intercalary with one or more sterile terminal cells.

3.10 Ralfsia Berkeley in Smith & Sowerby 1843 Suppl. III.

Type species: *Ralfsia deusta* (C. Agardh) Berkeley (=*Ralfsia fungiformis* (Gunnerus) Setchell & Gardner 1924)

Thallus: Outline orbicular when young, becoming irregular and confluent. Encrusting, surface smooth, bullate, verrucose or radial or concentric ridges. Structure pseudoparenchymatous, organisation dorsiventral, edges of thallus sometimes bilateral, construction monomerous. Basal layer of branched radiating filaments. Erect filaments branching from basal layer and either curving immediately to vertical or radially assurgent or forming a central core of horizontal filaments, occasionally branched, laterally adherent. Attached to substrate with or without rhizoids. Plastids one per cell, plate-like without obvious pyrenoid. Hairs absent, single or in tufts.

Reproduction: Unangia and plurangia on the same or different thalli. Unangia in discrete or expansive, slightly raised and gelatinous sori. Unangia sessile and lateral to paraphysis or terminal on a short stalk. Paraphysis differentiated from the vegetative filaments, multicellular, clavate. Plurangia superficial in slightly raised gelatinous sori, cylindrical uniseriate to biseriate with one or more sterile terminal cells. Plurangia closely packed without paraphyses, covered by a cuticle.

For reasons outlined in the introduction, I have not followed Batters (1890, 1893) division of *Ralfsia* into sub-genera *Stragularia* and *Eu-Ralfsia.* The nearly dimerous thallus and expansive sori of *R. confusa* Hollenberg would place it in *Stragularia* if this designation is not taken to imply a close relationship with the Scytosiphonacae, but as recent workers have linked *Stragularia* with microthalli of the Scytosiphonaceae (Wynne 1969, Fletcher 1987), and molecular information do not show a close relationship between the Ralfsiaceae and Scytosiphonaceae (Tan & Druehl 1994, Chapter Four of this study) this epithet is best avoided.

The arrangement of the locules of the plurangia is the most definitive character for distinguishing species of the New Zealand species of *Ralfsia* with the exception of *Ralfsia expansa* and *Ralfsia confusa*, which have very similar plurangia. However, the two species can be distinguished by the unangial sori, which are small and discrete in *Ralfsia expansa* and cover most of the thallus in *Ralfsia confusa*, and by the vegetative morphology of the thallus: *Ralfsia expansa* has a larger, thicker pale thallus while *Ralfsia confusa* has a small, thin dark thallus.

Key to the New Zealand species of *Ralfsia*

1. Plurangia and unangia in discrete sori.……………………………….…..*R. expansa*
1. Plurangia and unangia in expansive sori ………………………..………2
2. Plurangia biseriate with colourless sterile terminal cell; thallus smooth more than 225 μm thick……………………………………………………………….…..*R. sp.* “smooth”
2. Plurangia uniseriate or partially biseriate, sterile apical cell dark;
thallus less than 250 μm thick……….....…………………..……………..…. *R. confusa*

3.10.1 Ralfsia expansa (J. Agardh) J. Agardh

Plate 7 (A–C) & 8; Figs. 3.8–3.9.

A distinctive pale crust, usually 15–30 mm in diameter but at times 40 mm or more. Solitary or in groups, confluent adjoining thalli form a ridge, occasionally overgrowing one another. Orbicular crusts are identifiable in the field by the pale coloured outer thallus and reddish eroded centre. I have also found populations of this species that form a dark, irregular confluent crust among barnacles at Paekakariki on the Kapiti Coast and at Matheson Bay in Northland, the latter growing intermixed with *Pseudolithoderma*. Individual thalli cannot be distinguished in these populations, which probably result from grazing and regrowth.

Colour light brown or olive brown to fawn with very pale edges and pale yellow radial ridges, center often abraded to reveal the reddish to rust coloured basal layer, resulting in concentric bands of colour. Drying dark brown or reddish brown. Surface with pronounced radial ridges even in very young crusts. Young crusts can be peeled intact from rock, older crusts are crumbly with the centre often detaching from the substrate

Thallus: Outline orbicular, 300–400(–1000) μm thick. Young thalli attached to substrate without rhizoids, rhizoids prolific in older thalli especially where detaching from substrate. Structure pseudoparenchymatous, organisation dorsiventral, edges of crust sometimes bilateral, construction monomerous. Basal layer of branched radiating filaments. Erect filaments of 15–35 cells, branching acutely from basal layer and curving assurgently to vertical, occasionally branched, laterally adherent. Outer parts of some thalli with a medullary layer of several horizontal filaments curving both upward and downward forming a bilaterally symmetrical thallus. Rhizoids straight or sinuous up to 600 μm long and 10–15 μm diameter.

Basal cells irregular polyhedrals, 6–15 μm diameter and 1.5–3(–6) diameters long. Cells of erect filaments 5–13 μm diameter and 1–3 diameters long; lower cells rectangular, upper cells rounded. Epithallial cells 5–10(–12.5) μm wide and 1–2.5 diameters long. Cells with refractive bodies; lower cells often filled with reddish substance. Single parietal plastid in upper part of each cell without obvious pyrenoid.

Multicellular hyaline hairs absent to frequent, solitary or in tufts from scattered pits. Where present hairs up to 300 μm long with cells 4–6.5 μm diameter and 10–45(–55) μm long.

Reproduction: Unangia and plurangia on the same or different thalli. Unangia in slightly raised sori, gelatinous to pale yellow, drying matt, slightly raised in radial ridges or irregular patches with numerous clavate paraphyses. Sori usually less than 1 mm in diameter, but sometimes up to 3 mm. Unangia usually sessile on a terminal vegetative cell and lateral to a single paraphysis; rarely terminal on a single celled stalk, the stalk arising lateral to a paraphysis. Unangia pyriform to ovoid 22.5–30 μm diameter and 55–90(–105) μm long. Paraphyses clavate, 100–130 μm long, of 8–12 cells; apical cell swollen or rectangular, 7.5–12 μm diameter and 9–20 μm long; lower cells rectangular or barrel shaped, 3–8 μm diameter and 10–25 μm long; basal cells 3–6 μm diameter and 6–12.5 μm long.

Plurangia cylindrical, in small scattered sori without paraphyses, locules usually uniseriate, sometimes partially biseriate, 40–100(–112) μm long and 5–7 μm in diameter, with 8–10(–14) locules and a single dark coloured, slightly swollen, elongate domed cap cell 10–15 μm long. Covered by a cuticle.

This species is often found on soft substrates, such as shells of *Turbo* (Plate 7B), mussels and limpets, and also on concrete and PVC pipe. When growing on rock, it is often attached to and overgrowing other crusts. An epiphytic filamentous rhodophyte, probably *Erythrotrichia,* is common on all but very young thalli, often attached in hair pits and sometimes sufficiently abundant to give a reddish colour to the crust. *Ralfsia expansa* is usually found in low intertidal rock pools, on low intertidal rocks or shells or in the shallow subtidal, but I have found crusts growing in the upper intertidal on rock and on barnacles on very exposed rocks at Punakaiki on the West Coast of the South Island.

Distribution: North Island, South Island, Chatham Islands. This species is found on most coasts of New Zealand, although never in as large masses as in *Diplura*. The species is also found on the Chatham Islands (WELT A026471).

Discussion

This alga is consistent with *Eu-Ralfsia* Batters in having a crustose, monomerous thallus with unangia and plurangia in small discrete sori. It has characters in common with *Ralfsia pacifica* and *Ralfsia expansa,* and one herbarium specimen has been identified as *Ralfsia clavata*. The most distinctive character – the pale colour of orbicular crusts – has not been reported in other species of *Ralfsia*, but as some older or grazed and irregular crusts can be quite dark brown, this character should be considered variable. I have tentatively referred this alga to *Ralfsia expansa* (J. Agardh) J. Agardh largely due to the close agreement of New Zealand material with Sartoni & Boddi’s (1989) description of *Ralfsia expansa* from the Mediterranean material. Descriptions of this widely reported species vary and different authors have employed different diagnostic characters in separating *R. expansa* from related species, especially *R. verrucosa* and *R. hancockii* so I will discuss these characters in some detail.

A herbarium specimen of this species from Island Bay (WELT A18821) was identified by M. N. Clayton as *Ralfsia clavata*, presumably on the basis of the strongly clavate paraphyses. *Ralfsia clavata* (Harvey) P.L. Crouan & H.M. Crouan 1852 is based on *Myrionema clavata* described by Harvey in Hooker (1833) from British material. Fletcher (1987) transferred the species to the genus *Stragularia. Stragularia clavata* has been identified as the crustose phase of *Petalonia fascia* (e.g. Wynne 1969, Edelstein *et al*. 1970a, Yoneshigue-Valentin & Pupo 1994).

Fletcher’s (1987) description of *Stragularia clavata* differs from the current species in three respects: (1) Fletcher describes a thin (up to 180 μm) thallus of erect filaments arising at right angles from the basal layer and with a single terminal apical cell at the periphery of the thallus. The New Zealand alga has erect filaments branching from the basal layer, at first nearly prostrate and curving assurgently to vertical, forming a relatively thick thallus (up to 1mm); (2) Fletcher describes short plurilocular sporangia, up to 20 μm long with up to 7 locules and no terminal sterile cell. The New Zealand alga has long plurilocular sporangia, of up to 14 locules with a distinctive dark-coloured, elongate cap cell (Plate 8A, Fig. 3.9A); (3) The New Zealand alga has unilocular sori with strongly clavate paraphyses with very broad upper cells and thinner, elongate lower cells (Plate 8B, Fig. 3.9B). Fletcher describes and illustrates "elongate-clavate to elongate cylindrical" paraphyses with elongate lower cells but not markedly broadening at the tips, although the paraphyses on the New Zealand specimens do resemble paraphyses photographed from cultured crusts of *R. clavata* by Edelstein *et al*. (1970, Fig.7, Plate II). Morphological information is suspect, as *Stragularia* crusts have often been described from culture and may differ from specimens from nature, but I have examined many specimens of this alga, including very small crusts, presumably at an early stage of growth, and the differences from descriptions of *S. clavata* are consistent.

Aside from the pale colour, this alga is similar to *Ralfsia pacifica* Hollenberg (*in* Smith 1944). Both entities have large, monomerous thalli, usually sessile unangia and similar sized unangia and paraphyses. Hollenberg (1969) describes the plurangia of *R. pacifica* as regularly uniseriate, and regards this as a diagnostic character to separate the species from *R. verrucosa*. However his illustration (Hollenberg 1969, Fig.17, p. 294) shows several plurangia, some that are partly biseriate. Hollenberg also describes *R. pacifica* as having "prominent radial or concentric growth lines or ridges," a character shared with the New Zealand species. However photographs of *R. pacifica* published on the "Algaebase" website (www.algaebase.org, Guiry *et al.* 2005) show smooth, dark orbicular thalli, quite unlike the local species. Hollenberg also notes that thin specimens of *R. pacifica* resemble *R. confusa* Hollenberg. The New Zealand alga does not resemble *R. confusa* and the two entities are easily distinguishable. Womersley (1987) considers *R. pacifica* as probably not distinct from *Ralfsia verrucosa* as the regularly uniseriate state of the plurangia is doubtful.

Characters of the New Zealand species are consistent with Sartoni & Boddi's (1989) description of *Ralfsia expansa* (J. Agardh) J. Agardh. Both entities have partially biseriate plurilocular sporangia with a single, prominent and dark coloured cap cell (Fig. 3.9A) and, at least in some specimens, a thallus with a cortical layer of smaller cells above a medullary region of large cells. *Ralfsia expansa* has been widely reported from warmer seas (e.g. Dixit 1970, Littler & Littler 2000, Setchell 1926, Stephenson 1944, Wynne 1995, Price *et al.* 1978). However, few reports include detailed descriptions and many reports may be based on misidentifications of *R. verrucosa* (Stegenga *et al*. 1997), *R. hancockii* (León-Alvarez & González-González 2003) or other species. It is possible that a number of species exist within the *R. expansa* group.

The type specimen of *Ralfsia expansa* (J. Agardh) J. Agardh was collected by Liebman at Veracruz on the Mexican Atlantic coast. It was described by Agardh, first as *Myrionema expansum* (Agardh 1847) then renamed *Ralfsia expansa* (Agardh 1848). This specimen is not fertile and Agardh's descriptions are brief. Weber-van Bosse (1913) illustrated a specimen from the former Dutch East Indies and Børgeson (1914) provided a thorough description based on material from around St. Thomas in the former Danish West Indies. More recently Sartoni & Boddi (1989) published a description based on Mediterranean material, Rull Lluch (2002) described Namibian material and León-Alvarez & González-González (2003) published a description based on material collected from the same area of Mexico as the type specimen. These descriptions are summarised in Table 3.2, along with descriptions of similar algae from Japan, Brazil and India.

Børgeson's (1914) description is based on material from the same general area as the type material. He describes the sterile thallus as similar to *Ralfsia verrucosa* and agreed with Weber-van Bosse (1913) that *Ralfsia expansa* has a tendency to develop a bilaterally symmetrical thallus. Both authors regard this character as somewhat variable but Weber van Bosse used it to distinguish the species from *Ralfsia verrucosa*, while Børgeson regarded the longer, nearly clavate unangia and differences in the sterile terminal cell of the plurangia as diagnostic characters for *Ralfsia expansa*.

Some authors continued to use the bilaterally symmetrical thallus to distinguish *Ralfsia expansa*. Tanaka & Chihara (1980b) referred Japanese material to *Ralfsia expansa* using the symmetry of the thallus, the stalk cells of the unangia and the arrangement of plurangia as diagnostic characters. On the other hand Hollenberg (1968) and León-Alvarez & González-González (2003) place little value on the symmetry of the thallus, finding it variable in this and other species of *Ralfsia*. Sartoni & Boddi (1989) agree that bilateral thalli are present in *Ralfsia verrucosa*, but only where thalli are overgrowing irregularities in the substrate. They state that filaments of *R. verrucosa* are not "organised into a multiaxial growing region as seen in the marginal zone of *Ralfsia expansa*."

A second vegetative character used to distinguish *Ralfsia expansa* is the presence of a cortical layer of small cells that are distinct from the medulla of larger, elongate cells. León-Alvarez & González-González (2003) described *R. expansa* based on material from Veracruz in

Mexico, the same area as the type specimen. They found this character was shared with *Ralfsia hancockii* Dawson. A distinct cortical layer is present in some specimens of the New Zealand algae, while in others the cells grade from large to small, a character regarded by Sartoni & Boddi (1989) as typical of *R. verrucosa*. There may be a seasonal variation in this character. New Zealand material agrees in this regard to drawings of thalli in Sartoni & Boddi (1989, Fig. 5, p. 153 and Fig. 6, p. 154).

Rhizoids are prolific on some specimens from New Zealand. Rhizoids are also present in drawings of *R. expansa* by Børgeson (1914) and Weber-van Bosse (1913) and in descriptions by other authors (see Table 3.1), whereas *Ralfsia verrucosa* is “usually without rhizoids” according to Fletcher (1987) and lacks rhizoids in Womersley’s (1987) description.

Børgesen (1914, 1924), Sartoni & Boddi (1989) and Balakrishnan & Kinkar (1981, Figs. 130–131) describe *Ralfsia expansa* as having unangia either sessile on the vegetative filaments or with a single pedicel between the unangia and the vegetative cell that bears the paraphysis. Børgesen considered the single pedicel of the unangia a diagnostic character for the species in his original description, but revised his opinion in his account of Easter Island material (1924) in which he regards the presence of a pedicel as a variable character in the genus *Ralfsia*. He points out that a pedicel is present on unangia of *R. verrucosa* in descriptions of Harvey (1846), but not in those of Kuckuck (1894) or by Reinke (1889). Other authors describe *Ralfsia verrucosa* as having sessile unangia (Womersley 1987, Tanaka & Chihara 1980b) or up to three stalk cells (0–2 in Fletcher 1987). The New Zealand alga usually has sessile unangia, but occasionally unangia are borne on a single pedicel (Fig. 3.9A). León-Alvarez & González-González (2003) regard Tanaka & Chihara’s algae as *R. hancockii* based on the presence of several (usually three to seven) stalk cells supporting each unangium (the Hawaiian crust reported as *Ralfsia expansa* by Abbott & Huisman (2004) also has 2–4 stalk cells and is probably *R. hancockii).*

Sartoni & Boddi (1989) and Børgeson (1914) describe *R. expansa* as having more elongate unangia than *R. verrucosa* (see Table 3.2). The range of reported lengths is slightly higher than those reported for *Ralfsia verrucosa* (see Table 3.1). Unangia from New Zealand material, 55–105 μm long and 22.5–30 μm diameter (Fig. 3.9B), are within the range reported for either species.

Table 3.3. Dimensions of unangia reported for *Ralfsia verrucosa*

Author	Location	Unangia dimensions	
		Length	Width
Feldmann 1937	France	45–55 (or 80–90)[4] μm	30–37 (or 30) μm
Hamel 1931–39	France	60–100 μm	20–35 μm
Loiseaux 1968	France	60–100 μm	20–35 μm
Fletcher 1987	Britain	60–105 μm	15–37 μm
Tanaka & Chihara 1980b	Japan	50–60 (–72) μm	20–35 μm
Womersley 1987	South Australia	70–90 μm	18–26 μm

Børgeson regarded the sterile terminal cell in the plurangia of *R. expansa* as differing from that of *R. verrucosa*. His illustration does not show a prominent terminal plurangial cell. He refers to Kuckuck's (1894) description of plurangia of *Ralfsia verrucosa* with a colourless, sterile terminal cell. This is problematic as other authors (e.g. Hamel 1931–39, Loiseaux 1968, Fletcher 1987) describe plurangia of *Ralfsia verrucosa* as having a dark or coloured terminal cell, and other authors (e.g. Sartoni & Boddi 1989) have described *Ralfsia expansa* as having a prominent dark-coloured terminal plurangial cell. In New Zealand material (Plate 8A) the terminal cell is elongated, dark-coloured and more prominent than cells in micrographs of *Ralfsia verrucosa* in Fletcher (1978, Fig. 24, p. 388) and drawings by Jaasund (1964) from Norwegian material.

The plurangia of New Zealand specimens are nearly identical to those illustrated by Sartoni & Boddi (1989), who regard the prominence of the sterile terminal cell and the partially biseriate arrangement of the locules as characters which distinguish *Ralfsia expansa* from *Ralfsia verrucosa*, with plurangia of the latter only rarely biseriate. However, Hollenberg separated *Ralfsia pacifica* from *Ralfsia verrucosa* partly on the basis of *R. pacifica* having regularly uniseriate plurangia. Loiseaux (1968) described *Ralfsia verrucosa* as usually having two plurangia terminal on each vegetative cell, but this character has not been reported by other authors. The New Zealand species has a single plurangium (Fig. 3.9A) on each terminal cell of the vegetative filament, rather than 1–2 in most descriptions, but it is not clear whether these descriptions refer to two separate plurangia on a single terminal vegetative cell or to a single biseriate plurangium.

---

[4] Feldmann reported two forms of this species, one with short unangia, and the other with unangia 80–90 X 30 μm.

In New Zealand specimens, orbicular crusts can be easily identified in the field by the colour and the presence of radial ridges (Plate 7A–C), which are evident even in young specimens. *Ralfsia expansa* is usually described as dark or chocolate brown (Clayton & King, 1981). *Ralfsia expansa* is reported to coexist with *Ralfsia verrucosa* in South Africa by Kaehler & Froneman (1999) who state that *R. expansa* can be distinguished from *R. verrucosa* in the field by its darker colour.

Ralfsia expansa has been previously reported from the Pacific, in Fiji by Garbary *et al.* (1991), Tahiti by Setchell (1926), Samoa by Skelton & South (2002), the Marshall Islands by Dawson (1956), the Caroline Islands by Trono (1969), French Polynesia by Payri & Meinesz, (1985), and Queensland, Australia by Cribb (1996). The species has not been previously reported from New Zealand. Referring this alga to *Ralfsia expansa* would give this species a very wide distribution, from the Mediterranean and Caribbean, through the South Atlantic (John *et al.* 2004), India, and the South Pacific, with reports from the North Pacific probably *Ralfsia hancockii*.

Referring this species to *Ralfsia expansa* rather then *R. verrucosa* removes *R. verrucosa* from the New Zealand flora, as no other species resemble *Eu-Ralfsia*. Lindauer (1947) reported that *Ralfsia verrucosa* was “very common in several forms on smooth boulders on the coast of S. Taranaki.” It is possible that this observation and the description in Lindauer *et al.* (1961) is based on more than one species as several distinct species of crustose brown algae are present in South Taranaki. Lindauer *et al*. report characters consistent with *R. verrucosa* but also with other Ralfsiaceae. Their figures appear to be redrawn from previously published descriptions of *Ralfsia verrucosa* from the northern hemisphere (Fig. 38 2 & 3 from Kylin 1947, Fig. 38A–B, p. 44 and Fig. 38 4 & 5 from Hamel 1931–39, Fig. 26A–B, p. 109) and not drawn from New Zealand material. Other reports of *Ralfsia verrucosa* from New Zealand (e.g. Dellow & Cassie (1955), South & Adams (1976)) do not mention diagnostic characters. They are probably misidentifications of *Diplura* or other *Ralfsia* species.

Table 3.4. Morphological and reproductive characters of *Ralfsia expansa* (*n.i.*= no information)

Author		León-Alvarez & González-González 2003	Tórgo 1963	Sartoni & Boddi 1989	Børgesen 1914	Tanaka & Chihara 1980b[5]	Rull Lluch 2002	Balakrishnan & Kinkar 1981
Location		Veracruz, Mexican Atlantic Coast	Sao Paulo State, Brazil	Alboran Sea, Mediterranean Spain	Danish West Indies	Japan	Namibia	Visakhapatnam, India
Appearence	Colour	Dark brown	Yellow brown to dark brown	Dark brown	Dark brown	Light brown-reddish brown	Dark brown	Dark brown
	Surface	Rugose, coriaceous, no growth lines	Irregular	Smooth when young, later uneven or bullate	Even and smooth when young, older thalli uneven, bullate, folded	Smooth when young, later uneven	*n.i.*	Irregular, older thalli folded with concentric striations
Thallus diameter		*n.i.*	30 mm	30–40 mm	*n.i.*	40 mm or more	*n.i.*	*n.i.*
Thallus thickeness		180–252 μm (315–450 μm at sori)	Variable	300–700 μm	*n.i.*	200–800 (1100) μm	Up to 1400 μm	*n.i.*
Rhizoids		Irregularly distributed in isolated areas	Large number	abundant	few, short (Fig. 147, p .190)	yes	Lower medullary filaments free sinuous like rhizoids	Well developed
Thallus construction		Unilateral, bilateral in areas of irregular substrate	Bilateral	More or less bilateral	Often bilateral	Bilateral	Bilateral	Upwardly curving filaments
Hairs		Single hyaline hairs in pits	*n.i.*	Hairs in infrequent tufts	Abundant groups of hairs	Hairs in tufts, frequent	n.i.	Abundant, in groups
Cortical layer		Upper layer of 3–5 small cells	Upper layer of 4–5 small cells	Layer of small cells, 40–120 μm deep	Upper layer of small cells (Fig. 146–7, p. 190)	Upper layer of small cells 50–70 μm deep	Upper cells 4–8 μm diameter, thicker in below	Upper layer of 8–14 small cells (Fig. 127, p. 57)

---

[5] According to León -Alvarez & González-González 2003 this is probably *Ralfsia hancockii*.

Table 3.4. (Continued).

Author		León-Alvarez & González-González 2003	Tórgo 1963	Sartoni & Boddi 1989	Børgesen 1914	Tanaka & Chihara 1980b	Rull Lluch 2002	Balakrishnan & Kinkar 1981
Cortical cells	Length	4.2–5.7 μm	22–27 μm	5–8 μm		4–6 μm	*n.i.*	*n.i.*
	Length-diameter ratio	0.7–1.2	*n.i.*	subcuboid	*n.i.*	1–1.2	Oblong or squarish (medullary cells rectangular)	
Sub-cortical cells	Length	17.8–42 μm	22–27 μm	10–20 μm	*n.i.*	15–25 μm		
	Length-diameter ratio	1.4–3.3	Approx 4–5 (Fig. 2, p. 9)	3–4	*n.i.*	2.5–4	thicker	
Unangia	Shape	Absent	Oblong and pyriform	Oblong–pyriform	Oblong pyriform but varable	Ellipsoidal, or clavate or obovate	Not seen	Oblong–pyriform or ovoid–pyriform
	Length	Absent	35–71 μm	75–110 (130) μm	75–120 μm	75–95 μm		75–85 μm
	Diameter	Absent	*n.i.*	25–40 μm	30 μm	23–35 μm		15–19 μm
	Stalk cells	Absent	Single cell (but Fig. 4, p. 9 shows 2–3 stalk cells)[6]	None (sessile) or one	Single, occasionally absent	Pedicellate, 3–6 stalk cells		“nearly always stalked.” (Figs. 130–131, p. 57 show one pedicel
Paraphyses	Shape	Absent	Clavate (Fig. 3 & 5, p. 9)	Clavate	Clavate	Long, clavate slender		Clavate
	Length	Absent	111–138 μm	Up to 170 μm (10–16 (–21) cells)	100–170 μm (8–14 cells)	100–190(220) μm (12-16cells)		100–120 μm
	Diameter	Absent	*n.i.*	Upper cells 8–10 μm, lower cells 3–4 μm	Lower cells 3 μm wide, elongate, apical cells thicker, shorter	Lower cells 2.5–3 μm 4–7x long, apical cells 5–6 μm, 0.8–1.4x long		7–8 μm

---

[6] Tórgo’s figures of *R. expansa* (1963, Fig. 4, p. 9) show unangia with 2–3 stalk cells typical of *R. hancockii sensu* León-Alvarez & González-González or *R. verrucosa* sensu Fletcher.

Table 3.4. (Continued)

Author		León-Alvarez & González-González 2003	Tórgo 1963	Sartoni & Boddi 1989	Børgesen 1914	Tanaka & Chihara 1980b	Rull Lluch 2002	Balakrishnan & Kinkar 1981
Plurangia	Arrangement	1–2 per filament	One per filament (Fig 7, p. 9)	One per filament (Fig. 6B, p.154)	1–2 per filament (Fig. 148)	One per filament (Fig.2d)	*n.i.*	1–2 per filament (Fig. 132, p. 57)
	Length	25.2–87.5 μm	~50 μm (Fig. 8, p. 9)	40–80 μm	*n.i.*	40–65 μm	30–40 μm	Less than 20 μm
	Diameter	4.2–7.5 μm	*n.i.*	*ni*	5-6 μm	*ni*	2–3 μm	5–6 μm
	Locule arrangement	*n.i.*	Uniseriate-biseriate	Uniseriate, later partly biseriate	Uniseriate-biseriate (Fig. 148, p. 191)	Uniseriate, later biseriate	Uniseriate, exceptionally pluriseriate	Uniseriate
	Locule number	*n.i.*	*n.i.* 8–18 (Fig 8, p. 9)	10–16	15–16 (Fig. 148, p.191)	6–11 (x2) (Fig. 2, p. 6)	7–9	
	Sterile terminal cell	5.7–8.4 μm x 4.2–6.3 μm	swollen (Fig. 8, p.9)	one 8–15 μm long	unclear[7]	one 5–6 μm 1.2–2.2x long	One 6–8 x 2–4 μm	Absent

---

[7] Fig 148C shows a slightly swollen terminal cell or locule, usually with diagonal divisions.

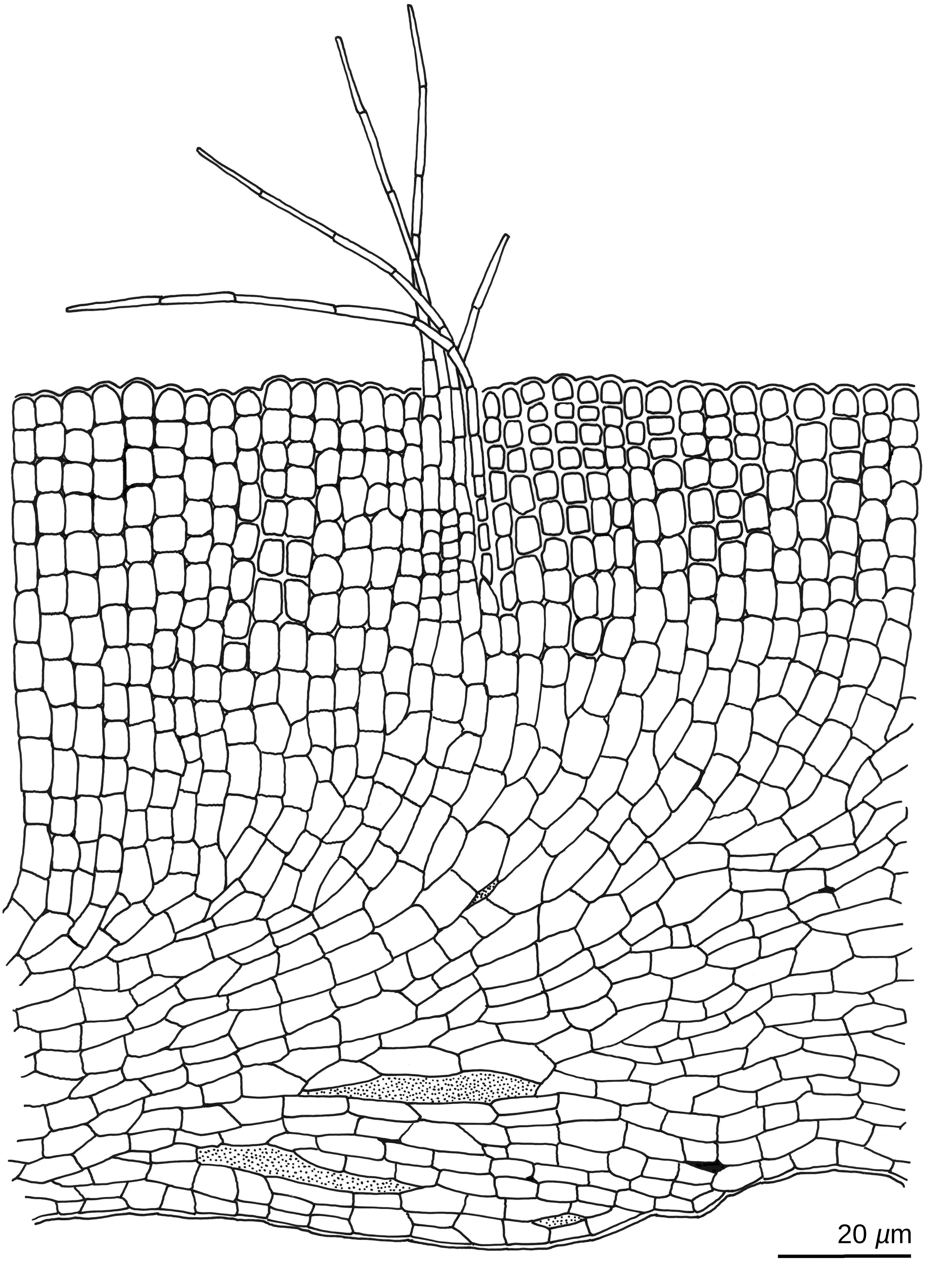

Fig. 3.8. Radial longitudinal section of *Ralfsia expansa* with hair pit.

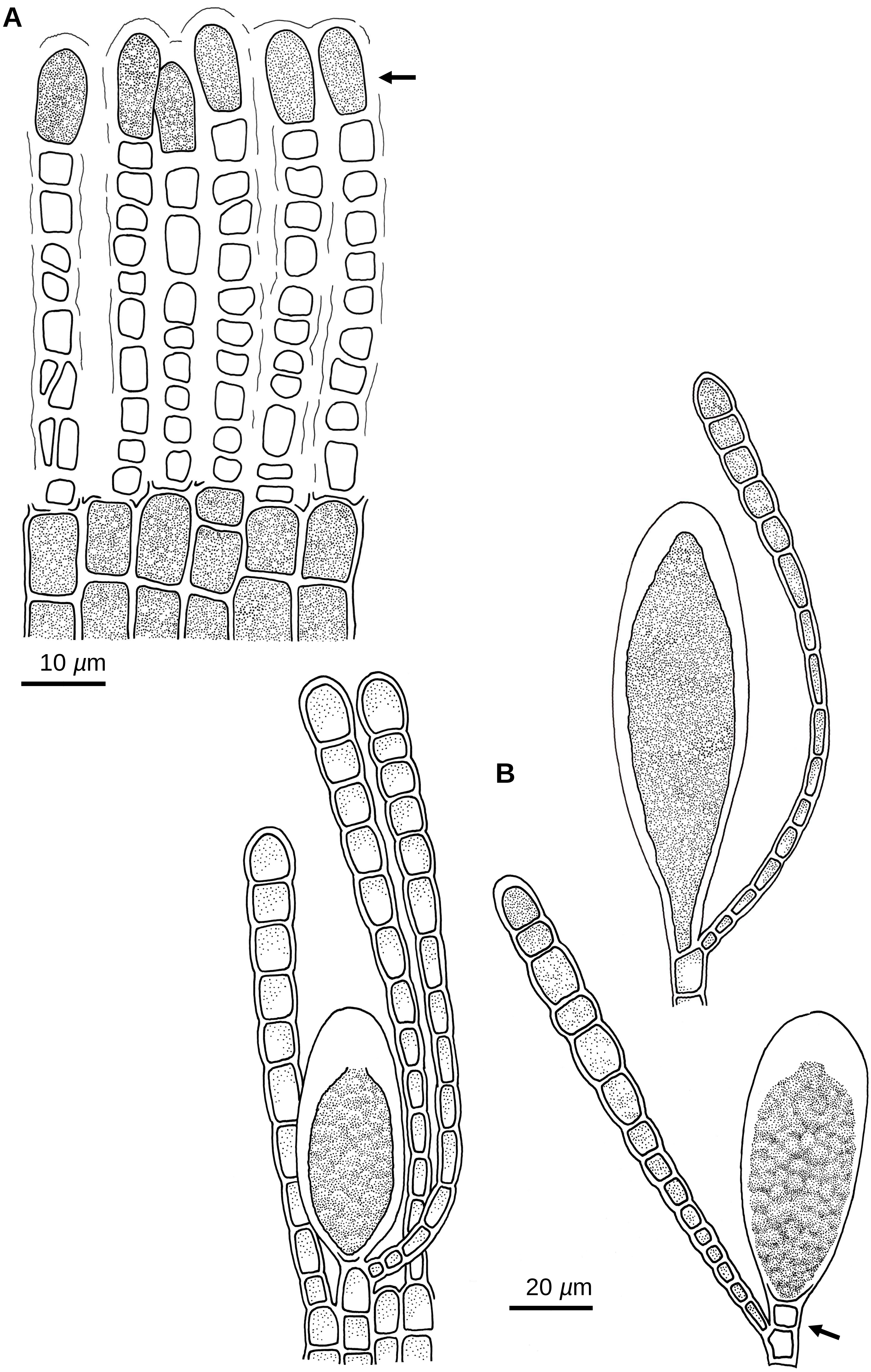

Fig. 3.9. *Ralfsia expansa* **A.** Plurangia, arrow indicates prominent sterile apical cell. **B.** Unangia with paraphyses, one figure with a pedicel (arrow).

3.10.2 Ralfsia sp. "smooth"

Plates 9 & 10; Fig. 3.10.

A locally common species, closely related to *R. confusa* (see Chapter 4), with a thick, smooth thallus (Plate 9B). On rock and shells, in tidal pools and in the lower intertidal and upper subtidal, often growing on non-geniculate coralline algae. Specimens growing over rough substrates, such as crustose coralline algae, may have a verrucose surface and resemble *Diplura*.

Thallus: Outline orbicular in young thalli or irregular when older or confluent. 10–30 mm diameter or larger. Thalli adhering tightly to the substrate without rhizoids. Confluent thalli indistinguishable from one another. Colour mid to dark brown with centre paler and often reddish, sometimes with paler radial stripes, edges pale. Surface smooth and glossy when dry, slight radial or concentric undulations but centre of thalli without pronounced ridges; sometimes with short raised radial ridges close to edge.

Infertile crusts up to 600 μm thick, slightly thicker when fertile. Thallus of a monostromatic or distromatic base of firmly united branched radiating filaments, giving rise to closely packed curved erect filaments of 20–35 cells. Upright filaments firmly united and do not separate easily under pressure. Basal cells cylindrical elongated or irregular polyhedrons 5–11 μm diameter and 0.8 to 3.85 diameters in length. Erect filaments branching from basal layer and curving to vertical. Filaments sometimes branching, cells (5–)8–15 μm wide and 0.9–3 diameters long. Sometimes with a distinct layer of small cortical cells. Epithallial cells domed, 5–13 μm diameter and 0.67–1.6 diameters long. Cells with a single, somewhat indefinite plastid, usually in upper part of cell, without obvious pyrenoid and often obscured by physodes.

Multicellular hyaline hairs in tufts, especially around edges of crust, visible as raised dots when dry. Hairs arising as thin filaments from the medulla, cells 4–6 μm diameter, 7.5–27.5 μm long.

Reproduction: Unilocular sporangia in summer in central or concentric sori, gelatinous and paler than surrounding crust, peeling off as single layer, drying matt. Unangia lateral to paraphyses and surrounded by many clavate paraphyses. Unangia 70–95 μm long and 25–35 μm diameter. Paraphyses up to 120 μm long, of 5–7 cells, apical cell swollen, 8–12 μm diameter, lower cells thinner and elongated. Plurangia late autumn or winter, one plurangium terminal on each erect filament, in expansive sori without paraphyses. Plurangia cylindrical

6–10 μm diameter, 50–82.5 μm long usually biseriate with 10–16 locules and one or more colourless cap cells, 9–20 μm long.

Discussion

This species is similar in appearance to *Ralfsia confusa* but has a thicker, monomerous, thallus and distinctive plurangia. Plurangia of *R. confusa* have a dark coloured cap cell and are uniseriate or partially biseriate, whereas those of *Ralfsia sp*. “smooth” are usually fully biseriate at maturity and have clear cap cells (Fig. 3.10C, Plate 10A).

Hollenberg (1969) described “Certain thicker specimens with assurgent thalli” from California, which were “at first believed to represent somewhat thicker specimens of *R. confusa*, but… are merely thinner specimens of *R. pacifica*.” Dethier (1987) and Dethier & Steneck (2001) also reported difficulty in distinguishing some specimens of *R. pacifica* from *R. confusa*. The New Zealand species also resembles a thicker *R. confusa*, and is similar in outward appearance to the thallus of *R. pacifica* Hollenberg illustrated on the algaebase website (Guiry *et al.* 2005) and to micrographs of sections of thalli in Wynne (1969; Plate 13e–g) but differs from *Ralfsia pacifica* Hollenberg in having biseriate plurangia in large expansive sori. Hollenberg described the plurangia of *R. pacifica* as “regularly uniseriate” but his illustration (Hollenberg 1969, Fig.17 p.294) shows some partially biseriate plurangia. However a micrograph of *R. pacifica* plurangia from Washington State (Dethier 1987, Fig. 4 p. 1846) shows plurangia that are apparently uniseriate. Hollenberg also states that plurangia of *R. pacifica* are “mostly about 1 mm in diameter or less” whereas plurangial sori of the New Zealand alga are expansive, covering most of the thalli and often over 10 mm in diameter.

The combination of monomerous thalli, a single plastid per cell and biseriate plurangia in expansive sori distinguish this species from any previously described crustose brown algae.

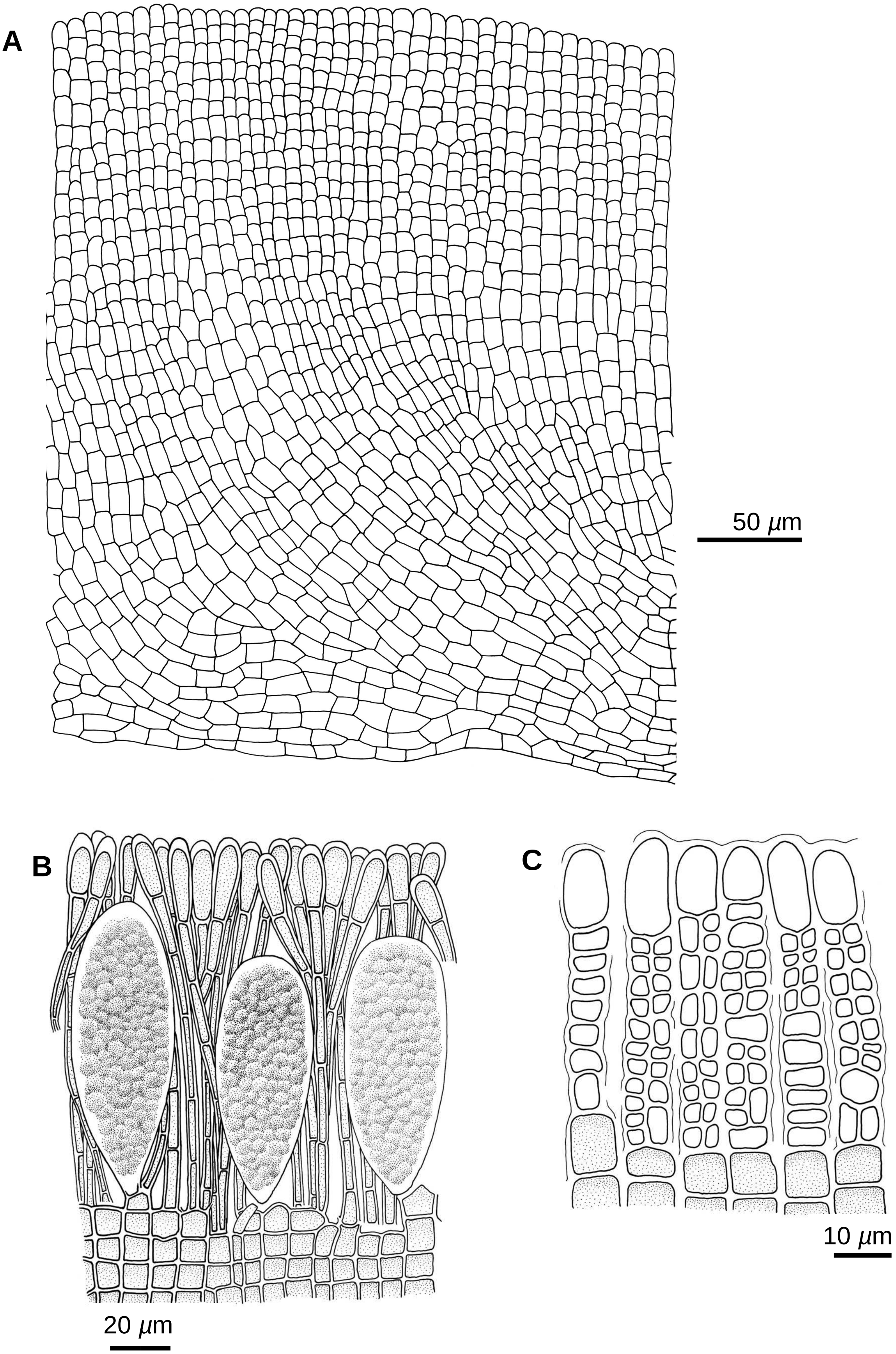

Fig. 3.10. *Ralfsia sp.* “smooth” **A.** Radial longitudinal section of thallus **B.** Unangia and paraphyses **C.** Plurangia.

3.10.3 Ralfsia confusa Hollenberg 1969

Plates 7(D–E), 11–12; Figs. 3.11–3.12

A relatively thin crust, up to 15 mm in diameter often gregarious and becoming confluent (Plate 7D). Usually epilithic, occasionally on shells. Thalli adhering tightly to substrate without rhizoids. Colour varying from light brown or tan to chestnut or dark olive brown. Basal areas reddish brown or rust coloured. Thallus firm, surface drying glossy or eggshell, centre smooth, periphery with low radial ridges and sometimes concentric ridges, edges pale with thick cuticle. Growing in shallow rock pools, often high in the intertidal on rock and loose cobbles.

Thallus: Outline orbicular in young thalli, irregular in older and confluent thalli. Vegetative thallus 100–250 µm thick, soral areas up to 400 µm thick. Structure pseudoparenchymatous, organization dorsiventral, construction monomerous or dimerous. Basal layer monostromatic or distromatic of firmly united branched radiating filaments, giving rise to closely packed erect filaments, often of 10–12 cells or less, but thicker crusts with up to 25 cells. Erect filaments either branching acutely from basal layer and curving sharply to vertical or dividing at right angles from basal filament. Erect filaments firmly united and not separating under pressure, occasionally branching. Basal cells rectangular or irregular polyhedrons, usually 7–11(–20) µm diameter and length 1–2 diameters. Cells of erect filaments 7–8(–12) µm diameter and 7–9(–12) µm in height. Epithallial cells domed, usually 6–8(–10) µm diameter and 7–9(–13) µm long. Epithallial cells covered by a thin cuticle, thickening near edge of thallus. Cells with single, indefinite plastid in upper part of cell, without obvious pyrenoid.

Hairs present or absent, either solitary or in tufts of less than five hairs, usually near the edge of the crust but occasionally among the sori, 2–5 µm diameter and up to 200 µm long, with cells 15–30 µm long.

Reproduction: Commonly found with unangia in extensive sori with many paraphyses. Sori slightly raised gelatinous patches, paler than the surrounding thallus, drying matt. Sori extending completely over the central part of the crust and spreading towards the edges in radial strips. Unangia pyriform to ovoid, sessile on terminal vegetative cell of an erect filament and lateral to a single paraphysis. Unangia 20–25(–30) µm diameter and 50–60(–80) µm long. Paraphyses clavate 60–75(–100) µm long, of 3–5 cells; apical cell usually swollen, 7–10 µm diameter and 15–25 µm long, sub-apical cells thinner, usually rectangular, occasionally barrel shaped, 3–6 µm diameter, 11–22.5 µm long. Cells of paraphyses with a single plastid occupying most of the cell. Unangia releasing pyriform biflagellate zoospores, 5–6 x 6–8.5 μm.

Rarely with plurangia, densely crowded in expanded slightly gelatinous sori, with a single plurangium terminal on each vegetative filament, without paraphyses. Plurangia 4–5 μm diameter and 22.5–37.5 μm long, terminating in a single dome shaped cap cell, slightly swollen, 6–7 μm diameter and up to 10 μm long covered by a thick cuticle. Each plurangium with 6–7(–8) locules. Locules uniseriate or partly biseriate, irregular or subquadrate. Unangia and plurangia not seen on the same thallus.

Type from Corona del Mar, Orange County, California.

Discussion

The New Zealand alga closely resembles *Ralfsia confusa* Hollenberg 1969, described from California. This species has also been reported from the Gulf of California (Cruz-Alaya *et al.* 2001), northern Chile (Medina *et al*. 2005) and India (Balakrishnan & Kinkar 1981). New Zealand specimens are consistent with Hollenberg’s description and illustrations of the upper filaments, plurangia and unangia but Hollenberg describes the erect filaments branching at right angles to the basal layer thus forming a dimerous crust. The New Zealand species has short filaments usually branching acutely from the basal layer and curving sharply to vertical (Fig. 3.11A, Plate 11A-B). However this character is somewhat variable. In many sections the thallus appears nearly or entirely dimerous (Fig. 3.11B), especially in sections from the centre of older thalli, or from confluent thalli where it is difficult to determine the plane for a radial longitudinal section. New Zealand specimens have paraphyses of 3–5 cells, whereas Hollenberg’s type has 10–12 celled paraphyses, but Hollenberg refers to variants with 3–4 or 4–6 cells. Hollenberg also refers to thicker specimens with assurgent erect filaments that he considers to be *Ralfsia pacifica*. Given the variations accepted by Hollenberg as *R. confusa*, and as some sections of New Zealand material appear dimerous it seems reasonable to refer the New Zealand species to *R. confusa*.

Hollenberg applied the epithet *confusa* due to similarities between this species and the crustose phases of some scytosiphonacean algae: the crust is thin, thalli are often found with expansive unangial sori (Plates 11B, 12A) and plurangia are seldom found. I also considered this species to be a member of the Scytosiphonaceae, until I collected specimens from Northland with plurangia and found ITS DNA sequences showed no close affinity with the Scytosiphonaceae. The plurangia appear similar to plurangia of *R. confusa* from Washington

State in micrograph in Dethier (1987, Fig. 7, p.1846), although plurangia of New Zealand specimens are somewhat shorter (Fig. 3.11B, Plate 12B).

Hollenberg placed *Ralfsia confusa* in the sub-genus *Stragularia* based on the expansive unilocular sori and thin, dimerous thallus. In younger orbicular crust the unangial sori of *R. confusa* cover most of the central part of the thallus and extend outward in irregular, partly confluent radial stripes. In older confluent thalli the sori are irregular, adjoining thalli are difficult to distinguish and sori are apparently confluent between thalli. However the coherent erect filaments, sterile apical cells of the plurangia, and assurgent erect filaments of New Zealand specimens are characteristic of *Ralfsia*.

Hollenberg (1969) placed *Ralfsia integra*, another species with expansive unangial sori but with a relatively thick thallus and assurgent filaments, in the genus *Ralfsia* without reference to *Stragularia*. He apparently regarded the arrangement of the filaments to be of greater importance than the type of sori. A separate genus within the Ralfsiaceae may be warranted for species with expansive unangial sori. For the present it seems better to retain this species in *Ralfsia* as the inclusion of microthalli of Scytosiphonaceae in *Stragularia* has confused the circumscription of this genus, and the Ralfsiaceae *sensu stricto* do not appear to be closely related to the Scytosiphonaceae (Tan & Druehl 1993).

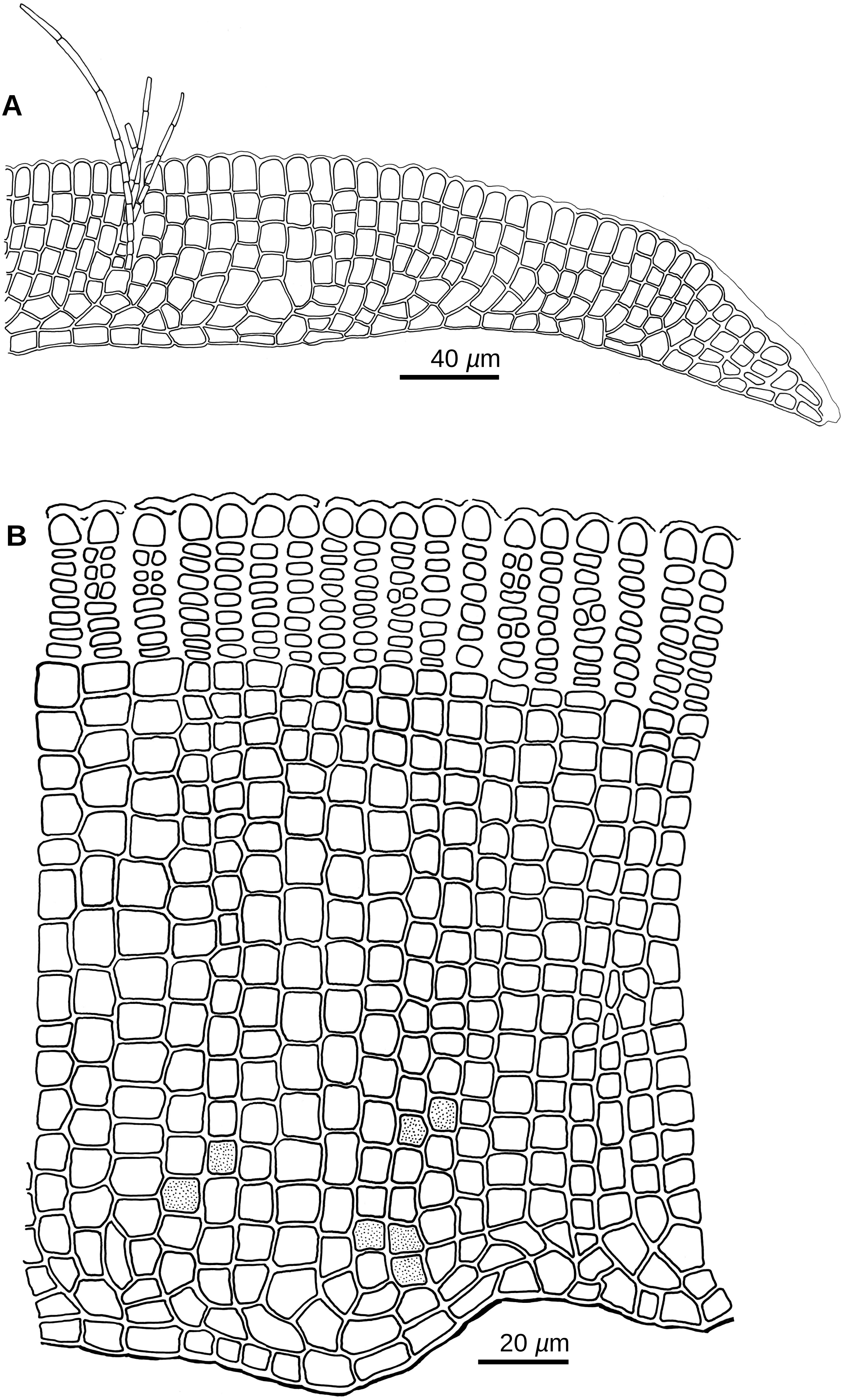

Fig. 3.11. *Ralfsia confusa*. **A.** Radial longitudinal section of edge of thallus. **B.** Radial longitudinal section of fertile thallus with plurangia.

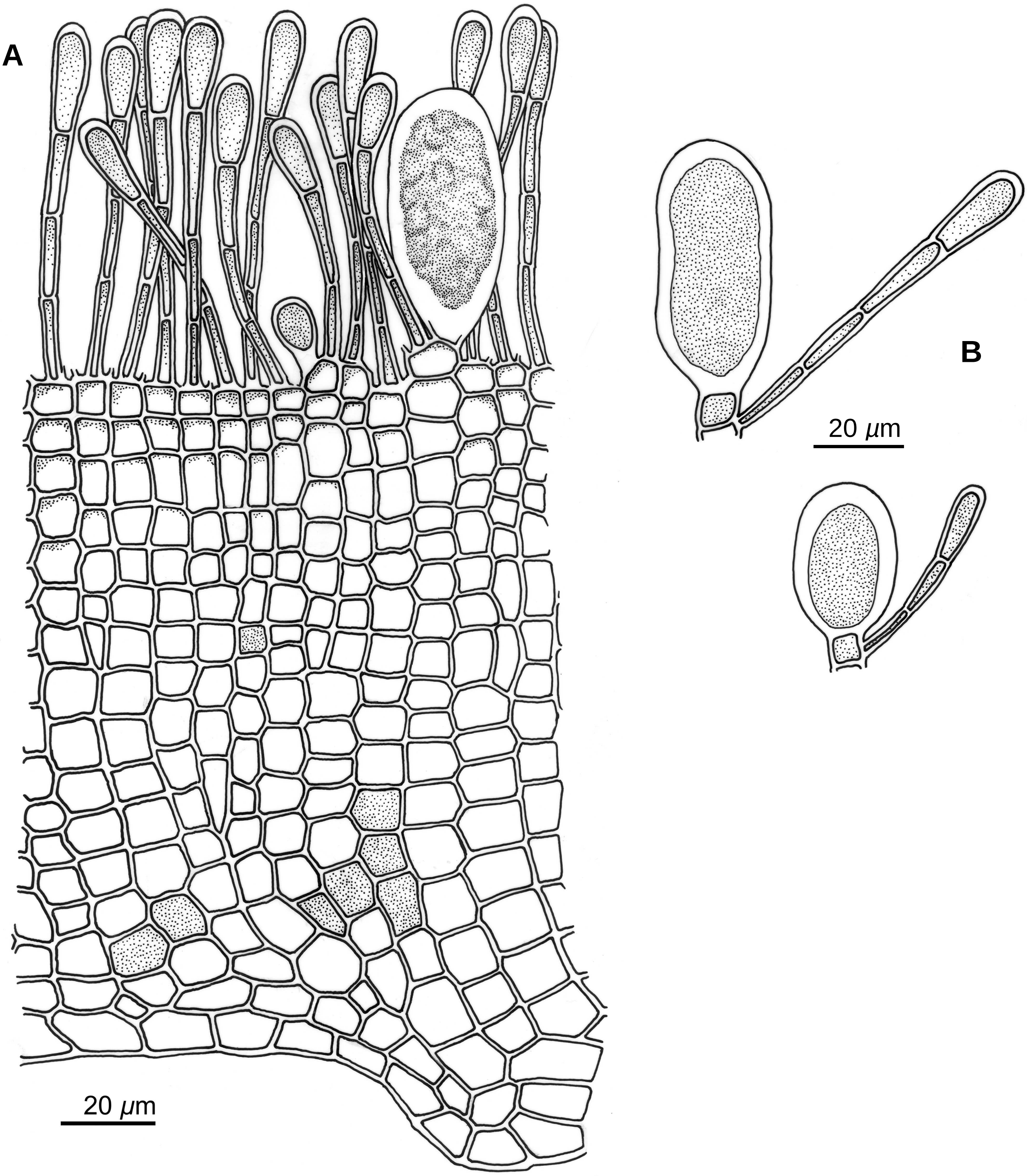

Fig. 3.12. *Ralfsia confusa* **A.** Radial longitudinal section of fertile crust. **B.** Two unangia with paraphyses.

3.11 Hapalospongidion **Saunders 1899**

Thallus: Crustose and gelatinous, outline orbicular in young thalli, older thalli confluent, irregular or eroded. Basal layer firmly attached to rock without rhizoids. Basal layer pseudoparenchymatous, two to several cells thick, giving rise to free filaments embedded in gelatinous matrix. Organisation dorsiventral, construction monomerous with a prostrate basal layer of laterally adherent, branched radiating filaments giving rise to free erect filaments, simple or rarely branched. Hairs absent, or single or in tufts. Plastids single per cell or possibly 1–3 per cell, plate-like.

Reproduction: Unangia terminal on a stalk or vegetative filament. Plurangia intercalary, uniseriate to multiseriate with one to few terminal sterile cells.

Type species: *Hapalospongidion gelatinosum* from California

Womersley (1987) combined *Hapalospongidion* with two genera of morphologically similar algae, *Mesospora* and *Basispora*. *Mesospora* was created by Weber-van Bosse based on *Mesospora schmidtii* (Weber-van Bosse 1911, 1913) from Indonesia and *Basispora* was created by John & Lawson (1974) based on *B. africana* John & Lawson from Ghana.

John & Lawson (1974) consider *Basispora* and *Mesospora* separate from *Hapalospongidion* on the basis of *Basispora* possessing several chloroplasts per cell and *Mesospora* having unangia attached laterally to the vegetative filaments. Womersley (1987) and León-Alvarez & Norris (2005) regard the difference in the attachment of the unangia as being a matter of interpretation and terminology, as all three genera have unangia terminal on a filament or stalk that may arise laterally from another filament. Womersley considers all genera to have one to three chloroplasts per cell, depending on the size and age of the cell. Rull Lluch (2002) agrees that *Mesospora* is synonymous with *Hapalospongidion* but retains *Basispora* as a separate genus based on the several discoid plastids reported by John & Lawson in *B. africana*. John & Lawson (1974) transferred *H. saxigenum* and *H. durvilleae* to *Basispora* on the basis of the several chloroplasts per cell reported by Lindauer *et al.* (1961). These were probably physodes misidentified as plastids, as all the New Zealand specimens I examined have a single, sometimes obscured, plastid in each cell. Rull Lluch (2002) considers it possible that the same mistake was made in the case of *Basispora*.

A fourth morphologically similar genus, *Acrospongium* Schiffer 1916, with one species, *A. ralfsioides*, has been reported from the Mediterranean (Sartoni & Boddi 1989). This species has a single plate-like plastid per cell and should probably be combined with *Hapalospongidion*.

Tanaka & Chihara (1982) erected a new family in the Ralfsiales, the Mesosporaceae to accommodate *Mesospora*, *Hapalospongidion* and *Basispora*. They separate these genera from other Ralfsiales by the intercalary plurilocular sporangia and terminal unilocular sporangia arising on a stalk or vegetative filament without paraphyses.

3.11.1 Hapalospongidion gelatinosum Saunders 1899

Plates 13 & 14; Fig. 3.13

A soft gelatinous crust, slippery when wet, thalli often coalescing to cover large areas. 10–30 mm diameter, but forming confluent patches with individual thalli indistinguishable (Plate 14C). Colour olive-green to tan, orbicular thalli with fine straw coloured radial stripes arranged in concentric bands, palest near the centre, but with a dark patch and often a reddish spot in the exact centre, confluent thalli mottled. Gelatinous when wet, drying matt or suede, turning to slime when removed from the rock and producing copious quantities of slime when cut.

Thallus: Outline orbicular in young thalli, older thalli often confluent, irregular or concentric ring with eroded centre, 250–750 μm thick. Basal layer firmly attached to rock without rhizoids. Structure of 1–2 or more pseudoparenchymatous basal layers giving rise to free filaments embedded in gelatinous matrix. Organisation dorsiventral, construction monomerous with a prostrate basal layer of laterally adherent, branched, radiating filaments 2–3 or more cells thick. Erect filaments of 25–65 cells branching acutely from basal layer, becoming free from one another and curving immediately to vertical. Erect filaments rarely branched.

Basal cells rectangular or irregular polyhedrons, 5–15 μm diameter and 0.33–2.5 diameters long. Lower cells of erect filaments cylindrical, upper cells rounded or barrel shaped, 4–8.5 μm long and 0.6–3.75 diameters long. Apical cells barrel shaped or swollen, 4–10 μm diameter and 0.4–2.2 diameters long. Single plastid per cell occupying most of the volume of the basal cells and upper cells of the erect filaments, plastid gradually reducing in size in lower cells of erect filaments. Cell contents somewhat granular with numerous physodes.

Hairs in tufts, visible when dry, arranged on thallus in irregular concentric circles. Hair cells 3–5 µm diameter and 5–22.5 µm long.

Reproduction: Unilocular sporangia not seen. Plurilocular sporangia uniseriate or partly biseriate, in groups, intercalary on erect filaments with two or three sterile cap cells. 8–12 locules in each plurangium, locules 7.5–15 µm diameter and 7.5–10 µm long.

Thin, occasionally branched hyphae-like filaments often present between erect filaments, no reproductive structures seen on these.

North Island, South Island, Stewart Island.
Type: *H. saxigenum* Specimen 11320, Herbarium Lindauer from Stewart Island, Herbarium of Auckland University College.

Discussion

Lindauer *et al*. (1961) recorded two species of *Hapalospongidion* from New Zealand, *H. saxigenum* and *H. durvilleae*. The latter, an epiphyte of *Durvillaea*, was transferred to *Herpodiscus* by South (1974). Adams (1994) describes *H. saxigenum* as localised to suitable (hard) rock types. I found thalli on various substrates in the Cook Strait region, including crumbly greywacke and soft sandstone. Thalli growing on irregular surfaces are less easily recognised and may resemble *Ralfsia* or *Diplura*. Populations at Houghton Bay, Wellington, tolerate surf, and abrasion and burying by sand.

Lindauer (1947) described the New Zealand alga as a new species, *H. saxigenum* Lindauer, that is “closely related to *H. gelatinosum* Saunders in habit and stature but differs principally in the absence of plurilocular bodies, and in the poorly developed basal layer.” Lindauer (1949) wrote that “the basal distromatic or tristromatic layer characteristic of the genus is barely distinguishable in this species, but it appears to exist.” The basal layer is tightly adherent to the substrate and difficult to section, but appears to consist of at least two layers of cells (Fig. 3.13D, Plate 13B), and in this regard New Zealand material is consistent with Saunders’ (1899) description of *Hapalospongidion gelatinosum*.

Unilocular sporangia were not present in any of my collections, but several specimens have uniseriate or biseriate plurangia, usually with three terminal cap cells (Fig. 3.13B, Plate 14B). I observed the release of motile spores from plurangia. The plurangia parted halfway up their length, the upper parts peeling away in groups that remained joined at the cap cells. This mode of spore release was observed by Jaasund (1964) in *Ralfsia verrucosa* and Edelstein *et* *al* (1968) in *Ralfsia fungiformis*. The biseriate plurangia are identical to those illustrated by Hollenberg (1942, p.530, Fig. 8) and Saunders (1889).

As there are no differences between New Zealand material and the description of the type specimen of *H. gelatinosum* (Saunders 1899), I regard the diagnostic characters used to erect *Hapalospongidion saxigenum* as unreliable and refer the New Zealand species to *Hapalospongidion gelatinosum* Saunders.

Womersley (1987) described a single new Australian species, *Hapalospongidion capitatum* that he separated from *H. gelatinosum* on the basis of capitate filaments (the uppermost two or three cells are enlarged), multiseriate plurilocular sporangia, and the absence of unilocular sporangia. Specimens from New Zealand have both capitate filaments identical to those illustrated by Womersley (Fig. 20F, p. 76) and non-capitate filaments – this character appears to be variable. Hairs are absent *in H. capitatum* but this character has been shown to be plastic in other brown algae, including *Ralfsia*. Only the multiseriate plurangia clearly separate *H. capitatum* from *H. gelatinosum*.

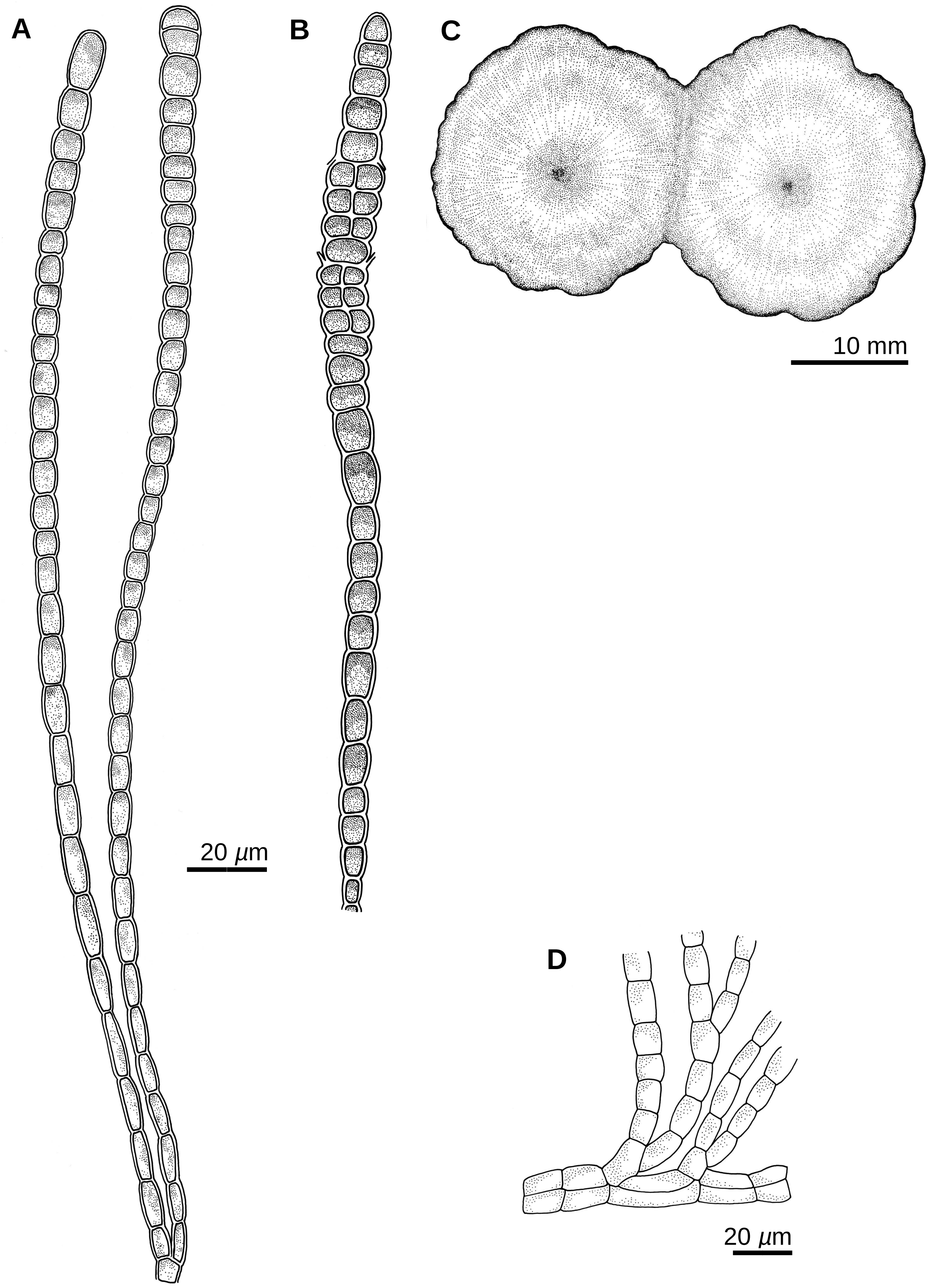

Fig. 3.13. *Hapalospongidion gelatinosum*. **A.** Vegetative filaments. **B.** Plurangium. **C.** Two orbicular thalli. **D.** Basal filaments with branching lower part of erect filaments

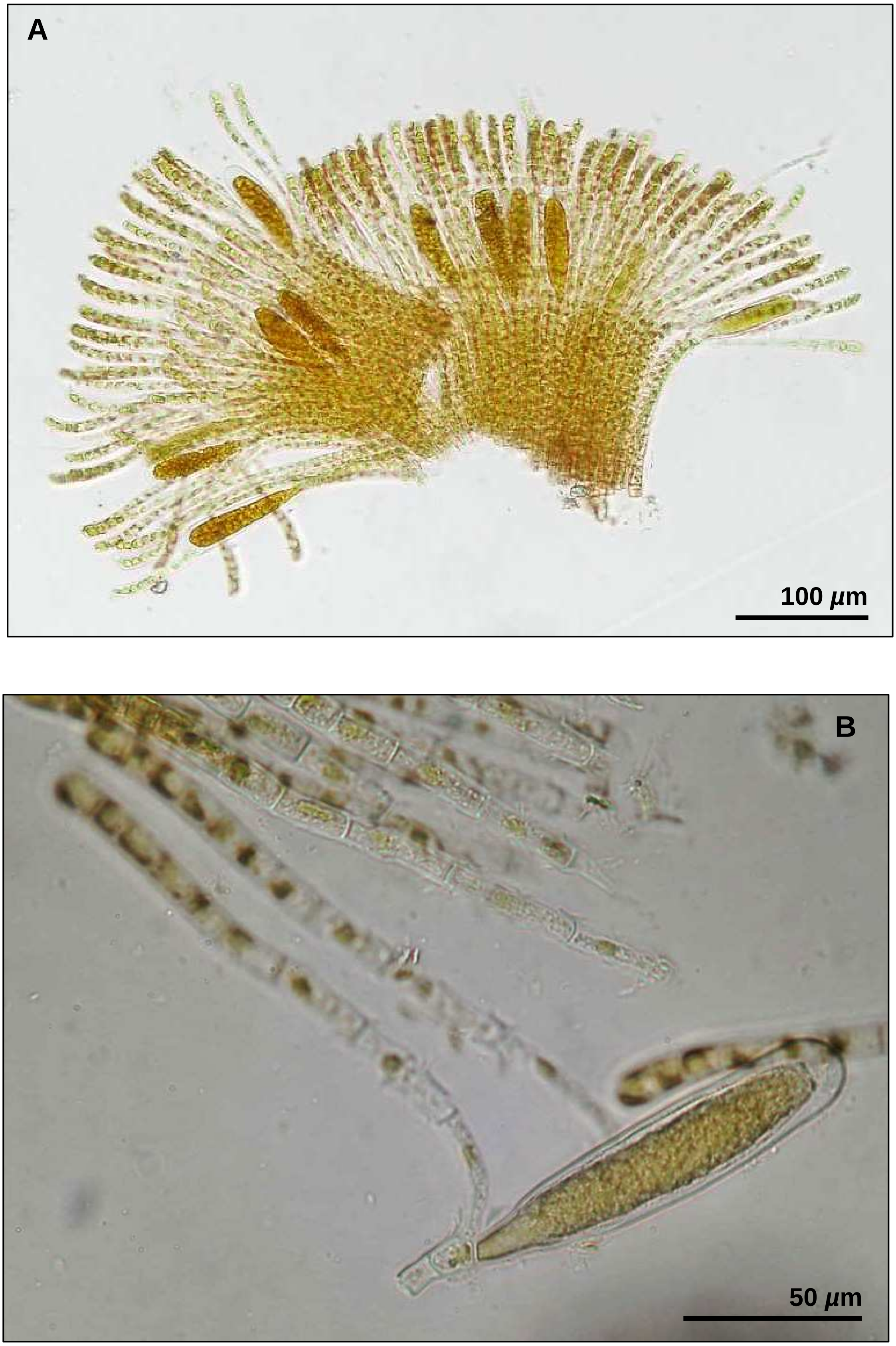

Plate 1. *Scytosiphon lomentaria* microthalli. A. Thallus with unangia. B. Unangium and paraphysis.

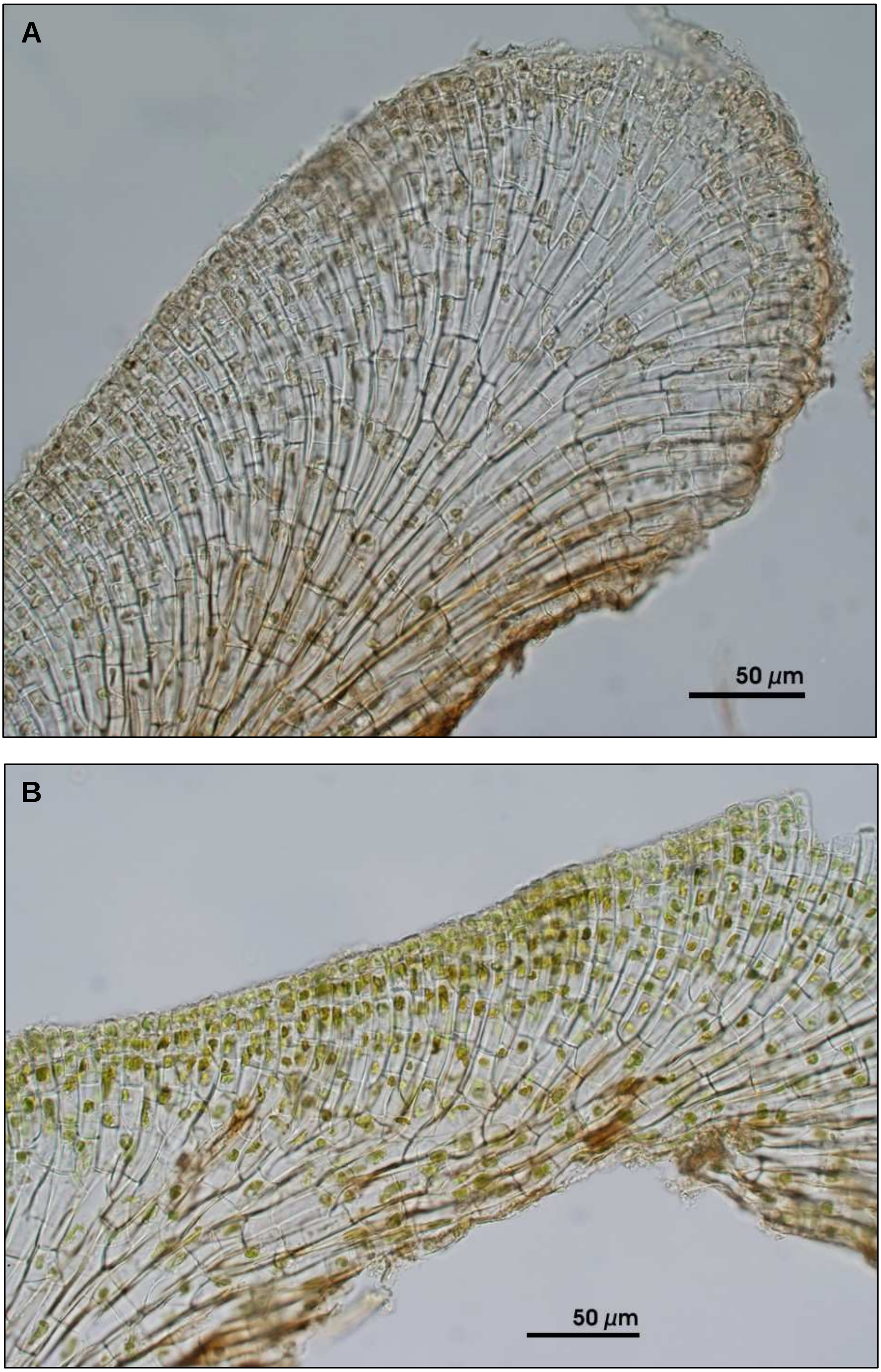

Plate 2. *Colpomenia bullosa*: young microthallus. **A**. Radial longitudinal section of edge of thallus. **B.** Radial longitudinal section of thallus.

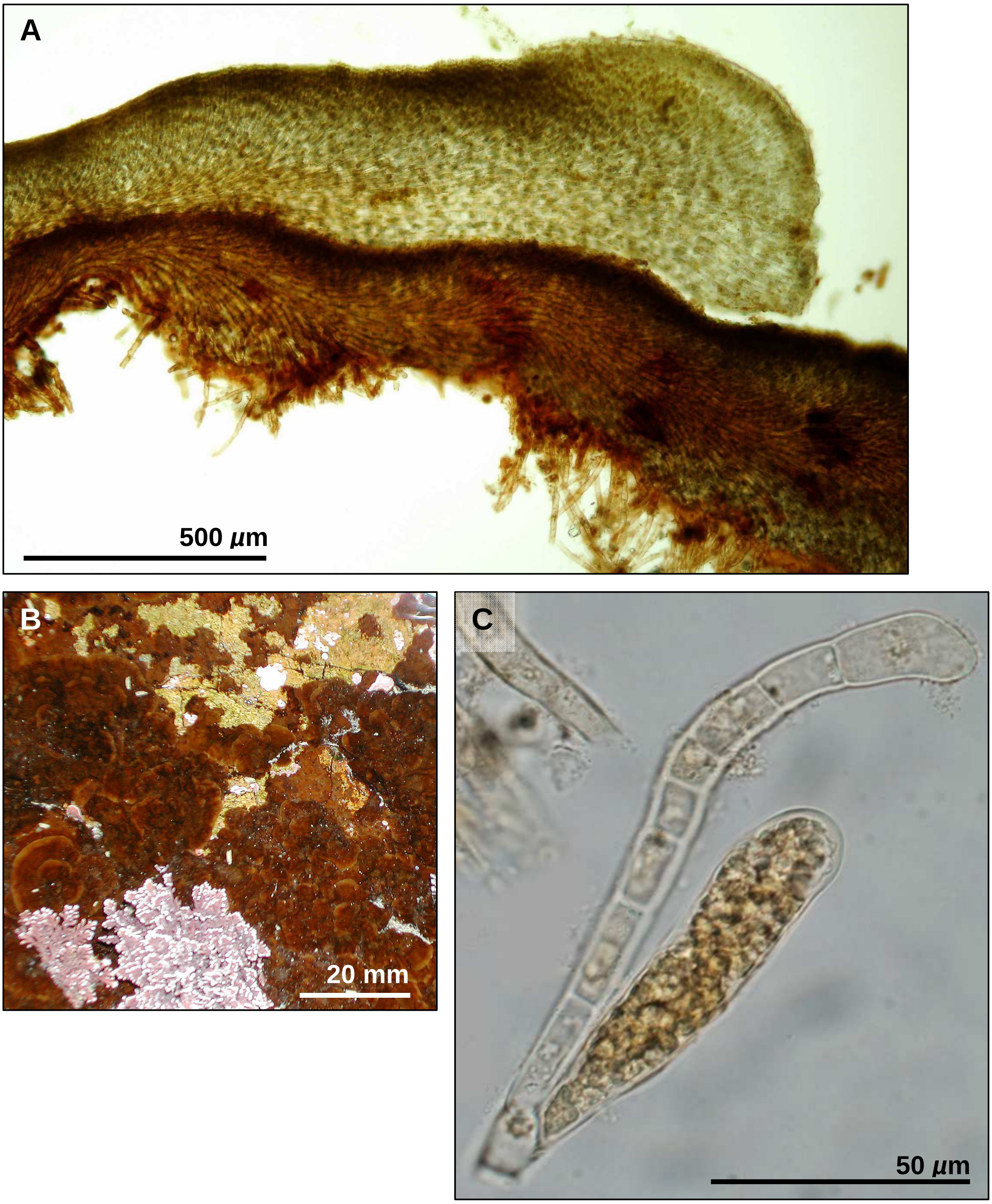

Plate 3. *Colpomenia bullosa* **A**. Older thallus with lobe and rhizoids. **B.** Lobed thalli in rock pool, Point Eldson, Wellington. **C.** Unangium and paraphysis.

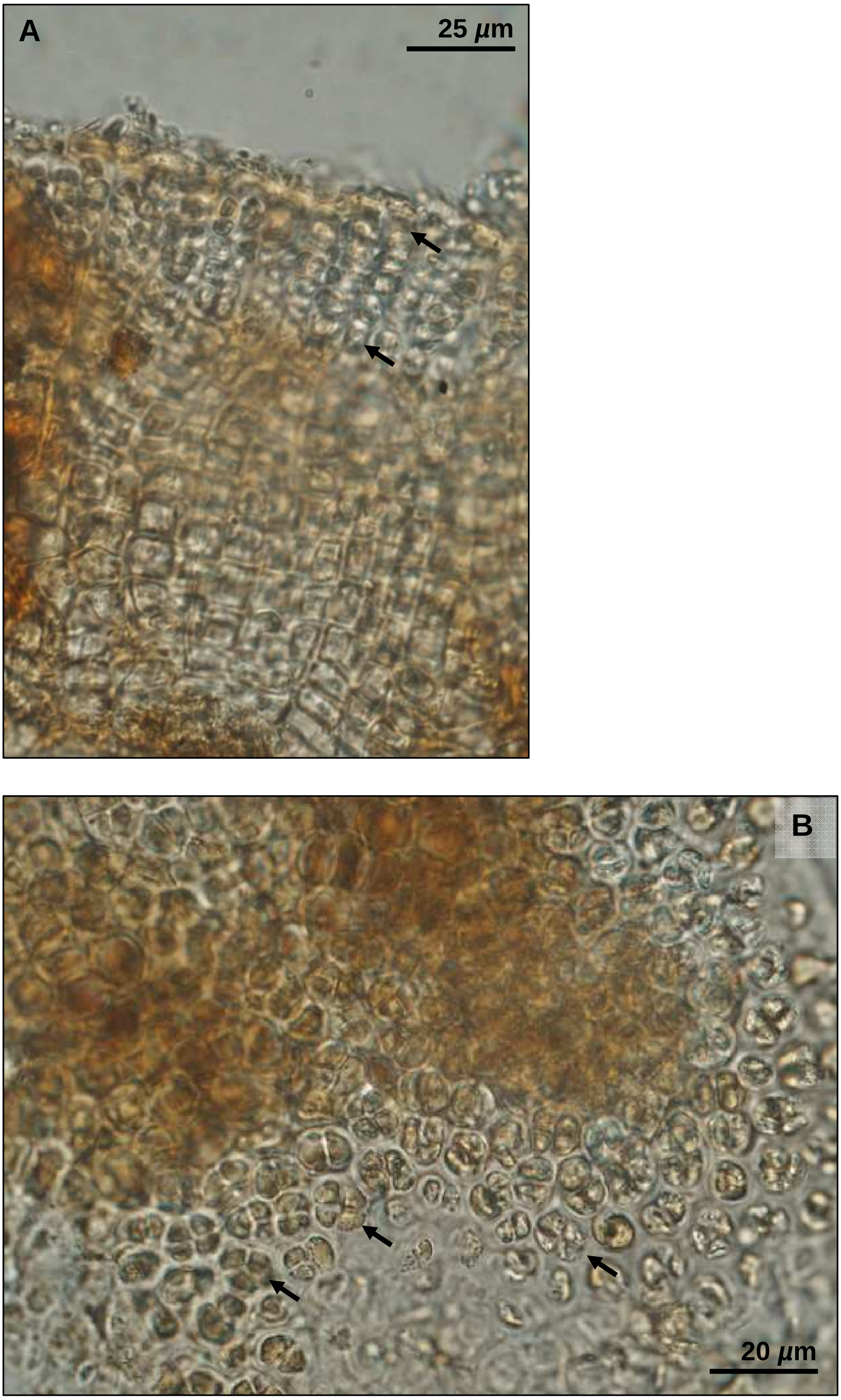

Plate 4. *Pseudolithoderma roscoffense*. **A.** Longitudinal section of thallus with plurangia (arrows). **B.** Thallus in surface view with plurangia (arrows).

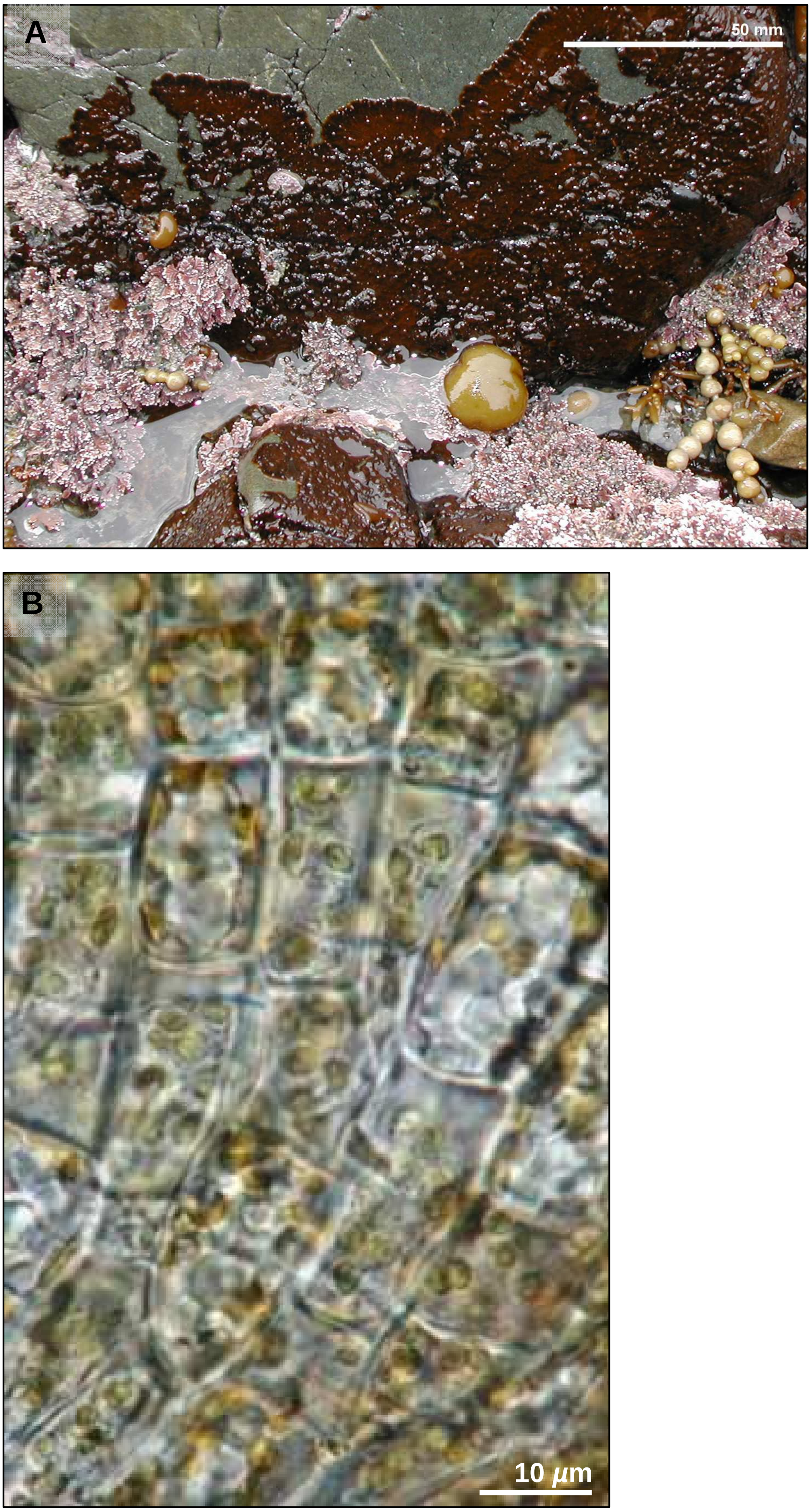

Plate 5. *Diplura sp*. **A**. Confluent thalli on rock, Point Elsdon, Wellington. **B**. Cells of erect filaments with discoid chloroplasts.

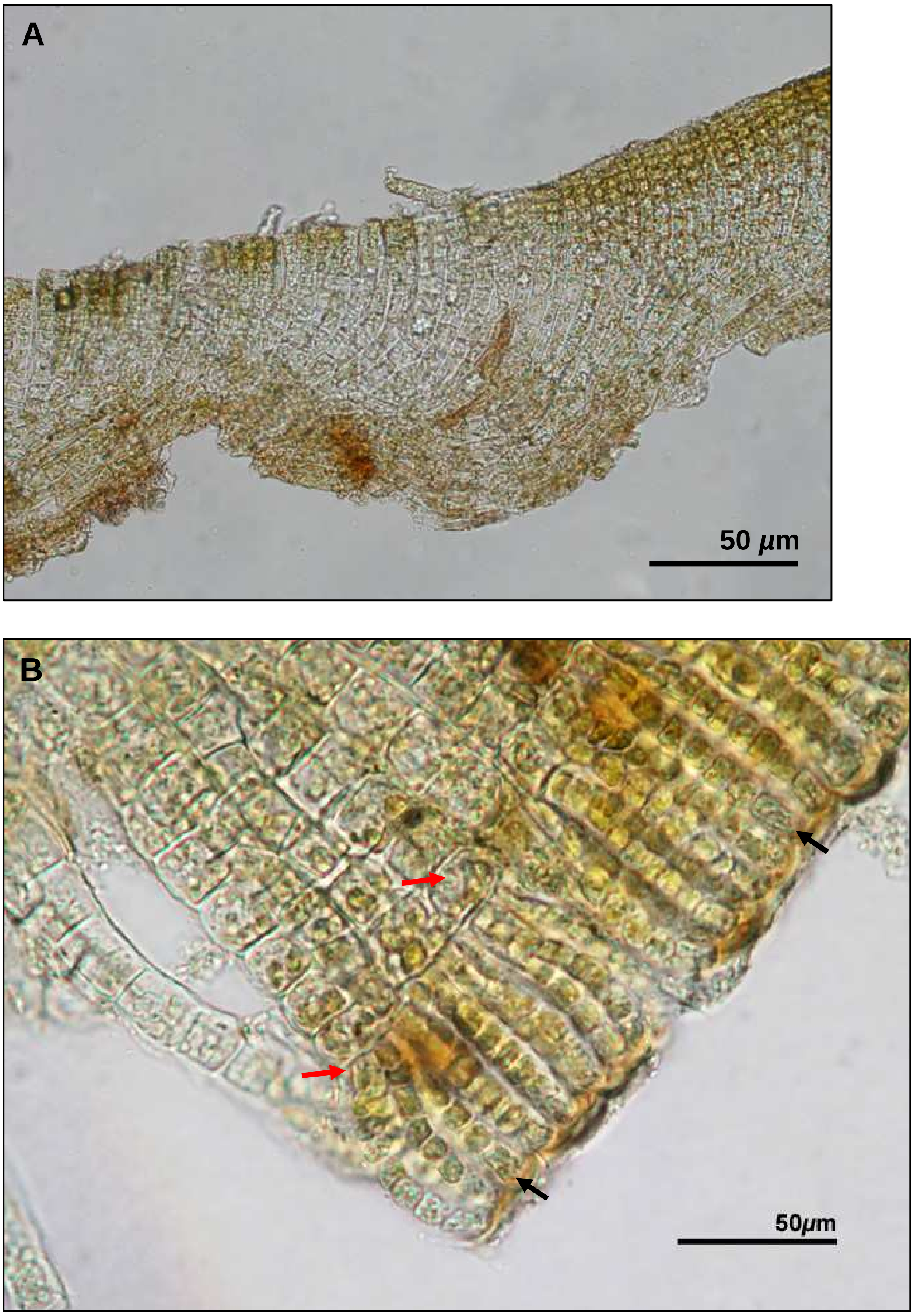

Plate 6. *Diplura sp.* **A.** Longitudinal section of thallus. **B.** Thallus with plurangia, red arrows: terminal vegetative cell; black arrows: sterile apical cell.

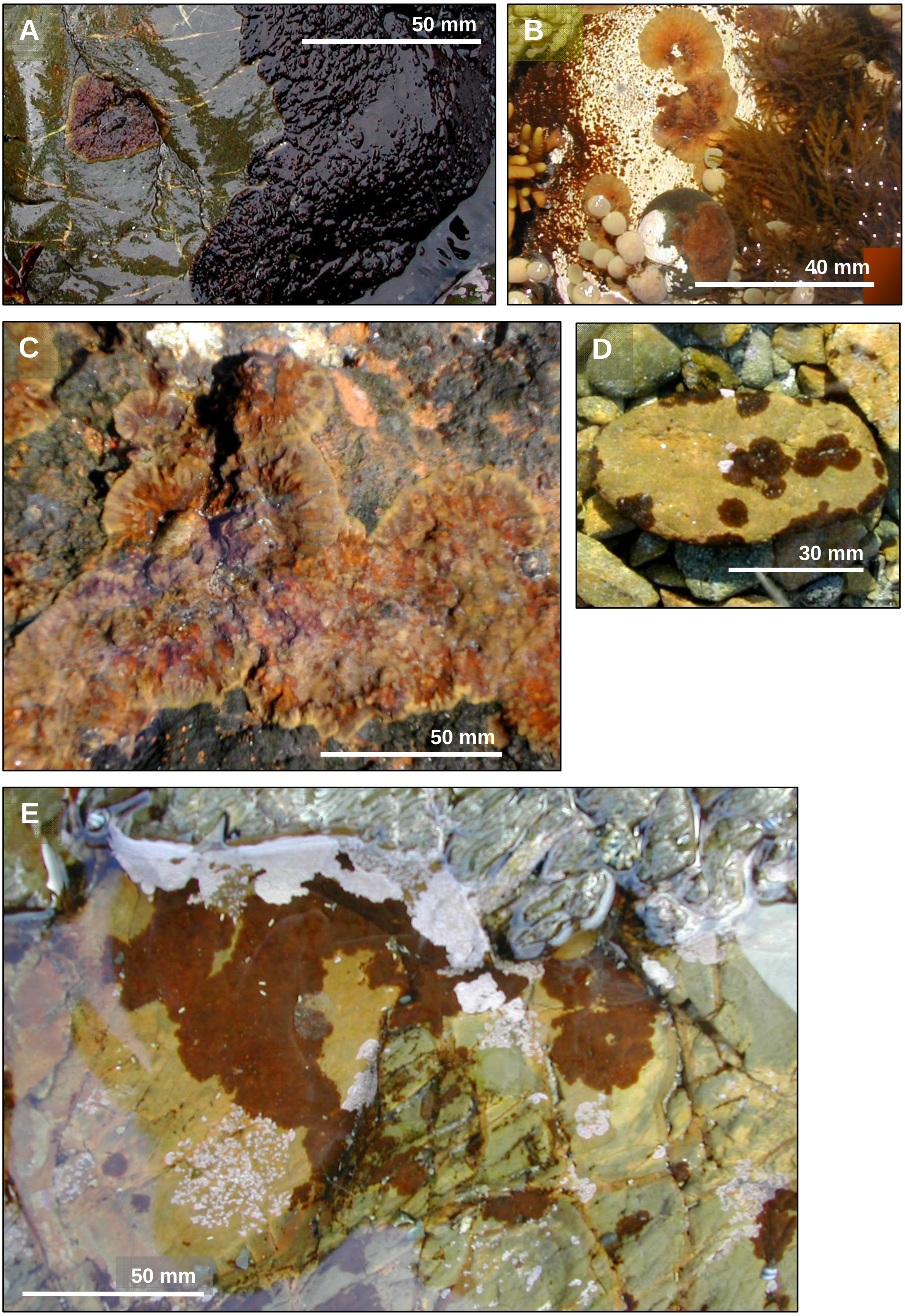

Plate 7. A–C. *Ralfsia expansa* **A.** Orbicular thallus with *Diplura sp.*, The Sirens, Wellington. **B.** Young thalli on rock and *Turbo*, Kaikoura. **C.** Confluent thalli. **D–E.** *Ralfsia confusa* **D.** Young thalli, Island Bay Wellington. **E.** Older confluent thalli in rock pool, Kau Bay, Wellington.

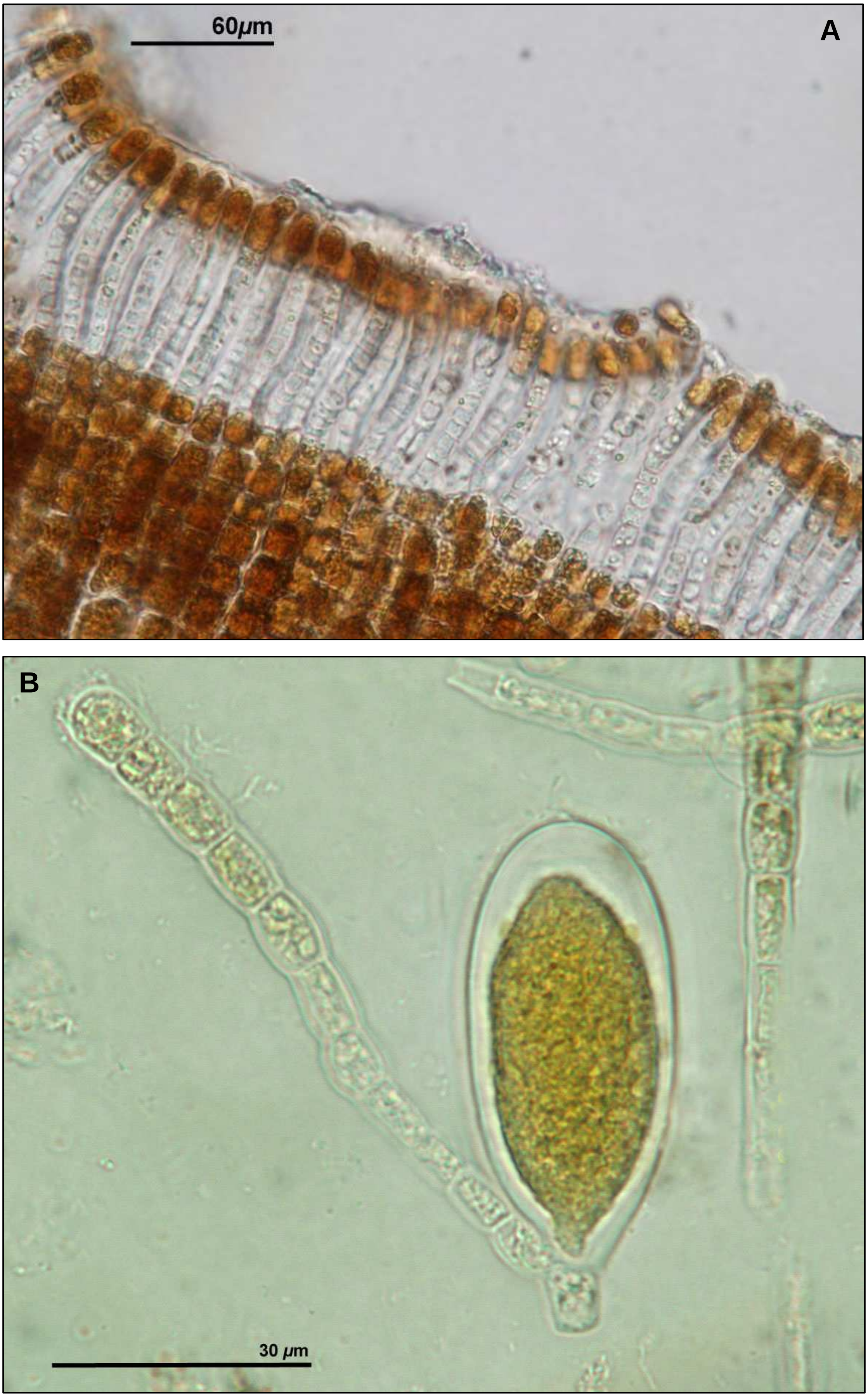

Plate 8. *Ralfsia expansa*. **A.** Plurangia. **B.** Detached unangium with paraphysis.

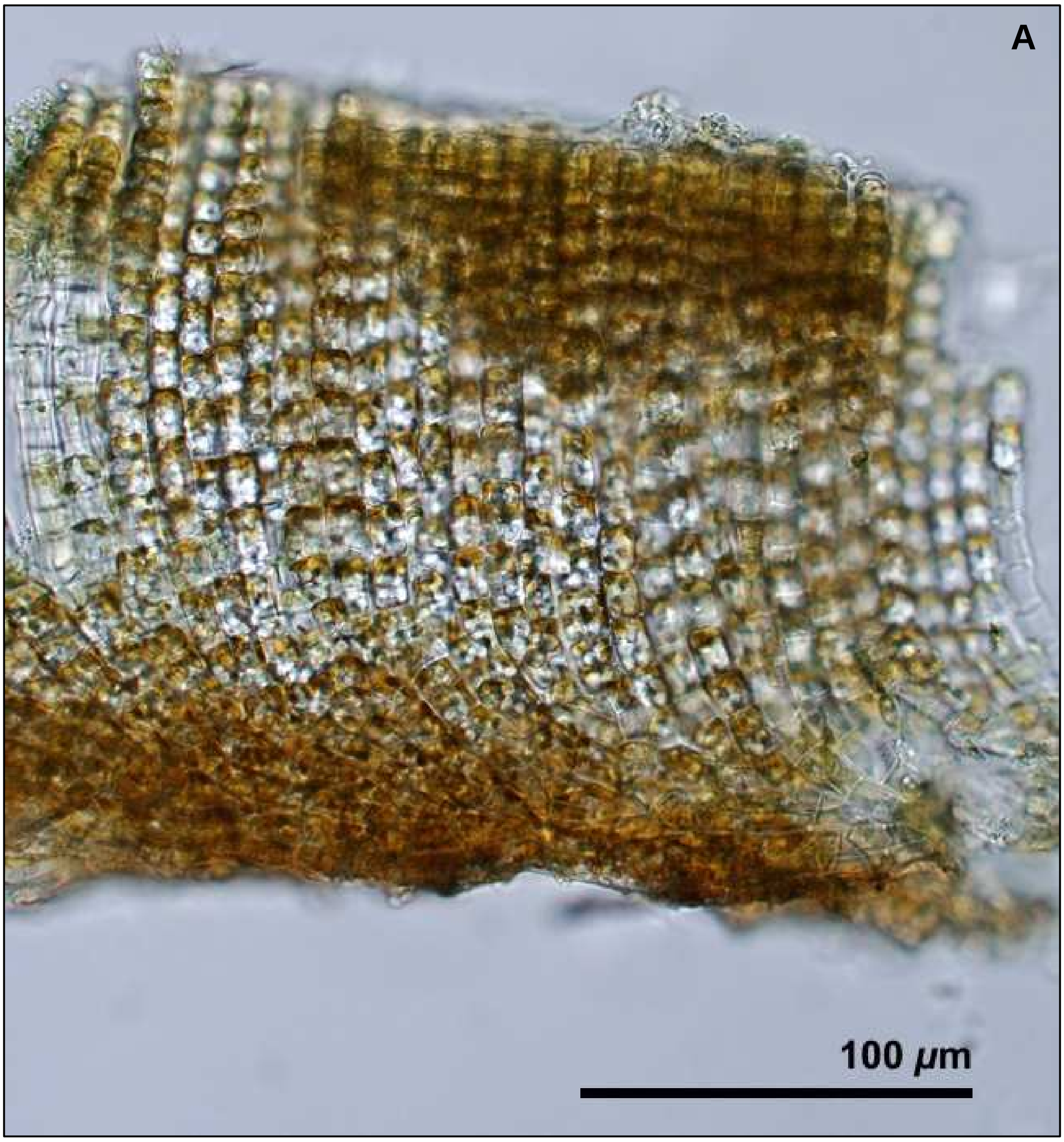

Plate 9. *Ralfsia sp.* “smooth”. A. Radial longitudinal section of thallus. **B.** Thalli growing on non-geniculate coralline algae, Elsdon Point, Wellington.

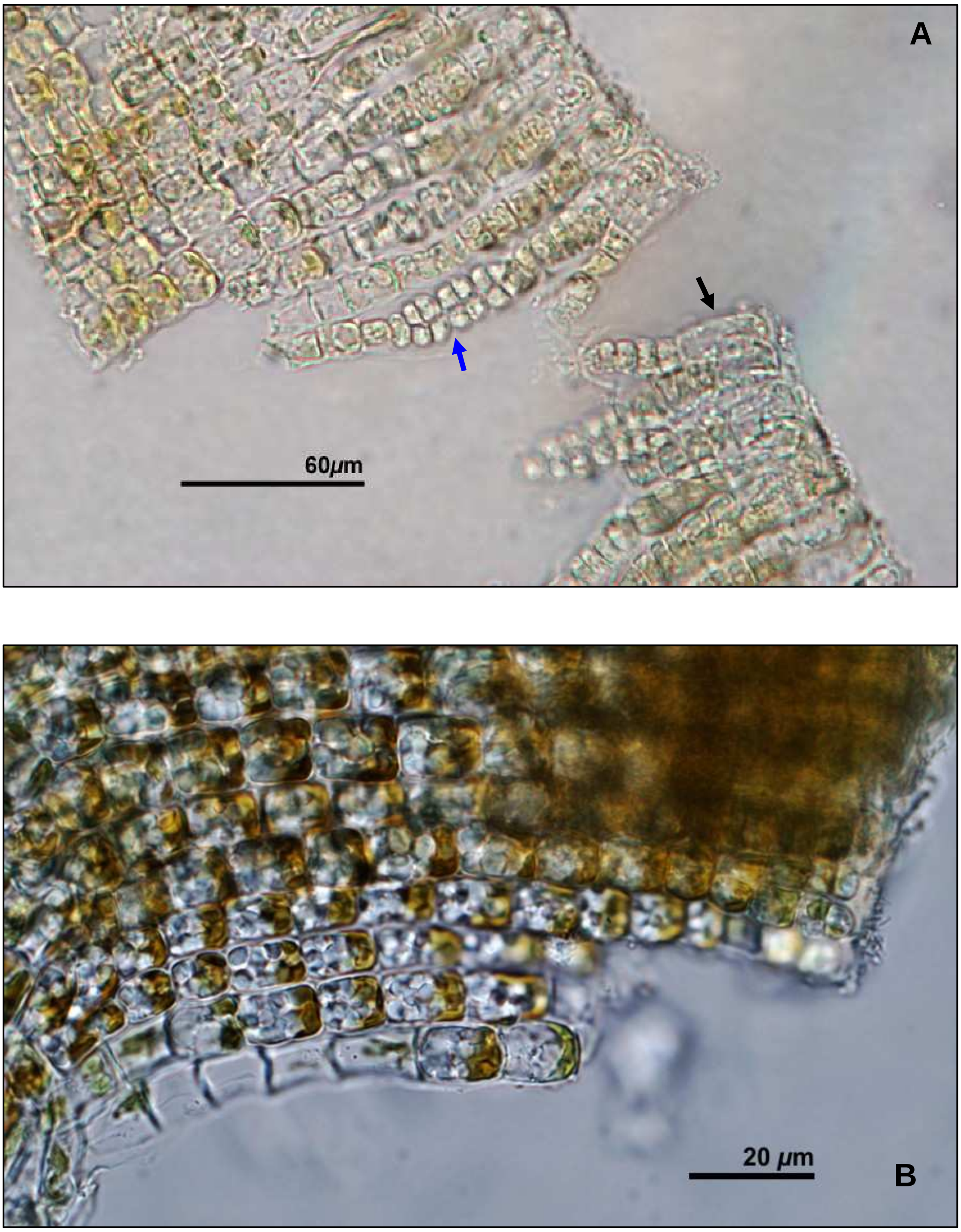

Plate 10. *Ralfsia sp.* “smooth”. **A.** Biseriate plurangia, blue arrow: locules; black arrow: terminal sterile cell. **B.** Cells of erect filaments with single plastid and physodes.

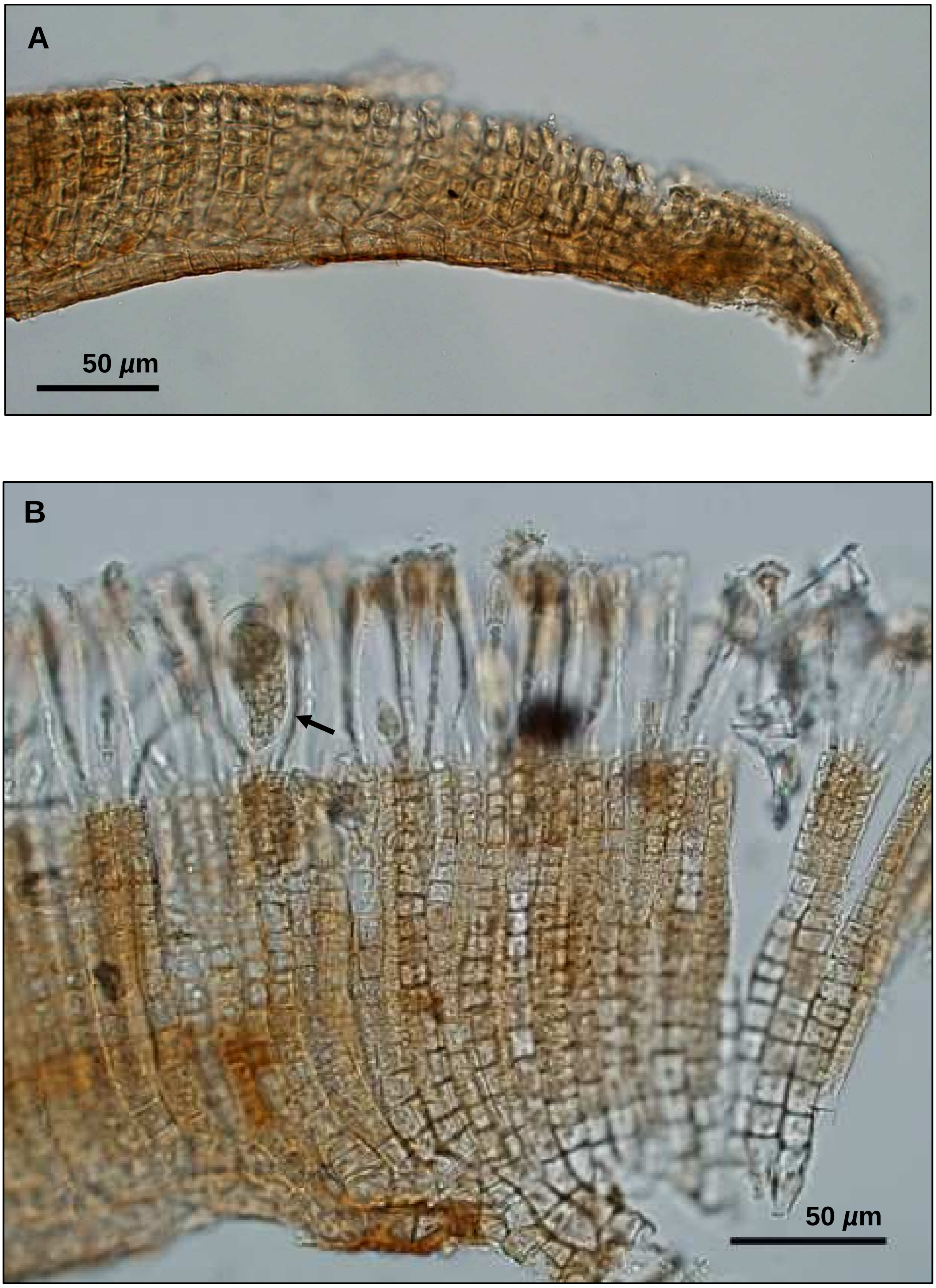

Plate 11. *Ralfsia confusa* **A.** Radial longitudinal section of edge of thallus. B. Radial longitudinal section with unangium (arrow) and paraphyses.

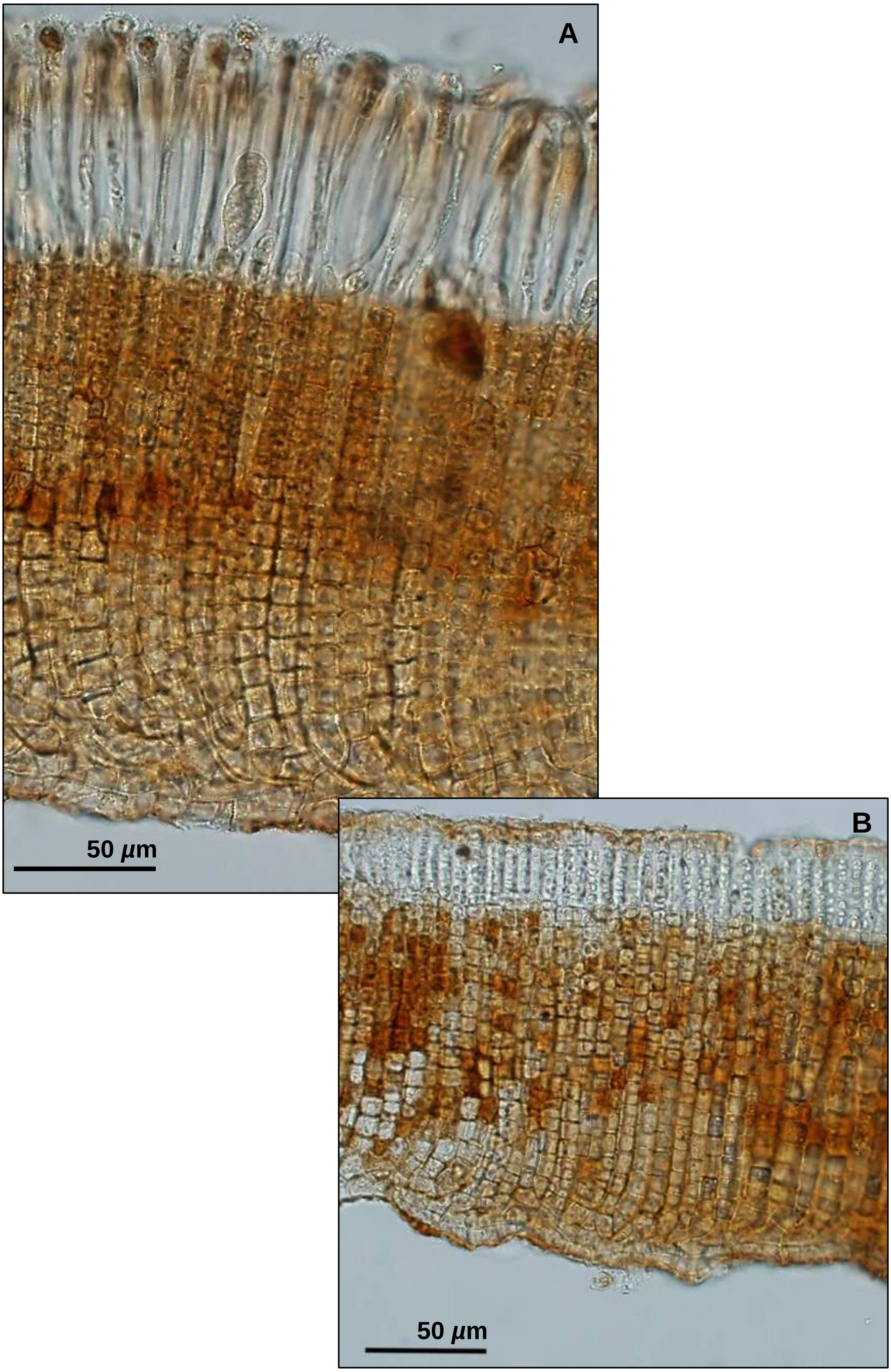

Plate 12. *Ralfsia confusa* **A.** Radial longitudinal section of thallus with unangia and paraphyses. **B**. Radial longitudinal section of thallus with plurangia.

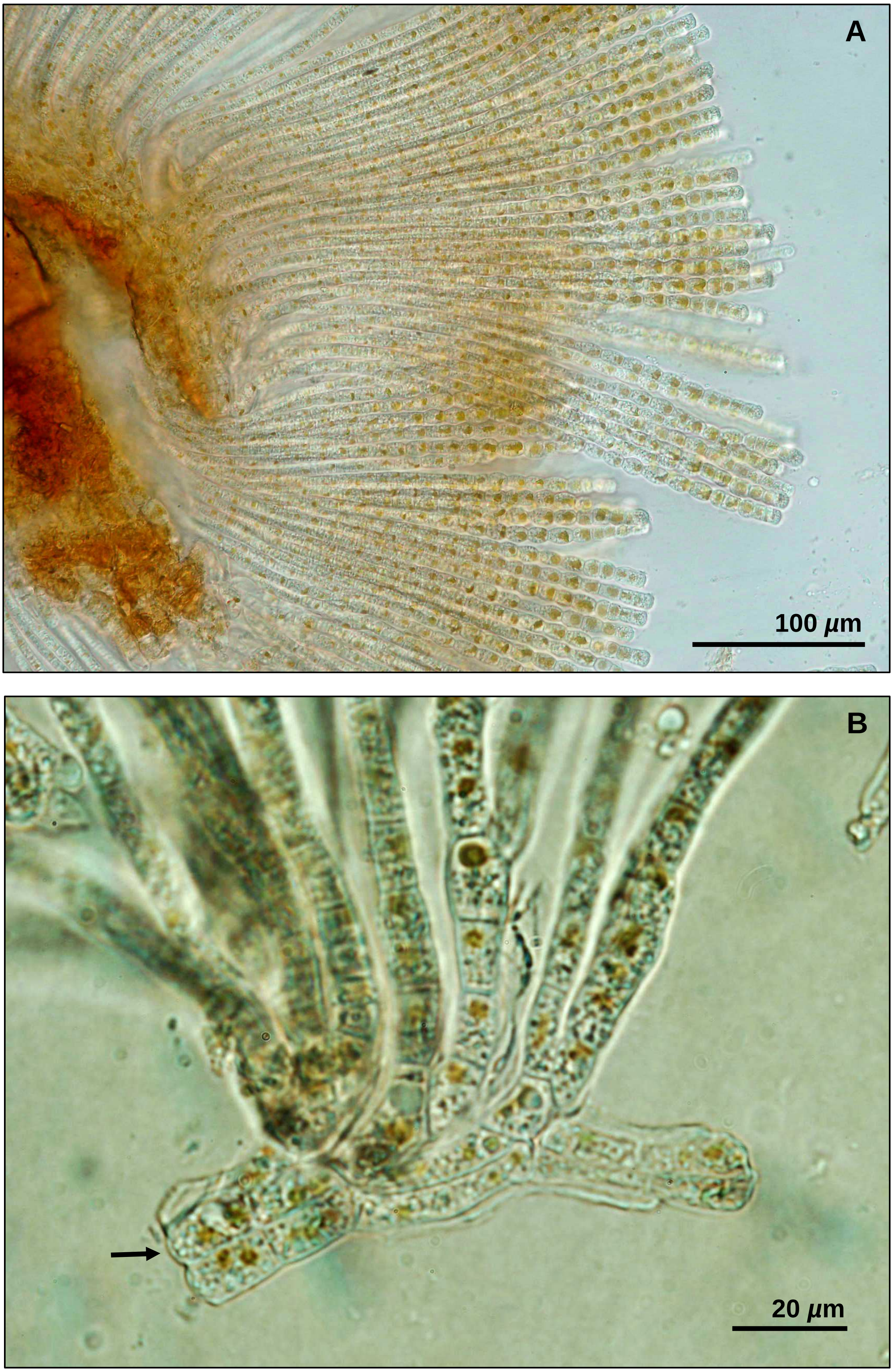

Plate 13. *Hapalospongidion gelatinosum*. A. vegetative thallus. B. Basal filaments (arrow) with lower part of erect filaments.

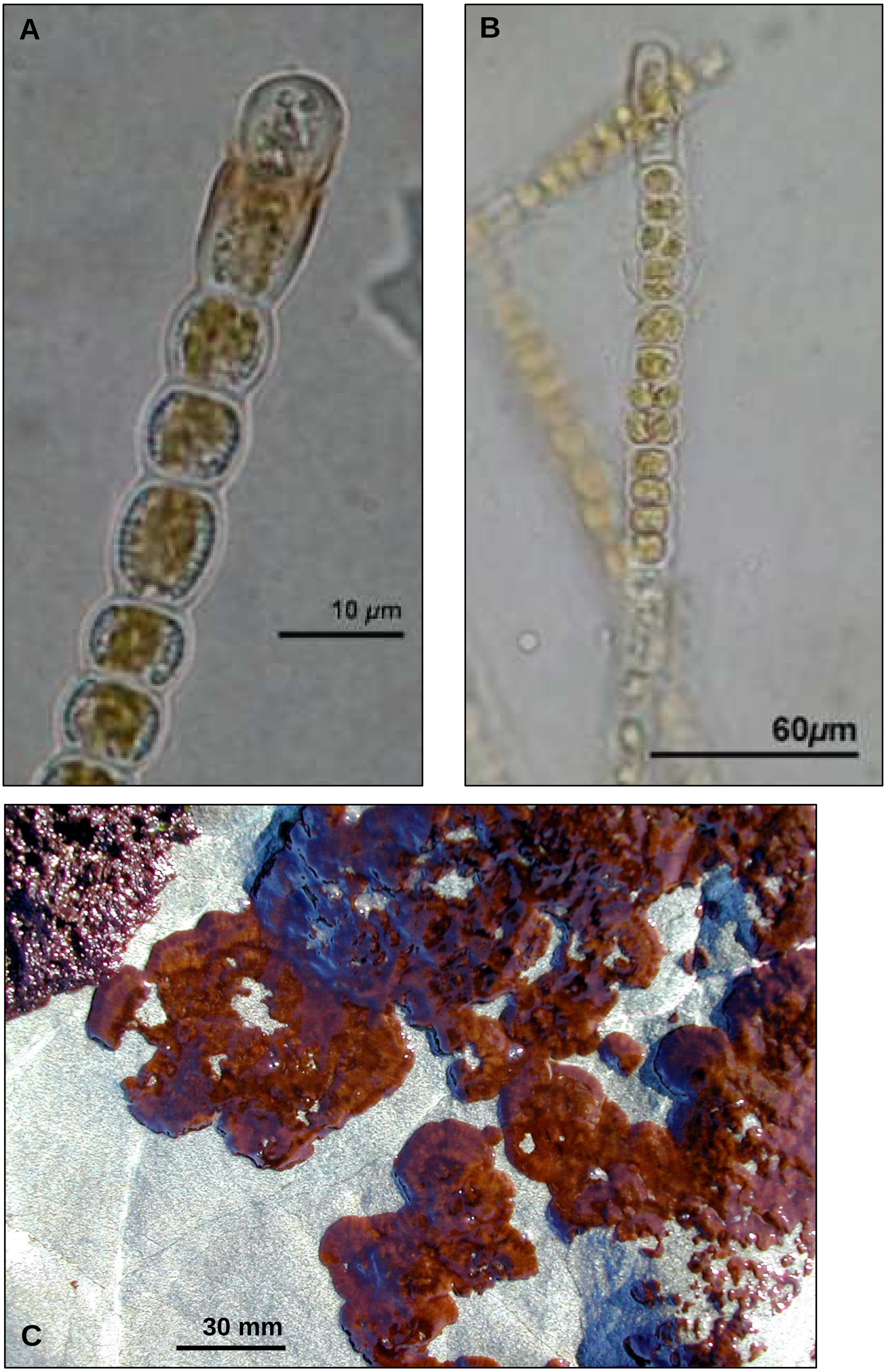

Plate 14. *Hapalospongidion gelatinosum* **A.** Apical cells of filament. **B.** Plurangium **C.** Confluent thalli, Houghton Bay, Wellington.

Chapter Four:
Molecular phylogenetics

4.1 Results

4.1.1 ITS Sequences

Ralfsiaceae/Lithodermataceae
ITS-2 sequences were obtained from all species. ITS-1 did not amplify well and fungal contamination was a problem. ITS-1 sequences from forward and reverse strands were obtained from *Hapalospongidion gelatinosum, Ralfsia expansa* and *Ralfsia sp.* "smooth." Complete ITS-1 sequences were not obtained from *Ralfsia confusa*, *Diplura sp*. and *Pseudolithoderma roscoffense*.

ITS regions of *Hapalospongidion gelatinosum* were longer than other Ralfsiaceae (Table 4.1), and contained many repeated motifs. ITS-2 regions of other species ranged from 329 nucleotides (in *Diplura sp.*) to 418 nucleotides (in *Ralfsia sp*. "smooth").

Scytosiphonaceae

ITS-2 sequences were obtained from *Colpomenia bullosa* from Point Elsdon (two specimens) and from Matheson Bay in Northland. All sequences were identical and were identical to ITS-2 sequences from this species from Muroran, Hokkaido, Japan, published by Kogame & Masuda (2001) (GenBank Accession number AB046577). One ITS-2 sequence of *Petalonia binghamiae* from Island Bay, Wellington was identical to sequences from Korea and California (in Cho e*t al*. 2002: California specimen from Shaw's Cove, GenBank accession number AY154723; Korean specimen from Sacheon, GenBank accession number AY154721).

4.1.2 LSU sequences

Sequences of approximately 1000 nucleotides of the 5′ end of the LSU nrDNA were obtained for all known New Zealand Ralfsiaceae and *Pseudolithoderma roscoffense* of the Lithodermataceae.

Table 4.1: Length of ITS-1 and ITS-2 regions of New Zealand Ralfsiaceae and Lithodermataceae. ITS borders according to Saunders & Druehl (1993a). ND: no complete data.

Species	**Length**	
	ITS-1	**ITS-2**
Ralfsia expansa	296–306	362–366
Ralfsia confusa	ND	370–379
Ralfsia sp. "Smooth"	395	418
Hapalospongidion gelatinosum	663	557
Diplura sp.	ND	329
Pseudolithoderma roscoffense	ND	361

4.1.3 Sequence alignment

ITS sequences

Alignment of ITS-2 sequences was possible within *Ralfsia*. Alignment required some gaps and alignment was ambiguous in some areas. The completed alignment included 462 sites of which 104 were parsimony informative. No outgroup taxon was alignable with *Ralfsia* sequences. Only a few short sections of ITS-2 sequences from *Hapalospongidion gelatinosum* could be aligned with sequences from other species. ITS-2 sequences of *Diplura sp.* and *Pseudolithoderma roscoffense* were alignable, and these sequences could be aligned, with several gaps and some ambiguity, with species of *Sphacelaria* obtained from GenBank. Alignments are shown in Appendix 1.

LSU alignment

Sequences were aligned according to Rousseau *et al.* 2001. This was not difficult, but required the addition of one additional long gap at positions 476 to 496 to accommodate *Diplura sp*. The alignment is shown in Appendix 2.

4.1.4 Phylogenetic relationships

ITS sequences

All trees had similar topology and branches between species had good bootstrap support (Fig. 4.1 and 4.2). Bayesian posterior probabilities were above 95%, except for the separation of *Ralfsia sp*. “smooth” from other taxa, which had 93% support.

Ralfsia confusa and *Ralfsia sp.* “smooth” are closely related but all analyses separated these species into two groups that are congruent with morphological differences. Two specimens of *R. confusa* from Northland (Russell and Whananaki), the only specimens found with plurangia, grouped with unangia-bearing specimens from Wellington Harbour and Wellington’s South Coast. Uncorrected pairwise distances varied from 0.3% to 1.3% within *R. confusa* and 0.3–0.6% within *Ralfsia sp*. “smooth.” Pairwise distances between the two species ranged from 6.5% to 7.6%. *Ralfsia expansa* is more distantly related, specimens from Otamure Bay, Northland and from Wellington’s south coast differed by 0.7%, and *Ralfsia expansa* differed from *Ralfsia confusa* by 35.6–37.4%, and from *Ralfsia sp*. “smooth” by 33.3–33.9%.

LSU Sequences

LSU sequences produced trees with generally similar arrangement of taxa as those of Rousseau *et al.* (2001), Draisma *et al.* (2001) and Cho *et al.* (2004), but relationships between orders and within orders were poorly resolved and some branches had little bootstrap support (Figs. 4.3 and 4.4). Maximum parsimony analysis produced a tree in which the early branching of the Dictyotales was well resolved. A second branch contained *Syringoderma phinneyi* of the Syringodermatales and a group containing the Sphacelariales, *Diplura sp.* and *Pseudolithoderma roscoffense*. This group had only moderate bootstrap support (72%). All other taxa formed a group corresponding to what de Reviers & Rousseau (1999) term the "brown algal crown radiation". Within this group the relationships between orders were not well supported. Some orders (Ectocarpales, Desmarestiales and Scytothamnales) separated into single groups, but often with low bootstrap support. Other orders (Fucales, Tilopteridales) had less than 50% bootstrap support. The Ralfsiaceae formed a well supported clade, with the exception of *Diplura sp.*, which grouped with *Pseudolithoderma roscoffense* and the Sphacelariales. The relationship of the Ralfsiaceae and *Nemoderma tingitanum,* a species referred to the Ralfsiales by Nakamura (1972), was not resolved.

A maximum likelihood analysis produced a tree with similar topology to the maximum parsimony tree (Fig.4.4), separating *Ralfsia* species and *Hapalospongidion* from *Diplura* and *Pseudolithoderma*, which grouped with the Sphacelariales.

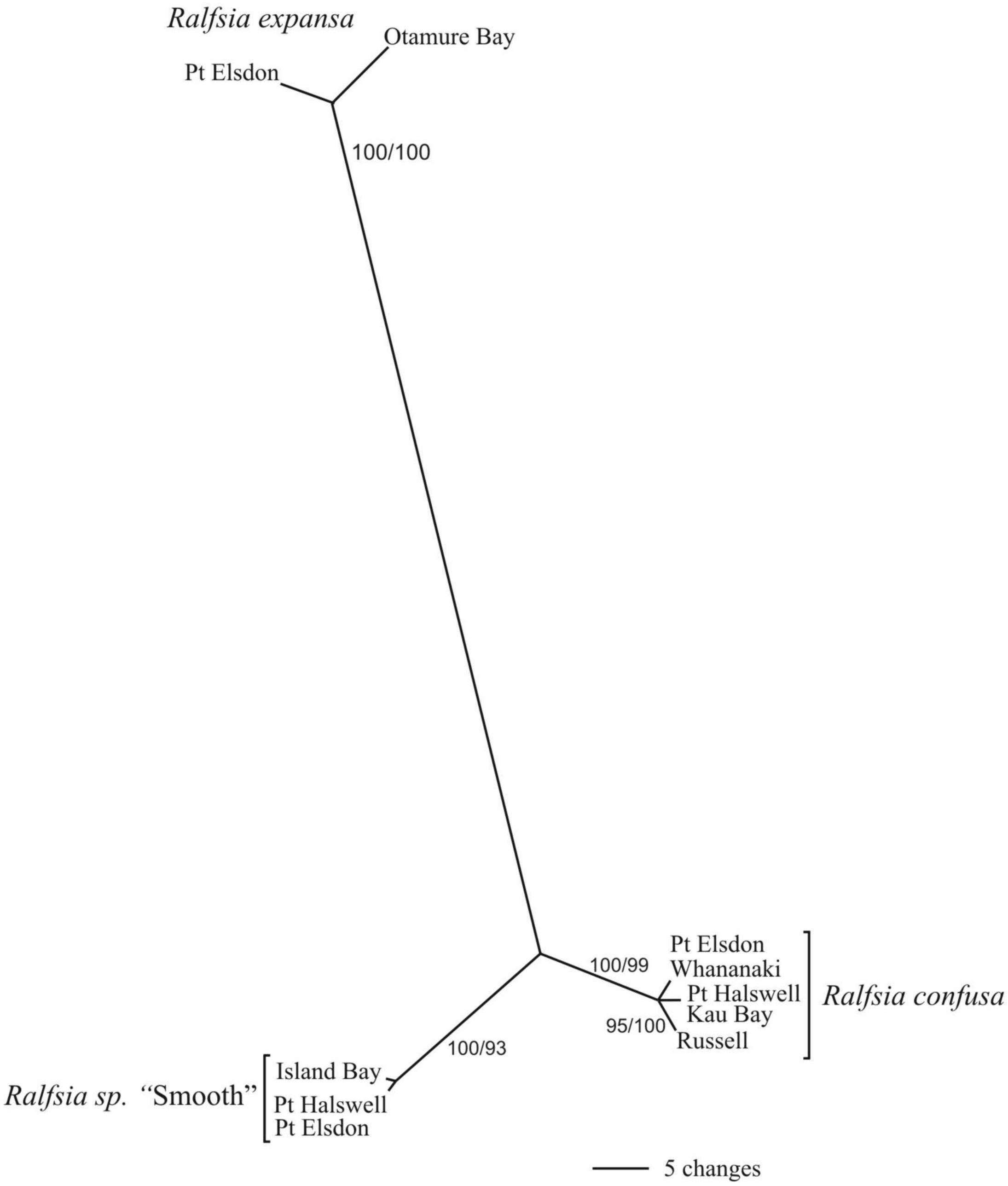

Fig. 4.1. Relationships of New Zealand species of *Ralfsia* based on ITS-2 sequences. One of 26 maximum parsimony trees inferred from a heuristic search. Nucleotide changes are indicated by branch lengths. Bootstrap values are shown beside branches (percentages of 1000 resamplings, left) and posterior probabilities from Bayesian analysis (right). Tree length=97; Consistency index=0.9897; Retention Index=0.9822.

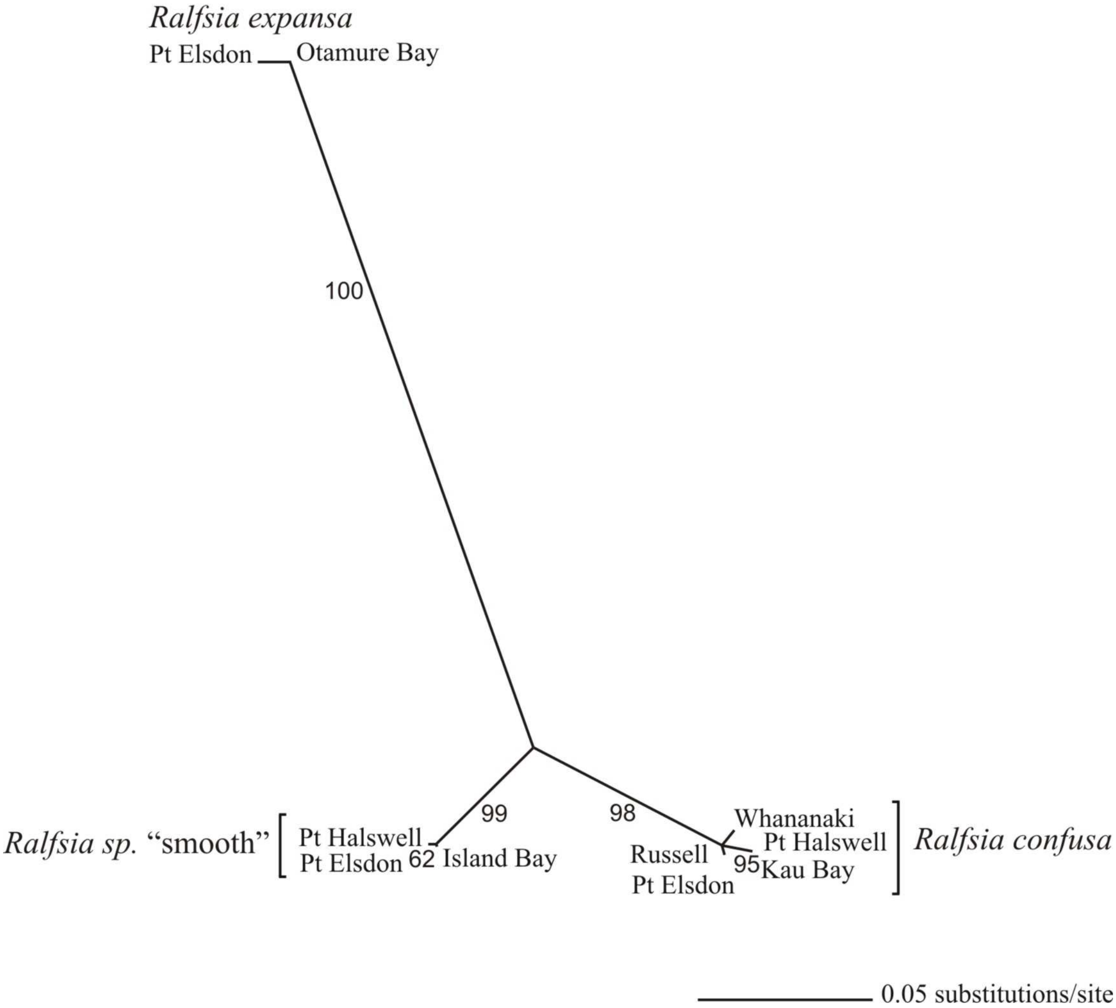

Fig. 4.2. Relationships of New Zealand species of *Ralfsia* based on ITS-2 sequences. Maximum likelihood tree inferred from heuristic search. -ln likelihood=1066.2353. Bootstrap values are shown below branches (percentages of 1000 resamplings).

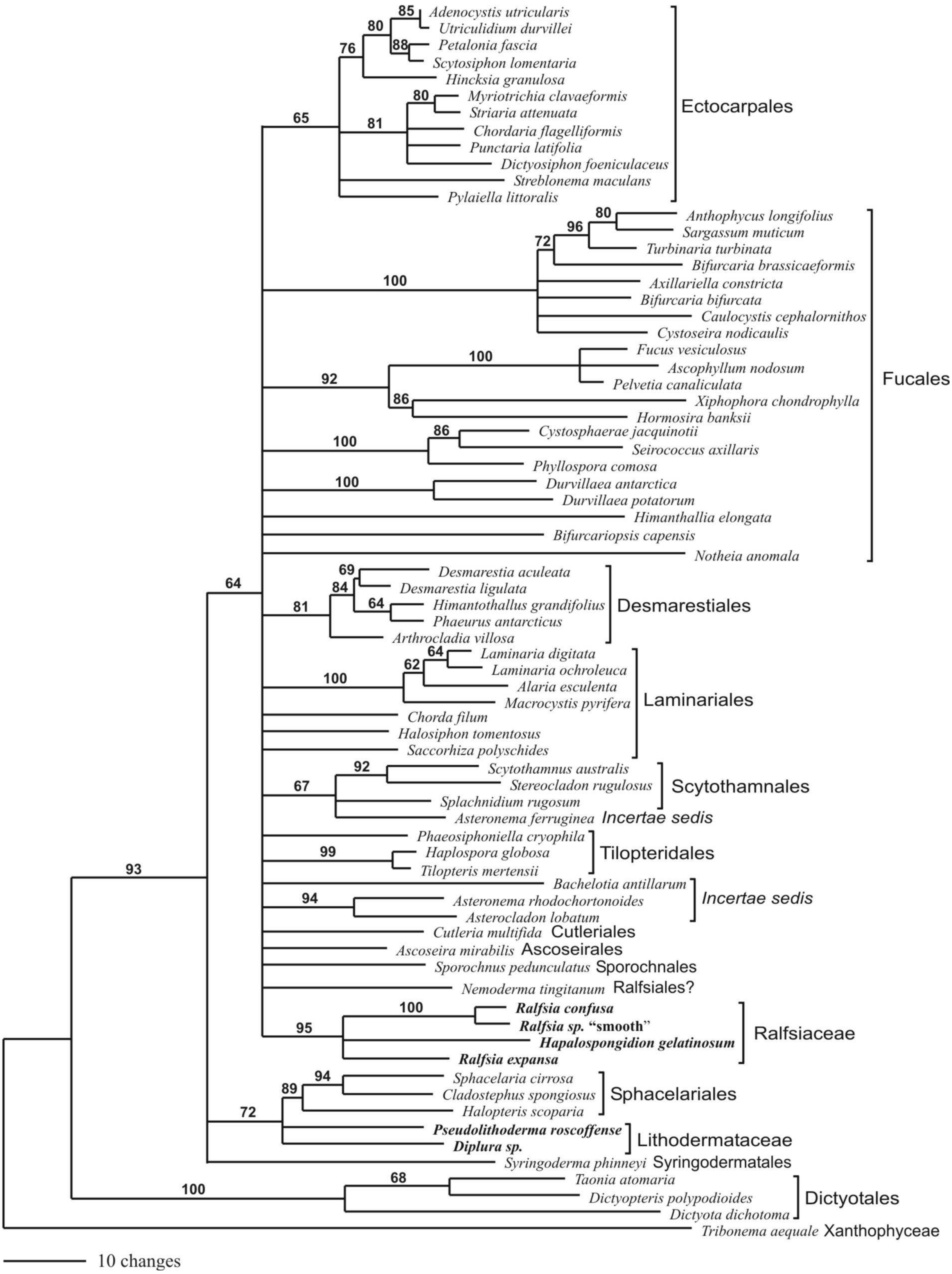

Fig. 4.3. Relationships of 73 phaeophycean species based on LSU nrDNA. Maximum parsimony tree inferred from heuristic search. Bootstrap values performed for 1000 replicates are indicated above branches. Branches with less than 50% support are collapsed. Tree length=1836; Consistency index=0.317; Retention Index=0.531. Species sequenced in this study are shown in bold type.

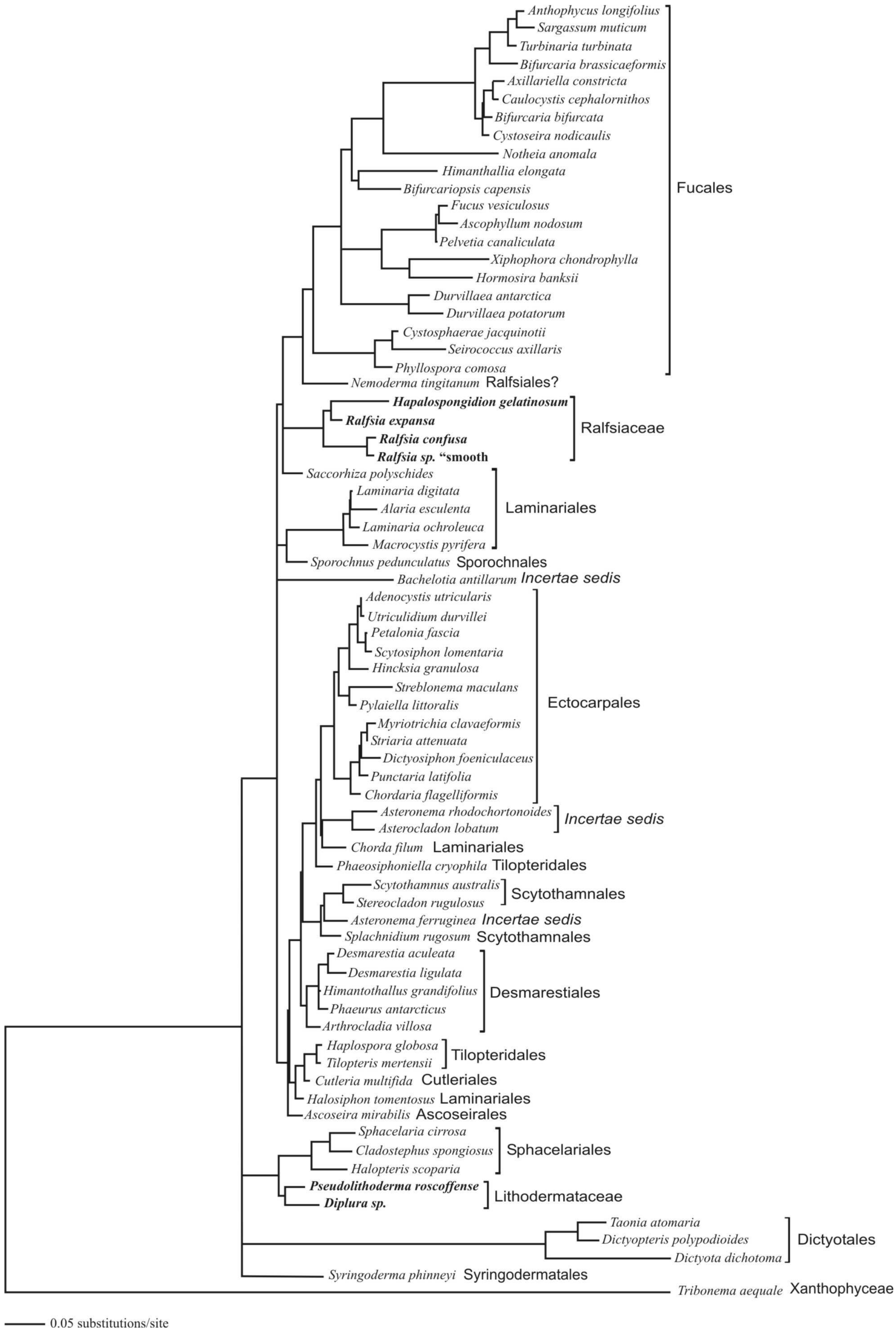

Fig. 4.4. Relationships of 73 phaeophycean species based on LSU nrDNA. Maximum likelihood tree inferred from heuristic search (-ln likelihood: 8113.51993). Species sequenced in this study are shown in bold type.

4.2 Discussion

4.2.1 Species and generic relationships

Divergence rates of ITS sequences in the Phaeophyta are very variable. Coyer *et al.* (2001) found a maximum of 3.3% divergence in *Macrocystis* species from the Northern and Southern Hemispheres, and van Oppen *et al.* (2002) found only 0.09% divergence in ITS sequences between *Desmarestia viridis/willi* between Northern and Southern Hemisphere populations. Conversely Cho *et al.* (2005) found between 9.2% and 11.01% divergence between ITS sequences of two lineages of *Colpomenia* and Cho *et al*. (2000) found up to 22.4% divergence between species of *Petalonia*. Coyer was unable to separate taxa usually regarded as separate species of *Macrocystis* using ITS data.

Divergence in ITS sequences in New Zealand *Ralfsia* is congruent with divergence in morphological characters. *Ralfsia confusa* and *Ralfsia sp.* “smooth” are the most morphologically similar species, distinguishable only by thallus thickness and the structure of the plurangia, and were considered as possibly conspecific, but analyses of ITS-2 sequences consistently separated the specimens sampled into two groups. *Ralfsia sp.* “smooth” was only collected from the Wellington region, but separated consistently from *Ralfsia confusa* from the same sites, and *Ralfsia confusa* from the same Wellington sites was more similar to Northland specimens than to *Ralfsia sp*. “smooth”. Both these species could be regarded as members of the genus or sub-genus *Stragularia* on the basis of having expansive sori and, in the case of *Ralfsia confusa*, short, nearly vertical filaments. I have not applied this name due to the confusion surrounding its use (see Chapter 1). *Ralfsia expansa* is more distantly related to other New Zealand *Ralfsia* (Figs. 4.1 and 4.2) and is consistent with Batters’ *Eu-Ralfsia* (Batters 1890).

Specific epithets were applied to local *Ralfsia* species on the basis of a limited number of morphological characters. The identity of local species could be confirmed by obtaining ITS sequences of specimens from the type locations. In particular *Ralfsia expansa* is reportedly widespread and descriptions are somewhat variable (León-Alvarez & González-González 2003), so a molecular study across the range of this species would clarify the identity of the New Zealand species.

4.2.2 Separation of the Ralfsiaceae and Scytosiphonacean microthalli

Studies by Kogame & Masuda (2001) and Cho *et al.* (2002, 2005) have provided a good data set of ITS sequences for the Scytosiphonaceae that are available on GenBank. ITS-2 sequences were adequate for discriminating between *Ralfsia* species and microthalli of the Scytosiphonaceae, and ITS-2 sequences obtained from of the two scytosiphonacean species in this study (*Petalonia binghamiae* and *Colpomenia bullosa*) were identical to sequences from North Pacific specimens. Microthalli of *Colpomenia bullosa* from New Zealand are larger than those reported by Kogame & Masuda (2001), with older thalli up to 30 mm diameter and forming extensive confluent crusts in rock pools. This exotic species is spreading in New Zealand (Parsons 1982, Nelson & Adams 1991, Adams 1994) and investigations of its spread and ecological impact should consider both life history phases.

4.2.3 Placement of **Hapalospongidion**

Hapalospongidion is morphologically distinct from *Ralfsia* and has been placed in a separate family, the Mesosporaceae (Tanaka & Chihara 1982). It was not possible to align ITS sequences of *Hapalospongidion* with any species of *Ralfsia.* LSU sequences did not separate *Hapalospongidion* from *Ralfsia*, but did separate this group from *Nemoderma tingitanum* (Nemodermataceae) and *Pseudolithoderma* (Lithodermataceae).

Tanaka & Chihara separated the Mesosporaceae from the Ralfsiaceae/Lithodermataceae on the basis of (1) intercalary plurilocular sporangia (separating the group from the Lithodermataceae) and (2) terminal unilocular sporangia on a stalk or vegetative filament (separating the group from the Ralfsiaceae). They included three genera, *Basispora*, *Hapalospongidion* and *Mesospora* in the family. The second character is somewhat ambiguous as it is not clear how the stalk should be defined and the meaning of *terminal* and *lateral* in relationship to the paraphysis (León-Alvarez & Norris 2005). Some *Ralfsia* species bear unangia on a stalk of several cells, but some workers describe these unangia as *lateral to the paraphysis* (e.g., Tanaka & Chihara 1980c). The vegetative filaments in *Hapalospongidion* are all similar to paraphyses of other Ralfsiaceae and scytosiphonacean microthalli and some workers (e.g., Abbott & Huisman 2004 on *Hapalospongidion pangoense*) have referred to all erect filaments of *Hapalospongidion* as paraphyses. It is not clear how the stalk or filament supporting the unangia is attached to the thallus. Rull Lluch (2002) found that the supporting filament of the unangia in *Hapalospongidion van-bosseae* branched off a vegetative filament near its base, so this vegetative filament could be regarded as laterally attached to a paraphysis, as in *Ralfsia*. Womersley (1987) regarded these characters and characters used to separate genera within the Mesosporaceae as inconclusive and merged these genera to a single genus, *Hapalospongidion*, which he placed in the Ralfsiaceae. The vegetative filaments of genera placed in the Mesosporaceae by Tanaka & Chihara are free from one another, but both the Lithodermataceae and the Ralfsiaceae contain members with more or less laterally adherent filaments and it is not clear that this character has any significance above the generic level.

The results of this study suggest that *Hapalospongidion* should be retained in the Ralfsiaceae until a wider study provides evidence otherwise.

4.2.4 Placement of **Diplura**

All analyses supported the separation of *Diplura* and *Pseudolithoderma* from the other Ralfsiaceae. ITS sequences from these two species were not alignable with other Ralfsiaceae but could be reasonably well aligned with one another. *Diplura* has previously been placed in the Ralfsiaceae (Hollenberg 1969, Tanaka & Chihara 1981b) based on having plurangia that have a terminal sterile cell. *Diplura* and a similar genus, *Endoplura,* possess several plastids per cell, unlike the other Ralfsiaceae *sensu stricto* (that is, not including the Lithodermataceae) with a single plastid per cell, but this character has been considered less important in the circumscription of the Ralfsiaceae than the intercalary organisation of the plurangia (Hollenberg 1969, Tanaka & Chihara 1981b). Some species of *Hapalospongidion* have been reported to contain more than one plastid per cell but this is not altogether clear (Rull Lluch 2002). Including more species and sequences from other regions of DNA should better resolve relationships, but these results suggest that the Lithodermataceae should be maintained as a separate family from the Ralfsiaceae and *Diplura* should be transferred to this family.

4.2.5 The Ralfsiales

Nakamura (1972) proposed the order Ralfsiales including three families, the Ralfsiaceae, the Lithodermataceae and the Nemodermataceae. These results suggest that Lithodermataceae and Nemodermataceae should be maintained as separate families, but do not resolve the relationship between the Nemodermataceae and the Ralfsiaceae. On the other hand *Diplura* and *Pseudolithoderma* were separated from the Ralfsiaceae in all analyses but were closely related to each other. The presence of several plastids per cell in *Diplura* and *Endoplura* has been raised as an objection to Nakamura’s proposed order Ralfsiales, which he characterized as having a single plate-like plastid per cell (Nelson 1982b). Transferring *Diplura* and *Endoplura* to the Lithodermataceae would overcome this objection, but would make the Lithodermataceae more diverse by including species with intercalary plurangia. These results suggest that the structure of the plurangia may be a less important character than the number of plastids per cell.

While the Ralfsiaceae were clearly separated from other orders, the relationship between the Ralfsiaceae *sensu stricto* (i.e. excluding *Diplura* and the Lithodermataceae) and other orders is unclear as analyses of LSU sequences alone did not resolve relationships between orders in the phaeophycean crown group. These relationships are well resolved in other studies that incorporate data from other regions of the genome (Rousseau *et al.* 2001, Draisma *et al.* 2001). However, this study did not show a close relationship between *Ralfsia*/*Hapalospongidion* and other phaeophycean orders. It is possible that the Ralfsiales should be recognized, strictly following Nakamura's diagnostic features (*See* Chapter One), and thus excluding species with more than one plastid per cell (*Diplura*, *Pseudolithoderma*) and those with pyrenoids, i.e. *Symphyocarpus* and *Sorapion* (Sears 2002).

4.2.6 Relationships of **Diplura***, the Lithodermataceae and the Sphacelariales*

The Phaeophyta can be divided into an early diverging group consisting of the Choristocarpaceae, Dictyotales, Sphacelariales, Onslowiaceae, Syringodermatales (Cho *et al.* 2004), the Ishigeales and the Phaeostrophiaceae (Kawai *et al.* 2005), and a second group consisting of the Ectocarpales, Fucales, Laminariales and several other orders, which de Reviers & Rousseau (1999) term the "brown algal crown radiation". This study suggests that a group including *Diplura* and at least some members of the Lithodermataceae are also part of this basal group.

The relationships within this basal group are only beginning to be resolved. Tan & Druehl (1996), in a phylogeny based on a limited number of small sub-unit nrDNA sequences found the Fucales were the first group to diverge from the phaeophycean lineage. Rousseau *et al.* 2001, using a larger data set of small and large sub-unit nrDNA sequences, found the Dictyotales were the earliest divergent group, followed by the Sphacelariales and the Syringodermatales. Draisma *et al.* (2001) added *rbc*L data and placed *Choristocarpus tenellus*, formerly placed in the Sphacelariales, as the earliest divergent taxon, followed by the Dictyotales and two separate clades of Sphacelariales and Syringodermatales. Recently, Cho *et al.* (2004) placed a newly established order, the Ishigeales between *Choristocarpus* and the Dictyotales and Syringodermatales. The Ishigeales is based on the Ishigeaceae, formerly placed in the Chordariales.

Kawai *et al.* (2005) found a weakly supported relationship between *Phaeostrophion irregulare* Setchell & Gardner and the Sphacelariales, based on large sub-unit and small sub-unit nrDNA and *rbc*L sequences. This little studied species has a perennial crustose base that develops erect blades. The cells possess several plastids without pyrenoids. Kawai *et al.* proposed a new family, the Phaeostrophiaceae, to accommodate this genus and declined to propose a new order. This result, and the results from this study, suggest morphologically diverse unresolved group that might include members of the Lithodermataceae, the Phaeostrophiaceae, and the Syringodermatales, with relationships to the Sphacelariales.

A relationship between Sphacelariales and other crustose brown algae has not been previously suggested. The Sphacelariales are small heterotrichous brown algae, with a basal part composed of creeping filaments, and usually with erect multiseriate filaments, with a prominent apical cell and tiers of cells formed by transverse and longitudinal cell divisions and hence parenchymatous. Cells of the Sphacelariales contain many disc-shaped chloroplasts (Prud'homme van Reine 1982) in common with *Diplura* and *Pseudolithoderma*. The genus *Sphacelaria* includes the crustose species, *Sphacelaria mirabilis* (Reinke ex Batters) Prud'homme van Reine. This species does not have erect axes, but has superficial reproductive filaments which were originally interpreted as an epiphyte, with the crustose base taken for a species of *Ralfsia* (Batters 1890[1]). This superficial resemblance to other crustose algae is interesting but may not imply a close relationship with other crustose species as it is clear that the crustose form has evolved several times (in the Scytosiphonaceae, the Ralfsiaceae, the Lithodermataceae and probably in the Phaeostrophiaceae).

4.2.7 Further work

LSU sequences are strongly conserved in the Phaeophyta. They are of limited value in resolving ordinal relationships (Draisma *et al*. 2001, Rousseau *et al*. 2001). Draisma *et al*. (2001) found *rbc*L sequences gave better resolution, although the reasons for this are not completely clear. Cho *et al*. (2004) also added *psa*A and *psb*A sequences and produced better resolved trees. Adding sequences from these regions, and including species from outside New Zealand should better resolve the relationships of the Ralfsiaceae among the brown algal crown group and the place of *Diplura* and the Lithodermataceae among the basal groups.

---

[1] A photocopy of the British Museum of Natural History's copy of Batters' *A List of the Marine Algae of Berwick-on-Tweed* (1890) included the following handwritten note beside this species (listed as *Battersia mirabilis* Reinke), presumably by Batters: *"What, in the above description, I have called "Ralfsia" is really the discoid base of the plant, the upright filaments are fruit-branches."*

5.0 References

ABBOTT, I. A. & HOLLENBERG, G. J. (1976). Marine algae of California. xii [xiii] + 827 pp. Stanford University Press, Stanford, California.

ABBOTT, I. A. & HUISMAN, J. M. (2004). Marine green and brown algae of the Hawaiian Islands. pp. xi + 259 +(1). Honolulu, Hawaií: Bishop Museum Press, 2004.

ADAMS, N. (1994). Seaweeds of New Zealand. Canterbury University Press.

AGARDH, J. G. (1847). Nya alger från Mexico. *Öfversigt af Kongl. Vetenskaps–Adademiens Förhandlingar, Stockholm* **4**: 5–17.

AGARDH, J. G. (1848). Species genera et ordines algarum. VIII + 363 pp. Lund, Sweden.

ANDERSON, R. J., SIMONS, R. H., & BOLTON, J. J. (1988). *Zeacarpa leiomorpha* (Ralfsiaceae), a new genus and species of crustose marine Phaeophyceae from southern Africa. *Phycologia* **27**: 319–326.

ARESCHOUG, J. E. (1875). Observationes phycologicae. Particula tertia. De algis nonnullis scandinavicis et de conjuctione Phaeozoosporarum Dictyosiphonis hippuroidis. *Nova Acta Regiae Societatis Scientiarum Upsaliensis Series 3* **10** (1): 1–36.

ATHANASIADIS, A. (1996). *Taxonomisk litteratur och biogeografi av Skandinaviska rödalger och brunalger.* 280. Algologia, Göteborg.

BALAKRISHNAN, M. S. & KINKAR, V. N. (1981). A taxonomic account of Indian Ectocarpales and Ralfsiales. *Seaweed Research and Utilisation* **4** (2): 1–57. Madras, India: Seaweed Research and Utilisation Association of India.

BARTON, E. S. (1903). List of marine algae collected at the Maldive and Laccadive Islands by J. S. Gardiner, Esq., M.A. *Journal of the Linnean Society, Botany* **35**: 475–482.

BATTERS, E. A. L. (1890). A list of marine algae of Berwick-on-Tweed. *History of the Berwickshire Naturalists' Club* **12**: 221–392. Alnwick.

BATTERS, E.A. (1893). New or critical British algae. *Grevillea* **21** (100): 102.

BENHISSOUNE, S., BOUDOURESQUE, C. F. & VERLAQUE, M. (2002). A Checklist of the Seaweeds of the Mediterranean and Atlantic Coasts of Morocco. II. Phaeophyceae. *Botanica marina* **45**: 217–230.

BOLD, H. C. & WYNNE, M. J. (1985). Introduction to the Algae. Structure and reproduction. pp. xvi + 720. Englewood Cliffs, New Jersey: Prentice Hall, Inc.

BONEY, A. D. (1982). Complementary association of an endophytic red alga and a shell encrusting green alga. *Annals of Botany* **50**: 179–183.

BØRGESEN, F. (1914). The marine algae of the Danish West Indies. Part II, Phaeophyceae. *Dansk Botanisk Arkiv* **2** (2): 1–66. Bianco Luno, Copenhagen.

BØRGESEN, F. (1924). Marine algae from Easter Island *In*: Skottsberg, C. (ed.) *The natural history of Juan Fernandez and Easter Island.* Almqvist & Wiksells, Uppsala.

BRITO, L.V.R. DE, SZÉCHY, M. T. M. DE & CASSANO, V. (2002). Levantamento taxonômico das macroalgas da zona das marés de costões rochosos adjacentes ao terminal maritimo almirante maximiano fomnesca, Baía da Ilha Grande, R. J. *Atlantica, Rio Grande* **24** (1): 17–26.

BROPHY, T. C. & MURRAY, S. N. (1989). Field and laboratory culture studies of a population of *Endarachne binghamiae* (Phaeophyta) from southern California. *Journal of Phycology* **25**: 6–15.

BURKHARDT, E. & PETERS, A. F. (1998). Molecular evidence from nrDNA ITS sequences that Laminariocolax (Phaeophyceae, Ectocarpales *sensu lato*) is a worldwide clade of closely related kelp endophytes. *Journal of Phycology* **34** (4): 682–691.

CHIHARA, M. (1970). Common Seaweeds of Japan in Colour. pp. xviii + 173. Osaka: Hoikusha Publishing Company.

CHO, G. Y., BOO, S. M., NELSON, W. & CLAYTON, M. N. (2005). Genealogical partitioning and phylogeography of *Colpomenia peregrina* (Scytosiphonaceae, Phaeophyceae) based on plastid *rbc*L and nuclear ribosomal DNA internal transcribed spacer sequences. *Phycologia* **44** (1): 103–111.

CHO, T. O., CHO, G. Y., YOON, H. S. & BOO, S. M. (2003). New records of *Myelophycus cavus* (Scytosiphonaceae, Phaeophyceae) in Korea and the taxonomic position of the genus on the basis of a plastid DNA phylogeny. *Nova Hedwigia* **76** (3–4): 381–397.

CHO, G. A., LEE, S. H. & BOO, S. M. (2004). A new brown algal order, Ishigeales (Phaeophyceae), established on the basis of plastid protein–coding rbcL, psaA and psbA region comparisons. *Journal of Phycology* **40** (5): 921–936.

CHO T. O., YANG, E. C., LEE, S. H. & BOO, S. M. (2002). First description of *Petalonia zosterifolia* and *Scytosiphon gracilis* (Scytosiphonaceae, Phaeophyceae) from Korea with special reference to nrDNA ITS sequence comparisons. *Algae* **17** (3): 135–144.

CHRISTENSEN, T. (1980). Algae: A taxonomic Survey. 1–216, Figs 1–69. Fasc. 1. Odense, Denmark: AiO Tryk.

CLAYTON, M. N. (1976). The morphology, anatomy and life history of a complanate form of *Scytosiphon lomentaria* (Scytosiphonales, Phaeophyta) from Southern Australia. *Marine Biology* **38**: 201–208. Springer-Verlag.

CLAYTON, M. N. (1978). Morphological variation and life history in cylindrical forms of *Scytosiphon lomentaria* (Scytosiphonaceae: Phaeophyta) from Southern Australia. *Marine Biology* **47**: 349–357.

CLAYTON, M. N. (1981). Studies in variability in Australian species of *Scytosiphon In:* Fogg, G. E. & Jones, W. E. (eds.) *Proceedings of the Eighth International Seaweed Symposium.* 67–75. Marine Science Laboratories, Menai Bridge.

CLAYTON, M. N. (1984). Evolution of the Phaeophyta with particular reference to the Fucales. Biopress Ltd.

CLAYTON, M. N. (1988). Evolution and life histories of brown algae. *Botanica Marina* **31**: 379–387.

CLAYTON, M. N. & KING R. J. (1981). Marine Botany: An Australasian perspective. Melbourne: Longman Cheshire.

COSTELLO, M. J., BOUCHET, P., BOXSHALL, G., EMBLOW, C., VANDEN BERGHE, E. (2004). European Register of Marine Species. Available online at http://www.marbef.org/data/erms.php. Consulted on 10/7/2005.

COYER, J. A., SMITH, G. J. & ANDERSEN, R. A. (2001). Evolution of *Macrocystis spp.* (Phaeophyceae) as determined by ITS1 and ITS2 sequences. *Journal of Phycology* **37**: 574–585.

CRIBB, A. B. (1996). *Seaweeds of Queensland – A naturalists guide.* 130. The Queensland Naturalist's Club Inc. Brisbane.

CRUZ–AYALA, M. B., NÚÑEZ–LÓPEZ, R. A. & LÓPEZ, G. E. (2001). Seaweeds in the Southern Gulf of California. *Botanica Marina* **44** (2): 2001.

DANGEARD, P. (1949). Les algues marines de la côte occidentale du Maroc. *Botaniste* **34**: 89–189.

DANGEARD, P. (1963). Recherches sur le cycle évolutif de quelques Scytosiphonacées. *Botaniste* **46**: 5–132.

DAWSON, E. Y. (1956). Some marine algae of the southern Marshall Islands. *Pacific Science* **10** (1): 25–66.

DE REVIERS, B. & ROUSSEAU, F. (1999). Towards a new classification of the brown algae. *Progress in Phycological Research* **13**: 107–201. Biopress Ltd.

DE TONI, G. B. (1895). Sylloge algarum omnium hucusque cognitarum. Vol. III. Fucoidae. 638. Padua.

DELLOW, V. & CASSIE, R. M. (1955). Littoral Zonation in two caves in the Auckland district. *Transactions of the Royal Society of New Zealand* **83** (2): 321–331.

DETHIER, M. N. (1981). Heteromorphic algal life histories: the seasonal pattern and response to herbivory of the brown crust, *Ralfsia californica*. *Oecologia* **49**: 333–339.

DETHIER, M. N. (1984). Disturbance and recovery in intertidal pools: Maintenance of mosaic patterns. *Ecological Monographs* **54**: 99–118.

DETHIER, M. N. (1987). The distribution and reproductive phenology of intertidal fleshy crustose algae in Washington. *Canadian Journal of Botany* **65**: 1838–1850.

DETHIER, M. N. (1994). The ecology of intertidal algal crusts: variation within a functional group. *Journal of Experimental Marine Biology and Ecology* **177**: 37–71. Elsevier.

DETHIER, M. N. & STENECK, R. S. (2001). Growth and persistence of diverse intertidal crusts: survival of the slow in a fast paced world. *Marine Ecology Progress Series* **223**: 89–100.

DIXIT, S. C. (1970). Species list of Indian marine algae–II. *Journal of the University of Bombay– III* **39 (Sc.)**: 99–130.

DRAISMA, S. G. A., VAN REINE, P. W. F., STAM, W. T. & OLSEN, J. L. (2001). A reassessment of phylogenetic relationships within the Phaeophyceae based on Rubisco large subunit and ribosomal DNA sequences. *Journal of Phycology* **37**: 586–603.

DRUEHL, L. D., MAYES, C., TAN, I. H. & SAUNDERS, G. W. (1997). Molecular and morphological phylogenies of kelp and associated brown algae. *Plant Systematics and Evolution* [Suppl.] **11**: 221–235. Springer-Verlag.

DREUHL, L. D. & SAUNDERS, G. W. (1992). Molecular explorations in kelp evolution. *Progress in Phycological Research* **8**: 47–83.

EARLE, S. A. (1969). Phaeophyta of the Eastern Gulf of Mexico. *Phycologia* **7** (2): 71–254.

EDELSTEIN, T., CHEN, L. & MCLACHLAN, J. (1968). Sporangia of *Ralfsia fungiformis* (Gunn.) Setchell et Gardner. *Journal of Phycology* **4**: 157–160.

EDELSTEIN, T., CHEN, L. C-M. & MCLACHLAN, J. (1970a). The life cycle of *Ralfsia clavata* and *R. borneti*. *Canadian Journal of Botany* **48**: 527–531.

EDELSTEIN, T., CHEN, L. C-M. & MCLACHLAN, J. (1970b). Investigations of the marine algae of Nova Scotia. VIII. The flora of Digby Neck peninsula, Bay of Fundy. *Canadian Journal of Botany* **48**: 621–629.

FARLOW, W. G. (1881). Marine Algae of New Englandand Adjacent Coast. Reprinted from Report of the U.S. Fish Commision for 1879. 1–210. Washington, Government Printing Office. (1969 Reprint, Lehre: Verlag Von J. Cramer, Biblioteca Phycologia, Band 8).

FELDMANN, J. (1937). Les algues marines de la Côte des Albères. I–III Cyanophycées, Chlorophycées, Phéophycées. *Revue Algologique* **9**: 141–335.

FELDMANN, J. (1949). L'ordre des Scytosiphonales. *Mémoires de la Société d'Histoire Naturelle de l'Afirique du Nord, hors série* **2**: 103–115.

FELSENSTEIN, J. (1981). Evolutionary trees from DNA sequences: A maximum likelihood approach. *Journal of Molecular Evolution* **17**: 368–376.

FELSENSTEIN, J. (1985). Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* **39**: 783–791.

FLETCHER, R. L. (1978). Studies on the family Ralfsiaceae (Phaeophyta) from around the British Isles *In*: Irvine, D. E. G. & Price, J. [Eds] *Modern approaches to the taxonomy of red and brown algae.* Academic Press, London, New York.

FLETCHER, R. L. (1987). Seaweeds of the British Isles. Vol. 3. Fucophyceae (Phaeophyceae). Part 1. x + 359 pp. British Museum (Natural History), London.

FLETCHER, R. L., MUNDA, I. M. & VUKOVIC, A. (1988). *Compsonema saxicolum* (Kuckuck) Kuckuck and *Microspongium gelatinosum* Reinke (Scytosiphonaceae, Fucophyceae): Two new records from the Mediterranean. *Botanica Marina* **31**: 1–8.

FRITSCH, F. E. (1945). *The Structure and reproduction of Algae, Vol. 2.* Cambridge University Press, Cambridge.

GARBARY, D. J., OLIVEIRA, J. C., SCAGEL, R. F. & VILLENEUVE, S. (1991). Notes and Distribution Records for the Marine Algae of Fiji. *Micronesica* **24** (2): 249–260. University of Guam.

GUIRY, M. D., NIC DHONNCHA, E. & RINDI, F. (2005). AlgaeBase version 3.0. World–wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; searched on 8 June 2005.

HAMEL, G. (1931–39). Phéophycées de France. Amsterdam: Linnaeus Press.

HARDY, F. G. & GUIRY, M. D. (2003). A Check-list and Atlas of the Seaweeds of Britain and Ireland. London: British Phycological Society.

HARVEY, A., WOELKERLING, W., FARR, T., NEILL, K. & NELSON, W. (2005). Coralline algae of Central New Zealand – An Identification Guide to Common 'Crustose' Species. *NIWA Information Series No. 57* 145 p. NIWA, Wellington.

HARVEY, W. H. (1846). Phycologia Brittanica Volume I. London: Reeve Bros., King William Street, Strand.

HAUCK, F. (1883–85). Die Meeresalgen Deutschlands und Österreichs. In: Rabenhorst, L. (Ed.) *Kryptogamen-Flora von Deutschland, Österreich und der Schweiz. Zweite Auflage*. Vol.2, pp. 513-575 + (I)-XXIII (XXIV). Leipzig: Euard Kummer.

HILLIS, D. M. & DIXON, M. T. (1991). Ribosomal DNA: molecular evolution and phylogenetic inference. *Quarterly Review of Biology* **66**: 411–453.

HOLLENBERG, G. J. (1942). Phycological Notes. *Bulletin of the Torrey Botanical Club* **69** (7): 528–538.

HOLLENBERG, G. J. (1968). Phycological notes III. New records of marine alage from the central tropical Pacific Ocean. *Brittonia* **20**: 74–82.

HOLLENBERG, G. J. (1969). An account of the Ralfsiaceae (Phaeophyta) of California. *Journal of Phycology* **5**: 290–301.

HOOKER, W. J. (1833). Class XXIV. Cryptogamma *In:* The English flora of Sir James Edward Smith. Vol. V (or Vol. II of Dr. Hooker's British flora). Part I. Comprising the mosses, Hepaticae, lichens, Characeae and algae. pp. x + 432. London:.

HSIAO, S. I. C. (1969). Life history and iodine nutrition of the marine brown alga, *Petalonia* fascia (O. F. Müll.) Kuntze. *Canadian Journal of Botany* **47**: 1611–1616.

HUELSENBECK, J. P. & RONQUIST, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17** (8): 754–755.

HURD, C. L., NELSON, W. A., FALSHAW, R. & NEIL, K. F. (2004). History, current status and future of marine macroalgal research in New Zealand: Taxonomy, ecology, physiology and human uses. *Phycological Research* **52**: 80–106.

JAASUND, E. (1964). Marine algae from northern Norway III. *Botanica Marina* **6**: 129–133.

JEFFS, A. (1985). The ecology of *Siphonaria* on Echinoderm Reef, with special reference to its association with the encrusting alga, *Ralfsia verrucosa*. MSc. Thesis, University of Auckland. Pp. 103 + xii.

JOHN, D. M. & LAWSON, G. W. (1974a). *Basispora*, a new genus of the Ralfsiaceae. *British Phycological Journal* **9**: 285–290.

JOHN, D. M. & LAWSON, G. W. (1974b). Observations on the marine algal ecology of Gabon. *Botanica Marina* **17**: 249–254.

JOHN, D. M., PRUD'HOMME VAN REINE, W. F., LAWSON, G. W., KOSTERMANS, T. B. & PRICE, J. H. (2004). A taxonomic and geographical catalogue of the seaweeds of the western coast of Africa and adjacent islands. *Beihefte zur Nova Hedwigia* **127**: 1–339.

KAEHLER, S. & FRONEMAN, P. W. (1999). Temporal variability in the effects of grazing by the territorial limpet *Patella longicosta* on the productivity of the crustose algae *Ralfsia verrucosa*. *South African Journal of Science* **95** (3): 121–122.

KAWAI, H., SASAKI, H., MAEBA, S., & HENRY, E. C. (2005). Morphology and molecular phylogengy of *Phaeostrophion irregulare* (Phaeophyceae) with a proposal for Phaeostrophiaceae fam. nov., and a review of the Ishigeaceae. *Phycologia* **44** (2): 169–182.

KJELLMAN, F. R. (1893). Fucaceae *In*: Engler, A. & Prantl, K. (Eds.) *Die natürlichen Pflanzenfamilien.* **I. Teil, Abt. 2.**: pp. 268–288. Leipzig.

KJELLMAN, F. R. & SVEDELIUS, N. L. (1910). Lithodermataceae Engler, A. & Prantl, K. Eds *Die natürlichen Pflanzenfamilien, Nachträge zum 1 T., 2 Abt.* **1** (2): 173–176. Leipzig.

KOGAME, K. (1996). Morphology and life history of *Scytosiphon canaliculatus* comb. nov. (Scytosiphonales, Phaeophyceae) from Japan. *Phycological Research* **44**: 85–94.

KOGAME, K. (1997a). Sexual reproduction and life history of *Petalonia fascia* (Scytosiphonales, Phaeophyceae). *Phycologia* **36**: 389–394.

KOGAME, K. (1997b). Life histories of *Colpomenia sinuosa* and *Hydroclathrus clathratus* (Scytosiphonaceae, Phaeophyceae) in culture. *Phycological Research* **45**: 227–231.

KOGAME, K. (1998). A taxonomic study of Japanese *Scytosiphon* (Scytosiphonales, Phaeophyceae) including two new species. *Phycological Research* **46**: 39–56.

KOGAME, K., HORIGUCHI, T. & MASUDA, M. (1999). Phylogeny of the order Scytosiphonales (Phaeophyceae) based onDNA sequences of *rbc*L, partial *rbc*S, and partial LSU nrDNA. *Phycologia* **38** (6): 496–502.

KOGAME, K., HORIGUCHI, H., YOSHIDA, T. & MASUDA, M. (1998). Morphology, phenology and culture of *Analipus gunjii* (Ralfsiales, Phaeophyceae). *Botanica Marina* **41**: 339–344.

KOGAME, K. & MASUDA, M. (2001). Crustose sporophytes of *Colpomenia bullosa* (Scytosiphonaceae, Phaeophyceae) in nature. *Cryptogamie Algologie* **22** (2): 201–208.

KOGAME, K. & YAMAGISHI, Y. (1997). The life history and phenology of *Colpomenia peregrina* (Scytosiphonales, Phaeophyceae) from Japan. *Phycologia* **36**: 337–344.

KORNMANN, P. & SAHLING, P–H. (1977). Meeresalgen von Helgoland, Benthische Grün–, Braun- und Rotalgen. *Helgoländer wissenschaftliche Meeresuntersuchungen* **29**: 1–289.

KRAAN, S. & GUIRY, M. D. (1998). Strain selection in the edible brown seaweed *Alaria esculenta*: Genetic fingerprinting and hybridization studies under laboratory conditions Marine Resources Series.

KRISTIANSEN, A. & PEDERSEN, P. M. (1979). Studies on life history and seasonal variation of *Scytosiphon lomentaria* (Fucophyceae, Scytosiphonales) in Denmark. *Botanisk Tidsskrift* **74**: 31–56.

KUKUCK, P. (1894). Bemerkungen zur marinen Algenvegetation von Helgoland. *Wissenschaftliche Meeresuntersuchungen. Neue Folge* **1** (1): 223–263.

KUMAR, S., TAMURA, K. & NEI, M. (2004). MEGA3: Integrated Software for Molecular Evolutionary Genetics Analysis and Sequence Alignment. *Briefings in Bioinformatics* **5**: 150–163.

KYLIN, H. (1947). Die Phaeophyceen der schwedischen Westküste. *Lunds universitets årsskrift. Acta Universitatis Lundensis. Nova series.* **43** (4): 1–99.

LAING, R. M. (1926). A reference list of New Zealand Marine Algae. *Transactions of the New Zealand Institute* **57**: 126–185.

LECLERC, M. C., BARRIEL, V., LECOINTRE, G. & DE REVIERS, B. (1998). Low divergence in rDNA ITS sequences among five species of *Fucus serratus* (Phaeophyceae) suggests a very recent radiation. *Journal of Molecular Evolution* **46**: 115–120.

LEE, E. G. & WILCOX, W. W. (2000). *Algae.* Prentice Hall, New Jersey.

LÉON-ALVAREZ, D. & GONZÁLEZ-GONZÁLEZ, J. (1993). Algas Costrosas del Pacifico Tropical. *In:* Salazar-Vallejo, S. I. y González, N. E. (eds.) *Biodiversidad Marina y Costera de México.* 456–474. Com. Nal. Biodiversidada y CIQRO, México.

LÉON-ALVAREZ, D. & GONZÁLEZ-GONZÁLEZ, J. (1995). Characterisation of the environmental distribution and morphs of *Ralfsia hancockii* Dawson (Phaeophyta) in the Mexican tropical Pacific. *Botanica Marina* **38**: 359–367.

LEÓN-ALVAREZ, D. & GONZÁLEZ-GONZÁLEZ, J. (2003). The morphological distinction of *Ralfsia expansa* and *R. hancockii* (Ralfsiaceae, Phaeophyta) from Mexico. *Phycologia* **42** (6): 613–621.

LEON-ALVAREZ, D. & NORRIS, J. N. (2005). Terminology and position of reproductive structures in crustose brown algae: Misapplication, confusion and clarification. *Cryptogamie, Algologie* **26** (1): 91–102.

LINDAUER, V. W. (1947). An annotated list of the brown seaweeds, Phaeophyceae, of New Zealand. *Transactions of the Royal Society of New Zealand* **76**: 542–566.

LINDAUER, V. W. (1949). Notes on the marine algae of New Zealand. *Pacific Science* **3**: 246–248. University of Hawaii.

LINDAUER, V. W., CHAPMAN, V. J. & AIKEN, M. (1961). The Marine Algae of New Zealand II: Phaeophyceae Nova Hedwigia III. Verlag Von J Cramer.

LITTLER, D. S. & LITTLER, M. M. (2000). Caribbean reef plants. An identification guide to the reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico. Offshore Graphics, Washington.

LITTLER, D. S. & LITTLER, M. M. (2003). South Pacific Reef Plants. A diver's guide to the plant life of the South Pacific Coral Reefs. 1–331. Washington, DC: OffShore Graphics, Inc.

LOISEAUX, S. (1967). Morphologie and Cytologie des Myrionémacées: Critères taxonomiques. *Revue Générale de Botanique* **74**: 329–347.

LOISEAUX, S. (1968). Recherches sur les cycles de développement des Myrionématacées (Phéophycées) III Tribu des Ralfsiées. *Revue Générale de Botanique* **75**: 295–318.

LUND, S. (1959). The marine algae of East Greenland. I. Taxonomic Part. *Meddelelser om Grønland* **156**: 247.

LUND, S. (1966). On a sporangia bearing microthallus of *Scytosiphon lomentaria* from nature. *Phycologia* **6** (1): 67–78.

LÜNING, K. & DRING, M. J. (1973). The influence of light quantity on the development of the brown algae *Petalonia* and *Scytosiphon*. *British Phycological Journal* **8**: 333–338.

MCLACHLAN, J., CHEN, L. C–M. & EDELSTEIN, T. (1971). The life history of *Microspongium sp. Phycologia* **10**: 83–87.

MEDINA, M., ANDRADE, S., FAUGERON, S., LAGOS, N., MELLA, D. & CORREA, J. A. (2005). Biodiversity of rocky intertidal benthic communities associated with copper mine tailing discharges in northern Chile. *Marine Pollution Bulletin* **50**: 396–409.

MORTON, O. (1994). *Marine algae of Northern Ireland. Ulster Museum Publication No. 271.* Ulster Museum, Botanic Gardens, Belfast.

MÜLLER, D. G., PARODI, E. R. & PETERS, A. F. (1998). *Asterocladon lobatum* gen. *et* sp. nov., a new brown alga with a stellate chloroplast arrangement, and its systematic position judged from nuclear rDNA sequences. *Phycologia* **37**: 425–432.

NAKAMURA, Y. (1965). Development of zoospores in *Ralfsia*-like thallus, with special reference to the life cycle of the Scytosiphonales. *Botanical Magazine Tokyo* **78**: 109–110.

NAKAMURA, Y. (1972). A proposal on the classification of the Phaeophyta. *In:* Abbott, I. A. & Kurogi, M. *Contributions to the systematics of benthic marine algae of the North Pacific.* 147–155. Japanese Society of Phycology, Kobe, Japan.

NAKAMURA, Y. & TATEWAKI, M. (1966). The occurrence of *Ralfsia*-like thallus with unilocular sporangia in *Colpomenia bullosa*. *Proceedings of the 11th Pacific Science Congress, Tokyo, Algae in the Pacific* **7**: 18.

NAKAMURA, Y. & TATEWAKI, M. (1975). The life history of some species of Scytosiphonales. *Scientific papers of the Institute of Algological Research, Faculty of Science, Hokkaido University* **6**: 57–93.

NELSON, W. A. (1982a). Morphology, anatomy and systematic affinities of *Caepidium antarcticum* J. Ag. (Phaeophyta). *Botanica Marina* **25**: 371–379. Walter de Gruyter & Co.

NELSON, W. A. (1982b). A critical review of the Ralfsiales, Ralfsiaceae and the taxonomic position of *Analipus japonicus* (Harv.) Wynne (Phaeophyta). *British Phycological Journal* **17**: 311–320.

NELSON, W. M. & ADAMS, N. M. (1991). Distribution of the adventive seaweed *Colpomenia bullosa*. *New Zealand Botanical Society Newsletter* **26**: 12–13.

NELSON, W. A. & PHILLIPS, L. (1996). The Lindauer legacy – current names for the Algae Novae-Zelandicae Exsiccatae. *New Zealand Journal of Botany* **34**: 553–582.

NEW ZEALAND DEPARTMENT OF CONSERVATION/MINISTRY FOR THE ENVIRONMENT (1998). New Zealand's biodiversity strategy: Our chance to turn the tide. New Zealand Department of Conservation/Ministry for the Environment, Wellington New Zealand.

NIZAMUDDIN, M. & FAROOQUI, P. B. (1968). The morhpology and structure of *Endarachne binghamiae* J. Agardh. *Botanica Marina* **11**: 40–53.

NODA, M (1987). Marine Algae of the Japan Sea. Kazama Shobo, Tokyo.

Norris, N. J. (1972). Marine algae from the 1969 cruise of the *Makarele* to the northern part of the Gulf of California. *Boletin Sociedad de la Botanica Mexico* 32: 1–30.

N'Yeurt, A. D. R., South, G. R. & Keats, D. W. (1996). A revised checklist of the benthic marine algae of the Fiji Islands, South Pacific (including the island of Rotuma). *Micronesica* **29**: 49–98.

Okamura, K. (1936). Nippon Kaiso-shi. Tokyo.

Papenfuss, G. F. (1951). Phaeophyceae *In:* Smith, G. M. (ed.) *Manual of Phycology*. Chronica Botanica Company, Waltham, Mass. USA.

Papenfuss, G. F. (1953). Problems in the classification of the marine algae *Proceedings of the Seventh International Botanical Congress, Stockholm.* 822–3.

Parente, M. I., Fletcher, R. L. & Neto, A. I. (2000). New records of brown algae (Phaeophyta) from the Azores. *Hydrobiologia* **440**: 153–157.

Parente, M. I., Neto, A. I. & Fletcher, R. L. (2003). Morphology and life history studies of *Endarachne binghamiae* (Scytosiphonaceae, Phaeophyta) from the Azores. *Aquatic Botany* **76**: 109–116.

Parke, M. (1953). A preliminary check–list of British marine algae. *Journal of the Marine Biological Association of the UK* **32**: 497–520.

Parke, M. & Dixon, P.S. (1976). Check–list of British marine algae – third revision. *Journal of the Marine Biological Association of the UK* **56**: 527–594.

Parsons, M. J. (1982). *Colpomenia* (Endlicher) Derbès et Solier (Phaeophya) in New Zealand. *New Zealand Journal of Botany* **20**: 289–301.

Payri, C. E. & Meinesz, A. (1985). Algae. *Proceedings of the 5th International Coral Reef Conference, Tahiti, 27 May–1 June 1985* **1**: 498–518.

Pedersen, P. M. (1976). Marine benthic algae from southernmost Greenland. *Meddelelser om Grønland* **199** (3): 1–80. Nyt Nordisk Forlag Arnold Busck, Kabenhavn.

Peters, A. F. (1998). Ribosomal DNA sequences support taxonomic separation of the two species of *Chorda*: reinstatement of *Halosiphon tomentosus* (Lyngbye) Jaasund (Phaeophyceae, Laminariales). *European Journal of Phycology* **33** (1): 65–71.

Peters, A. F. & Clayton, M. N. (1998). Molecular and morphological investigations of three brown algal genera with stellate plastids: Evidence for Scytothamnales ord. Nov. (Phaeophyceae). *Phycologia* **37** (2): 106–113.

Peters, A. F. & Ramírez, M. E. (2001). Molecular phylogeny of small brown algae, with special reference to the systematic position of *Caepidium antarcticum* (Adenocystaceae, Ectocarpales). *Cryptogamie Algologie* **22** (2): 187–200.

Peters, A. F., Ramírez, M. E. & Rülke, A. (2000). The phylogenetic position of the subantarctic marine macroalga *Desmarestia chordalis* (Phaeophyceae) inferred from nuclear ribosomal ITS sequences. *Polar Biology* **23** (2): 95–99.

Phillips J. A. & Price I. R. (1997). A catalogue of Phaeophyta (brown algae) from Queensland, Australia. *Australian Systematic Botany* **10** (5): 683–721.

Phillips, N., Smith, C. M. & Morden, C. (2001). An effective DNA extraction protocol for brown algae. *Phycological Research* **49**: 97–102.

Posada, D. & Crandall, K. A. (1998). Modeltest: Testing the model of DNA substitution. *Bioinformatics* **14** (9): 817–818.

Price, J. H., John, D. M. & Lawson, G. W. (1978). Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment. II. Phaeophyta. *Bulletin of the British Museum (Natural History) Botany* **6**: 87–182.

PRUD'HOMME VAN REINE, W. F. (1982). A taxonomic revision of the European Sphacelariaceae (Sphacelariales, Phaeophyceae). *Leiden Botanical Series* **6**. x + 293pp.

RAMIREZ, M. G. & ROJAS, V. (1991). El género *Colpomenia* en Chile. *Boletin de la Museo Nacional de Natural Historia de Chile* **42**: 11–24.

RAVANKO, O. (1970). Observations on the taxonomy and ecology of the epilithic crustaceous brown algae in the SW Archipelago of Finland (Seili Islands). *Botaniska Notiser* **123**: 220–230.

RAVANKO, O. (1975). The effect of the environment on the morphological expressions of brown algae Harold Barnes *Ninth European Marine Biology Symposium.* 629–636. Aberdeen University Press.

REINKE, J. (1889). Atlas deutscher Meeresalgen. Vol. Heft 1pp. (I–IV +) 1–34, Plates 1–25. Berlin.

RIBERA, M. A., GÓMEZ–GARRETA, A., GALLARDO, T.,CORMACI, M., FURNARI, G. & GIACCONE, G. (1992). Check–list of Mediterranean Seaweeds. I. Fucophyceae (Warming 1884). *Botanica Marina* **35**: 109–130.

RICKER, R. W. (1987). Taxonomy and Biogeography of Macquarie Island Seaweeds. **vi + [2]**: 344. British Museum (Natural History), London.

ROUSSEAU, F., BURROWES, R., PETERS, A. F.,KUHLENKAMP, R., & DE REVIERS, B. (2001). A comprehensive phylogeny of the Phaeophyceae based on nrDNA resolves the earliest divergences. *Comptes Rendues de la Acadamie des Sciences de Paris – Sciences de la vie* **324**: 305–319. Elsevier.

ROUSSEAU, F. & DE REVIERS, B. (1999). Circumscription of the order Ectocarpales (Phaeophyceae): bibliographical synthesis and molecular evidence. *Cryptogamie Algologie* **20** (1): 5–18.

RUENESS, J., BRATTEGARD, T., LEIN, T. E., KÜFNER, R., PEDERSEN, A. & SØRLIE, A. C. (2001). Class Phaeophyceae (division Chromophyta) – brown algae (brunalger) *In:* Brattegard, T. & Holthe, T. [Eds] *Distribution of marine, benthic macro-organisms in Norway. A tabulated catalogue. preliminary Edition. Research Report No. 1997-1.* Direktoratet for Naturforvaltninhg, Trondheim.

RULL LLUCH, J. (2002). Marine benthic algae of Namibia. *Scientia Marina* **66 (**suppl**.)**: 5–256.

SANDERS, W. B., MOE, R. L. & ASCASO, C. (2004). The intertidal marine lichen formed by the pyrenomycete fungus *Verrucaria tavaresiae* (Ascomycotina) and the brown alga *Petroderma maculiforme* (Phaeophyceae): thallus organization and symbiont interaction. *American Journal of Botany* **91**: 511–522.

SANTELICES, B., RAMIREZ, M. E. & ABBOTT, I. A. (1989). A new species and new records of marine algae from Chile. *British Phycological Journal* **24** (1): 73–82.

SARTONI, G. & BODDI, S. (1989). *Acrospongium ralfsioides* Schiffner & *Ralfsia expansa* (J. Agardh) J. Agardh (Ralfsiaceae, Phaeophyta): two new records from the Alboran Sea. *Gionarle Botanico Italiano* **123** (3–4): 145–155.

SAUNDERS, DE A. (1898). Phycological memoirs. *Proceedings of the California Academy of Sciences. Series 3, Botany* **1**: 147–168.

SAUNDERS, DE A. (1899). New and little known brown algae of the Pacific Coast. *Erythea* **7**: 37–40.

SAUNDERS, G. W. (1993). Gel purification of red algal genomic DNA – an inexpensive and rapid method for the isolation of polymerase chain reaction friendly DNA. *Journal of Phycology* **29**: 251–254.

SAUNDERS, G. W. & DRUEHL, L. D. (1992). Nucleotide sequences of the small sub-unit ribosomal RNA genes from selected Laminariales (Phaeophyta): implications for kelp evolution. *Journal of Phycology* **28**: 544–549.

SAUNDERS, G. W. & DRUEHL, L. D. (1993a). Nucleotide sequences of the internal transcribed spacers and 5.8S rRNA genes from *Alaria marginata* and *Postelsia palmaeformis* (Phaeophyta: Laminariales). *Marine Biology* **115**: 347–352.

SAUNDERS, G. W. & DRUEHL, L. D. (1993b). Revision of the kelp family Alariaceae and the taxonomic affinities of *Lessoniopsis* Reinke (Laminariales, Phaeophyta). *Hydrobiologia* **260/261**: 689–697.

SAUNDERS, G. W. & KRAFT, G. T. (1995). The phylogenetic affinities of *Notheia anomala* (Fucales, Phaeophyceae) as determined from partial small sub-unit RNA sequences. *Phycologia* **34**: 383–389.

SCAGEL, R. F. (1966). The Phaeophyceae in perspective. *Oceanography and Marine Biology*. **4**: 123–194.

SCAGEL, R. F., GABRIELSON, P. W., GARBARY, D. J., GOLDEN, L., HAWKES, M. W., LINDSTROM, S. C., OLIVEIRA, J. C. & WIDDOWSON, T. B. (1989). A synposis of the benthic marine algae of British Columbia, southeast Alaska, Washington and Oregon. *Phycological Contributions, 3:vi + 532*. University of British Columbia.

SEARS, J. R. (2002). NEAS keys to the benthic marine algae of the northeastern coast of North America from Long Island Sound to the Strait of Belle Isle.

SEARS, J. R. & WILCE, R. T. (1973). Sublittoral benthic marine algae of southern Cape Cod and adjacent islands: *Pseudolithoderma paradoxum* sp. nov. (Ralfsiaceae, Ectocarpales). *Phycologia* **12**: 75–82.

SERRÃO, E. A., ALICE, L. A. & BRAWLEY, S. H. (1999). Evolution of the Fucaceae (Phaeophyceae) inferred from nrDNA–ITS. *Journal of Phycology* **35**: 382. 394.

SETCHELL, W. A. (1926). Tahitian Algae collected by W. A. Setchell, C. B. Setchell and H. E. Parks. *University of California Publications in Botany* **12** (5): 61–142 (Plates 7–22. University of California.

SETCHELL, W. A. & GARDNER, N. L. (1924). Expedition of the California Academy of Sciences to the Gulf of California in 1921. The marine algae. Proceedings of the California Academy of Sciences Series **4** (12): 695–949.

SETCHELL, W. A. & GARDNER, N. L. (1925). The marine algae of the Pacific coast of North America, Part III, Melanophyceae. *University of California Publications in Botany* **8**: 383–898.

SIEMER, B. L., STAM, W. T., OLSEN, J. L., & PEDERSEN, P. M. (1998). Phylogenetic relationships of the brown algal orders Ecotocarpales, Chordariales, Dictyosiphonales and Tilopteridales (Phaeophyceae) based on Rubisco large subunit and spacer sequences. *Journal of Phycology* **34**: 1038–1048.

SILVA, P. C., BASSON, P. W. & MOE, R. L. (1996). Catalogue of the benthic marine algae of the Indian Ocean. *University of California Publications in Botany* **79**: 1–1259. University of California.

SILVA, P. C. & DE REVIERS, B. (2000). Ordinal names in the Phaeophyceae. *Cryptogamie Algologie* **21** (1): 49–58. Elsevier SAS.

SILVA, P. C., MEÑEZ, E. G. & MOE, R. L. (1987). Catalog of the benthic marine algae of the Philippines. *Smithsonian Contributions to Marine Sciences* **27**: iv + 179, 2 figs, 1 table.

SKELTON, P. A. & SOUTH, G. R. (2002). Annotated catalogue of the benthic marine algae of the Palolo Deep National Marine Reserve of Samoa. *Australian Systematic Botany* **15**: 135–179.

SKOTTSBERG, C. (1921). Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. VIII. Marine algae. I. Phaeophyceae. *Kungl. svenska vetenskapsakademiens handlingar* **61** (11): 1–56. Uppsal, Stockholm, Almqvist & Wiksells Boktryckeri.

SMITH, G. M. (1944). Sublittoral marine algae of the Monterey Peninsula. *Proceedings of the California Academy of Sciences Series* **4** (25): 171–176.

SMITH, J. E. & SOWERBY, J. (1837–1843). English botany; or, coloured figure of British plants, with their essential characters, synonyms and places of growth. Supplement to Volume 3. London.

SOUTH, G. R. (1974). *Herpodiscus* gen.nov and *Herpodiscus durvilleae* (Lindauer) comb. nov., a parasite of *Durvillea antarctica* (Chamisso) Hariot endemic to New Zealand. *Journal of the Royal Society of New Zealand* **4** (4): 455–461.

SOUTH, G. R. & ADAMS, N. M. (1976). Marine algae of the Kaikoura Coast – A list of species *National Museum of New Zealand Miscellaneous Series.* **No. 1** (October 1976).

SOUTH, G. R., SKELTON, P.A. & YOSHINAGA, A. (2001). Subtidal benthic marine algae of the Phoenix Islands, Republic of Kiribati, Central Pacific. *Botanica Marina* **44**: 559–570.

SOUTH, G. R. & TITTLEY, I. (1986). A checklist and distributional index of the benthic marine algae of the North Atlantic Ocean. Huntsman Marine Laboratory and British Museum (Natural History), St Andrews and London.

STEGENGA, H., BOLTON, J. J. & ANDERSON, R. J. (1997). Seaweeds of the South African west coast. 655 pp. Bolus Herbarium, University of Cape Town, Cape Town.

STEPHENSON, T. A. (1944). The constitution of the intertidal flora and fauna of South Africa Part II. *Annals of the Natal Museum* **10**: 261–358.

STIGER, V., HORIGUCHI, T., YOSHIDA, T., COLEMAN, A. W. & MASUDA, M. (2000). Phylogenetic relationships of *Sargassum* (Sargassaceae, Phaeophyceae) with reference to a taxonomic revision of section Phyllocystae based on ITS-2 nrDNA sequences. *Phycological Research* **48**: 251–260.

STRÖMFELT, H. F. G. (1886). *Om algvegetationen vid Islands Kuster.* pp. 1–89. Göteborg: Akademisk Afhandling.

SUSSMANN, A. V. & DEWREEDE, R. E. (2001). Seasonality of the red algal crust '*Petrocelis franciscana'* (Gigartinales, Rhodophyta) on boulder-strewn shores of southern British Columbia, Canada. *Phycological Research* **49**: 51–59.

SWOFFORD, D. L. (2002). PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

TAN, I. H. & DRUEHL, L. D. (1993). Phylogeny of the Northeast Pacific brown algae (Phaeophycean) orders as inferred from 18S rRNA gene sequences. *Hydrobiologia* **260/261**: 699–704.

TAN, I. H. & DREUHL, L. D. (1994). A molecular analysis of *Analipus* and *Ralfsia* (Phaeophyceae) suggests the order Ectocarpales is polyphyletic. *Journal of Phycology* **30**: 721–729.

TAN, I. H. & DREUHL, L. D. (1996). A ribosomal DNA phylogeny supports the close evolutionary relationships among the Sporochnales, Desmarestiales and Laminariales (Phaeophyceae). *Journal of Phycology* **32**: 112–118.

TANAKA, J. & CHIHARA, M. (1980a). Taxonomic study of the Japanese crustose brown algae (1) General account and the order Ralfsiales. *The Journal of Japanese Botany* **55**: 193–202.

TANAKA, J. & CHIHARA, M. (1980b). Taxonomic study of the Japanese crustose brown algae (2) *Ralfsia* (Ralfsiaceae, Ralfsiales) (Part 1). *The Journal of Japanese Botany* **55**: 225–236.

TANAKA, J. & CHIHARA, M. (1980c). Taxonomic study of the Japanese crustose brown algae (3) *Ralfsia* (Ralfsiaceae, Ralfsiales) (Part 2). *The Journal of Japanese Botany* **55**: 337–342.

TANAKA, J. & CHIHARA, M. (1981a). Taxonomic study of the Japanese crustose brown algae (4) *Ralfsia* (Ralfsiaceae, Ralfsiales) (Part 3). *The Journal of Japanese Botany* **56**: 97–104.

TANAKA, J. & CHIHARA, M. (1981b). Taxonomic study of the Japanese crustose brown algae (5) *Endoplura* and *Diplura* (Ralfsiaceae, Ralfsiales). *The Journal of Japanese Botany* **56**: 153–160.

TANAKA, J. & CHIHARA, M. (1981c). Taxonomic study of the Japanese crustose brown algae (6) *Pseudolithoderma* (Lithodermataceae, Ralfsiales). *The Journal of Japanese Botany* **56**: 376–381.

TANAKA, J. & CHIHARA, M. (1982). Morphology and taxonomy of *Mesospora schmidtii* Weber van Bosse, Mesosporaceae fam.nov. (Ralfsiales, Phaeophyceae). *Phycologia* **21** (3): 382–389. Blackell Scientific Publications.

TATEWAKI, M. (1966). Formation of a crustaceous sporophyte with unilocular sporangia in *Scytosiphon lomentaria*. *Phycologia* **6** (1): 62–66.

TAVARÉ, S. (1986). Some probabilistic and statistical problems in the analysis of DNA sequences *In:* Miura, R. M. (ed.) *Some mathematical questions in biology – DNA sequence analysis.* pp. 57–86. American Mathematical Society, Providence, RI.

TAYLOR, W. R. (1957). Marine algae of the northeastern coast of North America. (vii) 509. The University of Michigan Press, Ann Arbor.

TAYLOR, W. R. (1960). Marine algae of the eastern tropical and subtropical coasts of the Americas. xi + 870 pp. The University of Michigan Press, Ann Arbor.

TORGO, FLAVIA M. DE S. (1963). Observações sôbre *Ralfsia expansa* (Phaeophyceae) e *Hyella caespitosa* (Cyanophyceae). *Boletim do Museu Nacional* **30**: 1–11.

TOSTE, M. F., PARENTE, M. I., NETO, A. I. & FLETCHER, R. L. (2003). Life history of *Colpomenia sinuosa* (Scytosiphonaceae, Phaeophyceae) in the Azores. *Journal of Phycology* **39**: 1268–1274.

TRONO, G. C. (JR) (1969). The marine benthic algae of the Caroline Islands, II. Phaeophyta and Rhodophyta. *Micronesica* **5** (1): 25–119.

VAN OPPEN, M. J. H., OLSE, J. L., STAM, W. T. & VAN DEN HOEK, C. & WIENCKE, C. (1993). Arctic-Antarctic disjunctions in the benthic seaweeds *Acrosiphonia arcta* (Chlorophyta) and *Desmarestia viridis/willii* (Phaeophyta) are of recent origin. *Marine Biology* **115**: 381–386.

VANDERMEULEN, H., DEWREEDE, R. E. & COLE, K. (1984). Nomenclatural recommendations for three species of *Colpomenia* (Scytosiphonales, Phaeophyta). *Taxon* **33**: 324–329.

VERLAQUE, M. (1988). Végétation marine de la Corse (Méditerranée). VII. Documents pour la flore des algues. *Botanica Marina* **31**: 187–194.

WAERN, M. (1949). Remarks on Swedish *Lithoderma*. *Svensk Botanisk Tidskrift* **43** (2–3): 633–670.

WEBER-VAN BOSSE, A. (1911). Notice sur quelques genres nouveaux d'algues de l'Archipel Malasien. *Annales du Jardin Botanique de Buitenzorg* **24**: 25–33.

WEBER-VAN BOSSE, A. (1913). Liste des algues de Siboga. I. Myxophyceae, Chlorophyceae avec le concours de M. Th. Reinbold. *Siboga–Expeditie Monographie 59a*. Leiden.

WEHR, J. D. (2002). Phylum Phaeophyta (Brown Algae) In: John, D. M., Whitton, B. A. & Brook, A. J. *The freshwater algal flora of the British Isles.* 278–280. Natural History Museum (London, England); British Phycological Society.

WHITE, T. J., BRUNS, T., LEE, S., TAYLOR, J. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In:* Innis, M. A., Gelfand, D. H., Shinsky, J. J., White, T. J., (eds.) *PCR Protocols: A Guide to Methods and Applications.* 315–322. Academic Press, San Diego.

WIENCKE, C. & CLAYTON, M. N. (2002). Antarctic Seaweeds. 239 pp. A.R.G. Gantner Verlag KG, Ruggell.

WILCE, R. T., WEBBER, E. E. & SEARS, J. R. (1970). *Petroderma* and *Porterinema* in the New World. *Marine Biology* **5**: 119–135.

WILLIAMSON, J. E. (1992). Distribution patterns and life history features of the intertidal encrusting alga *Pseudolithoderma sp*. MSc. Thesis in Zoology, University of Auckland.

WILLIAMSON, J. E. (1994). Nutritional interaction in an alga-barnacle association. *Oecologia* **99**: 16–20.

WILLIAMSON, J. E. & CREESE, R. G. (1996a). Colonisation and persistence of patches of the crustose bown alga *Pseudolithoderma sp*. *Journal of Experimental Marine Biology and Ecology* **203**: 191–208.

WILLIAMSON, J. E. & CREESE, R. G. (1996b). Small invertebrates inhabiting the crustose alga *Pseudolithoderma sp*. (Ralfsiaceae) in northern New Zealand. *New Zealand Journal of Marine and Freshwater Research* **30**: 221–232. The Royal Society of New Zealand.

WOMERSLEY, H. B. S. (1987). The marine benthic flora of southern Australia. Part II. 481 pp. South Australian Government Printing Division, Adelaide.

WOMERSLEY, H. B. S. (1996). The Marine Benthic Flora of Southern Australia: Rhodophyta Part IIIB Gracilariales, Rhodymeniales, Corallinales, and Bonnemaisoniales. *Flora of Australia Supplementary Series No. 5.* Australian Biological Resources Study Canberra/State Herbarium of South Australia.

WOMERSLEY, H. B. S. & BAILEY, A. (1970). Marine algae of the Solomon Islands. *Philosophical Transactions of the Royal Society of London. B Series (Biological Science)* **259**: 257–352. London.

WYNNE, M. J. (1969). Life history and systematic studies of some Pacific North American Phaeophyceae (brown algae). *University of California Publications in Botany* **50**: 1–88.

WYNNE, M. J. (1972). Studies on the life forms in nature and in culture of selected brown algae. *In*: Abbott, I. A. & Kurogi, M. *Contributions to the systematics of benthic marine algae of the North Pacific.* 133–145. Japanese Society of Phycology, Kobe, Japan.

WYNNE, M. J. (1982). Phaeophyceae In: Parker, S. P. (ed) *Synopsis and classification of living organisms Vol I.* McGraw–Hill, New York.

WYNNE, M. J. (1995). Benthic marine algae of the Seychelles collected during the RV Te Vega Indian Ocean Expedition. *Contributions of the University of Michigan Herbarium* **20**: 261–346.

WYNNE, M. J. (1998). A checklist of the benthic marine algae of the tropical and subtropical western Atlantic: first revision. *Nova Hedwigia* 116: iii + 155, 5 figs.

WYNNE, M. J. & LOISEAUX, S. (1976). Recent advances in life history studies of the Phaeophyta. *Phycologia* **15**: 435–452.

WYNNE, M. J. & NORRIS, J. N. (1976). The genus *Colpomenia* Derbès et Solier (Phaeophyta) in the Gulf of California. *Smithsonian Contributions to Botany* **35**: 1–18.

YAMADA, Y. (1948). Marine Algae No.1 (*Colpomenia bullosa*) Yamada, Y. & Kinoshita, S. *Icones of the Marine Animals and Plants of Hokkaido: 6.* Yoichi, Hokkaido: Hokkaido Fisheries Scientific Institution.

YONESHIGUE–VALENTIN, Y. & PUPO, D. (1994). Estudos in situ e in vitro de fase Ralfsióide *Stragularia clavata* (Harv. in Hook.) Hamel de *Petalonia fascia* (O.F. Müller) Kuntze (Scytosiphonales – Phaeophyta). *Revista Brasil. Biol.* **54**: 489–496.

6.0 Appendices

Appendix 1: Sequence alignments

New Zealand *Ralfsia* species, ITS2 Alignment

```
                                             111 111 111 122 222 222 223 333 333 333 444 444 444 455 555 555 556 666 666 666 777 777 777
                                 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678
Ralfsia_confusa_(Russell)        ACA CCA CTC GCA GTC TTG TGC CCT CCC CC- --- --T TCT TCC TTG TTG TCT TGT CTT TG- --- --- --- --- --- ---
Ralfsia_confusa_(Whananaki)      ... ... ... ... ... ... ... ... ... ..- --- --. ... ... ... --- ... ... ... ..- --- --- --- --- --- ---
Ralfsia_confusa_(Kau_Bay)        ... ... ... ... ... ... ... ... ... ..- --- --. C.. ... ... --- ... ... ... ..- --- --- --- --- --- ---
Ralfsia_confusa_(Pt_Halswell)    ... ... ... ... ... ... ... ... ... ..- --- --. C.. ... ... --- ... ... ... ..- --- --- --- --- --- ---
Ralfsia_confusa_(Pt_Elsdon)      ... ... ... ... ... ... ... ... ... ..- --- --. ... ... ... ... ... ... ... ..- --- --- --- --- --- ---
Ralfsia_sp._smooth_(Pt_Halswell) ... ... ... ... ... ... ... ... --- --- --- --. .T. ..T C.C .AT .TG .TC G.. ..T TGT TAT TTG CCG CTC GTT
Ralfsia_sp._smooth_(Island_Bay)  ... ... ... ... ... ... ... ... --- --- --- --. .T. ..T C.C .AT .TG .TC G.. ..T TGT TAT TTG CCG CTC GTT
Ralfsia_sp._smooth_(Pt_Elsdon)   ... ... ... ... ... ... ... ... --- --- --- --. .T. ..T C.C .AT .TG .TC G.. ..T TGT TAT TTG CCG CTC GTT
Ralfsia_expansa_(Otamure_Bay)    ... ... A.. C.- --- -C. .T. ... .AT --- -CG AC- --- --- C.C --- .T. .TC G-- --- --- --- --- --- --- ---
Ralfsia_expansa_(Pt_Elsdon)      ... ... A.. C.- --- -C. .T. ... .AT GAA TCA AC- --- --- C.C --- .T. .TC G-- --- --- --- --- --- --- ---

                                                             111 111 111 111 111 111 111 111 111 111 111 111 111 111 111 111 111 111 111
                                 788 888 888 889 999 999 999 000 000 000 011 111 111 112 222 222 222 333 333 333 344 444 444 445 555 555
                                 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456
Ralfsia_confusa_(Russell)        --- --- --- --- --- --- --- --- --- --A GCA GGA GGA GGA --- GGA GGA GGA GGG GGG G-- ACA -CG ACG GCG GAC
Ralfsia_confusa_(Whananaki)      --- --- --- --- --- --- --- --- --- --. ... ... ... ... --- ... ... ... ... ... .-- ... -.. ... ... ...
Ralfsia_confusa_(Kau_Bay)        --- --- --- --- --- --- --- --- --- --. ... ... ... ... --- ... ... ... ... ... .-- ... -.. ... ... ...
Ralfsia_confusa_(Pt_Halswell)    --- --- --- --- --- --- --- --- --- --. ... ... ... ... --- ... ... ... ... ... .-- ... -.. ... ... ...
Ralfsia_confusa_(Pt_Elsdon)      --- --- --- --- --- --- --- --- --- --. ... ... ... ... GGA ... ... ... ... ... .-- ... -.. ... ... ...
Ralfsia_sp._smooth_(Pt_Halswell) GCT TAC GCA GCG GTG GTG GTG GTG GCA TG. ... A.. A.. .-- --- --- --- ... ... ... .AA ... AG. ... ... ...
Ralfsia_sp._smooth_(Island_Bay)  GCT TAC GCA GCG GTG GTG GTG GTG GCA TG. ... A.. A.. .-- --- --- --- ... ... ... .AA ... AG. ... ... ...
Ralfsia_sp._smooth_(Pt_Elsdon)   GCT TAC GCA GCG GTG GTG GTG GTG GCA TG. ... A.. A.. .-- --- --- --- ... ... ... .AA ... AG. ... ... ...
Ralfsia_expansa_(Otamure_Bay)    --- --- --- --- --- --- --- --- --- -G. .-- -.. ... A.. CGA --- --- --- ... CTT .-- --- --- ... .G. ...
Ralfsia_expansa_(Pt_Elsdon)      --- --- --- --- --- --- --- --- --- -G. .-- -.. ... A.. CGA C.. --- --- ... CTT .-- --- --- ... .G. ...

                                 111 111 111 111 111 111 111 111 111 111 111 111 111 111 122 222 222 222 222 222 222 222 222 222 222 222
                                 555 666 666 666 677 777 777 778 888 888 888 999 999 999 900 000 000 001 111 111 111 222 222 222 233 333
                                 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234
Ralfsia_confusa_(Russell)        TAT GCG TGG TCC GGG --- AGC TTG AGT GCT GCC GAG TTC ACC CAA GCC CAG AGA ATC GCC CCG CGG C-C GAT GGA CAA
Ralfsia_confusa_(Whananaki)      ... ... ... ... ... --- ... ... ... ... ... ... ... ... ... ... ... ... ... A.. ... ... .-. ... ... ...
Ralfsia_confusa_(Kau_Bay)        ... ... ... ... ... --- ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .-. ... ... ...
Ralfsia_confusa_(Pt_Halswell)    ... ... ... ... ... --- ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .-. ... ... ...
Ralfsia_confusa_(Pt_Elsdon)      ... ... ... ... ... --- ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .-. ... ... ...
Ralfsia_sp._smooth_(Pt_Halswell) ... ... ... ... ... --- ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .-. ... ... ...
Ralfsia_sp._smooth_(Island_Bay)  ... ... ... ... ... --- ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .-. ... ... ...
Ralfsia_sp._smooth_(Pt_Elsdon)   ... ... ... ... ... --- ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .-. ... ... ...
Ralfsia_expansa_(Otamure_Bay)    .T. .A. C.A ... ... CTT ... ..A ... ... T.. ... ... GT. T.. TAA ... .C. CA. ... ... ..A AA. .G. ... AGG
Ralfsia_expansa_(Pt_Elsdon)      .T. .A. C.A ... ... CTT ... ..A ... ... T.. ... ... GT. T.. TAA ... .C. CA. ... ... ..A AA. .G. ... AGG

                                 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 223 333 333 333 333
                                 333 334 444 444 444 555 555 555 566 666 666 667 777 777 777 888 888 888 899 999 999 990 000 000 000 111
```

```
                                 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012
Ralfsia_confusa_(Russell)        GTT CAT CGC ACG GAG TTG TTG ACG GCG CTC --G CTT CAC GGC CTG CGA TAC GAC GAC TCA CCC CAA ACG TGC GTG CCT
Ralfsia_confusa_(Whananaki)      ... ... ... ... ... ... ... ... ... ... --. .C. ... ... ... ... ... ... ... ... ... ... ... ... ... ...
Ralfsia_confusa_(Kau_Bay)        ... ... ... ... ... ... ... ... ... ... --. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
Ralfsia_confusa_(Pt_Halswell)    ... ... ... ... ... ... ... ... ... ... --. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
Ralfsia_confusa_(Pt_Elsdon)      ... ... ... ... ... ... ... ... ... ... --. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
Ralfsia_sp._smooth_(Pt_Halswell) ... ... ... ... ... ... ... ... ... ... --. ... ... ... ... ... ... ... ... ... ... ... ... ... --C ..-
Ralfsia_sp._smooth_(Island_Bay)  ... ... ... ... ... ... ... ... ... ... --. ... ... ... ... ... ... ... ... ... ... ... ... ... --C ..-
Ralfsia_sp._smooth_(Pt_Elsdon)   ... ... ... ... ... ... ... ... ... ... --. ... ... ... ... ... ... ... ... ... ... ... ... ... --C ..-
Ralfsia_expansa_(Otamure_Bay)    T.. ... ... ... ... ... ... ... ... ... TT. TCC TCG ... AG. ... ... ... ... ... T.. ... ... ... ..- --.
Ralfsia_expansa_(Pt_Elsdon)      T.. ... ... ... ... ... ... ... ... ... TT. TCC TCG ... AG. ... ... ... ... ... T.. ... ... ... ..- --.

                                 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333
                                 111 111 122 222 222 223 333 333 333 444 444 444 455 555 555 556 666 666 666 777 777 777 788 888 888 889
                                 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890
Ralfsia_confusa_(Russell)        TTG GAG CTT GCC --- TGT TGT T-G TTG C-C GCG AGG TCC GAA AGG AGG GGA G-- GGC A-- --- --- --- --- CTG CAC
Ralfsia_confusa_(Whananaki)      ... ... ... ... --- ... ... .-. ... .-. ... ... ... ... ... ... ... .-- ... .-- --- --- --- --- ... ...
Ralfsia_confusa_(Kau_Bay)        ... ... ... ... --- ... ... .-. ... .-. ... ... ... ... ... ... ... .-- T.. .-- --- --- --- --- ... ...
Ralfsia_confusa_(Pt_Halswell)    ... ... ... ... --- ... ... .-. ... .-. ... ... ... ... ... ... ... .-- T.. .-- --- --- --- --- ... ...
Ralfsia_confusa_(Pt_Elsdon)      ... ... ... ... CGT ... ... .-. ... .-. ... ... ... ... ... ... ... .-- ... .-- --- --- --- --- ... ...
Ralfsia_sp._smooth_(Pt_Halswell) -.. C.. ... .TT --- ... CAC CA. ... .-. ... ... ... ... ... .A. ..G .CA ... .GT CAT T-- --- -GA .C. ...
Ralfsia_sp._smooth_(Island_Bay)  -.. C.. ... .TT --- ... CCC CA. ... .-. ... ... ... ... ... .A. ..G .CA ... .GT CAT T-- --- -GA .C. ...
Ralfsia_sp._smooth_(Pt_Elsdon)   -.. C.. ... .TT --- ... CAC CA. ... .-. ... ... ... ... ... .A. ..G .CA ... .GT CAT T-- --- -GA .C. ...
Ralfsia_expansa_(Otamure_Bay)    GA. C.A .A. .G. C-- .TC C.C .T. .CC .T. ..T C.. CA. ... C.. GAC C.C CGC C.. CGC CGC CTC GGC GAC GAC G..
Ralfsia_expansa_(Pt_Elsdon)      GA. C.A .A. .G. C-- CTC C.C .T. .CC .T. ..T C.. CA. ... C.. GAC C.C CGC C.. CGC CGC --- --- --- --- G..

                                 333 333 333 444 444 444 444 444 444 444
                                 999 999 999 000 000 000 011 111 111 112
                                 123 456 789 012 345 678 901 234 567 890
Ralfsia_confusa_(Russell)        CAC CCA TCC GAC GAT CT- TCT ACT TTC GTT
Ralfsia_confusa_(Whananaki)      ... ... ... ... ... ..- ... ... ... ...
Ralfsia_confusa_(Kau_Bay)        ... ... A.. ... ... ..- ... ... ... ...
Ralfsia_confusa_(Pt_Halswell)    ... ... A.. ... ... ..- ... ... ... ...
Ralfsia_confusa_(Pt_Elsdon)      ... ... ... ... ... ..- ... T.. ... ...
Ralfsia_sp._smooth_(Pt_Halswell) GCA ... ... ... ... ..- ..A ... ... ...
Ralfsia_sp._smooth_(Island_Bay)  GCA ... ... ... ... ..- ... ... ... ...
Ralfsia_sp._smooth_(Pt_Elsdon)   GCA ... ... ... ... ..- ... ... ... ...
Ralfsia_expansa_(Otamure_Bay)    G.. GGC C.. A.. ... .GA .G. ... ... ...
Ralfsia_expansa_(Pt_Elsdon)      GG. GGC C.. A.. ... .GA .G. ... ... ...
```

Appendix 2: LSU Alignment

```
                                             111 111 111 122 222 222 223 333 333 333 444 444 444 455 555 555 556 666 666 666 777 777 777 ]
                                 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 ]
#Tribonema_aequale               ATA ACT AAG CGG AGG AAA AGA AAC TAA CCA GGA TTC CCC TAG TAA CGG CGA GTG AAG CGG GAA GAG CCC ACG ATG GTA
#Dictyota_dichotoma              ... ... ... ... ... ... ... ... ... .A. ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TG.
#Sphacelaria_cirrosa             --- --- --- -.. ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Fucus_vesiculosus               ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ..A T.T AA.
#Laminaria_digitata              ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Splachnidium_rugosum            ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Streblonema_maculans            ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ..A ... TA.
#Ascophyllum_nodosum             ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ..A T.T AA.
#Pelvetia_canaliculata           ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ..A T.T AA.
#Xiphophora_chondrophylla        ... ... ... ... ... ..G ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ..A T.. TA.
#Hormosira_banksii               ... ... ... ... ... ..G ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.T .A.
#Himanthallia_elongata           ... ... ... ... ... ... ... ... ... .T. ... ... ... C.. ... ... ... ... ... ... ... ... .T. .T. T.. TA.
#Anthophycus_longifolius         ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. .T. ... AG.
#Sargassum_muticum               ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. .T. ... TA.
#Turbinaria_turbinata            --- --- --- --- --- --- --- --- --. ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... ... AG.
#Axillariella_constricta         ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. GT. T.. TA.
#Bifurcaria_bifurcata            ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. GT. T.. TG.
#Bifurcaria_brassicaeformis      ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. GT. ... TA.
#Bifurcariopsis_capensis         --- --- --- --- --- ... ... ... ... .A. ... ... ... C.. ... ... ... ... ... ... ... ... .T. .TA T.. TA.
#Caulocystis_cephalornithos      ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. G.. ... TG.
#Cystoseira_nodicaulis           ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. GT. T.. TG.
#Notheia_anomala                 ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ..A C.. TA.
#Cystosphaerae_jacquinotii       ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Phyllospora_comosa              ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Seirococcus_axillaris           ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Durvillaea_antarctica           ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ..A T.. TA.
#Durvillaea_potatorum            ... ... ... ... ... ... ... ... ... ... ... ... ..T C.. ... ... ... ... ... ... ... ... .T. ..C T.. TG.
#Taonia_atomaria                 ... ... ... ... ... ... ... ... ... .A. ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... ... TG.
#Dictyopteris_polypodioides      --- --. ... ... ... ... ... ... ... .A. ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... ... TA.
#Cladostephus_spongiosus         --- --- --- --- --- ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Halopteris_scoparia             --- --- --- -.. ... ... ... ... ... .A. ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Syringoderma_phinneyi           --- --- --- --- --- ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Nemoderma_tingitanum            --- --- --- --- ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Bachelotia_antillarum           ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Haplospora_globosa              --- --- --- --- -.. ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Phaeosiphoniella_cryophila      --- --- --- --- -.. ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Tilopteris_mertensii            --- --- --- --- --- --- --- --. ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Alaria_esculenta                --- --- --- --- --- ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Laminaria_ochroleuca            ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Macrocystis_pyrifera            --- -.. ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ..G ... .T. ... T.. TA.
#Chorda_filum                    ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Halosiphon_tomentosus           ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Saccorhiza_polyschides          ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Cutleria_multifida              ... ... ... ... ... ... ... ... ... .A. ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Ascoseira_mirabilis             ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Arthrocladia_villosa            --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- ---
#Desmarestia_aculeata            ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
```

```
#Desmarestia_ligulata            --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- ---
#Himantothallus_grandifolius      ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Phaeurus_antarcticus            --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --. ... ... ... ... ... .T. .T. T.. TA.
#Sporochnus_pedunculatus         --- --- --- --- --- ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Scytothamnus_australis          --- --- --- -.. ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Stereocladon_rugulosus          ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Asteronema_ferruginea           ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Asteronema_rhodochortonoides    ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Asterocladon_lobatum            ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ..A C.. TA.
#Hincksia_granulosa              --- --- --- --- --- --- --. ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Pylaiella_littoralis            ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Adenocystis_utricularis         --- --- --- --- --- --- --- --- --- --- --- --- -.. C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Utriculidium_durvillei          --- --- --- --- --- --- --- --- --- --- --- --- --- C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Petalonia_fascia                --- ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Scytosiphon_lomentaria          --- --- --- --- --- --- --. ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Chordaria_flagelliformis        ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Punctaria_latifolia             --- --- --- --- --- ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Myriotrichia_clavaeformis       ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Dictyosiphon_foeniculaceus      ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T- --- T.. TA.
#Striaria_attenuata              ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Pseudolithoderma_PS5            ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Ralfsia_confusaTH21             ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Ralfsia_expansaPS6              ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Ralfsia_smoothSR6               ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.
#Hapalospongidion_gelatinosumHP4 ... ... ... ... ... ... ... ... ... .T. ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. .A.
#Diplura_australisRV16           ... ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... ... ... ... ... ... .T. ... T.. TA.

                                                             111 111 111 111 111 111 111 111 111 111 111 111 111 111 111 111 111 111 111 ]
                                 788 888 888 889 999 999 999 000 000 000 011 111 111 112 222 222 222 333 333 333 344 444 444 445 555 555 ]
                                 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 ]
#Tribonema_aequale               ATC GAT GCG CC- CCT G-C GGC CAC CGA ATT GTA GTC TGT AGA GGG TCG -TC C-A CTG CGC ACC GCC GA- -CT CAA GTC
#Dictyota_dichotoma              ... TGG C.- --- .TC .-- --G GC. -.. ... ... CA. ..G ... ..C GT. -G. .-. GC- ... TGT C.G CG- -GC ... ...
#Sphacelaria_cirrosa             ... TGG C.- --- TTC .-- --G GT. ... ... ... ... ... ... ..C GT. -G. .-. GC- ..G CG. C.G AG- -GC G.. ...
#Fucus_vesiculosus               ... TGG CA- --- .TC .-- --T GC. -.. ... ... ... .AA ... ..T AG. -A. .C. GC- A.A CGA -GG TGC TTC G.. ...
#Laminaria_digitata              ... TG- C.- --- TTC .-- --G G-. ... ... ... ... ..G ... ..C G.. -A. .-. GC- ..T GG. CGG .G- -GC G.. ...
#Splachnidium_rugosum            ... TGA C-- --- TTC .-- --- GT. ... ... ... ... ..G ... ..C GA. -A. .-. GC- ..G CGG CGG .G- -GC G.. ...
#Streblonema_maculans            ... TGA C.C --- T.. .-- --G GT. ... ... ... ... ..G ... ..C GTA -A. .-. GC- T.G .G. CGG .G- -GC G.. ...
#Ascophyllum_nodosum             ... TGG CA- --- .TC .-- --T GC. -.. ... ... ... .AA ... ..T AG. -G. .C. GC- A.A CGA -GG TGA TTC G.. ...
#Pelvetia_canaliculata           ... TGG CA- --- .TC .-- --T GC. -.. ... ... ... .AA ... ..T GG. -G. .C. GC- A.A CGA -GG TGC TTC G.. ...
#Xiphophora_chondrophylla        ..T TG. CAC --- AA. .-- -.T G.. A.. ... ... ... ..A ... ..C GA. -A. .-. GC- -.G .TG AGA TG- -GC T.. ...
#Hormosira_banksii               ... TGG CAC GGG TT. .-T T.T GT. ... ... ... ... ... ... ..C GA. -A. .-G GC- ..G ..G AGG TG- -GC A.. ...
#Himanthallia_elongata           ... TG- C.- --- .TC .-- -TG G-. ... ... ... ... ..G ... ..C GT. -G. T-. GA- ..T GGA CGG .G- -A. G.. ...
#Anthophycus_longifolius         .C. CGG C.- --- .TC .-- --G GT. G.G ... ... ... ..G ... ..C GTT -G. .-. GC- ..G CGG CGG .G- -TC G.. ...
#Sargassum_muticum               .C. CGG C.- --- .TC .-- --G GT. G.G -.. ... ... ..G ... ..C GTT -G. .-. GC- ..G CGG CGG .G- -TC G.. ...
#Turbinaria_turbinata            .C. CGG C.- --- TTC .-- --G GT. G.G ... ... ... ..G ... ..C GTT -G. .-. GC- ..G CGG CGG .G- -TC G.. ...
#Axillariella_constricta         .C. CGG C.C --- .T. C-- -.G GT. G.G ... ... ... ..G ... ..C GTT -G. .-. GC- ..G CGG CGG .G- -TC G.. ...
#Bifurcaria_bifurcata            .C. CGG C.- --- TTC .-- --G GT. T.G ... ... ... ..G ... ..C GTT -G. .-. GC- ..G CG- CGG .G- -TC G.. ...
#Bifurcaria_brassicaeformis      .C. CGG C.C --- T.C .-- --G GT. G.G G.. ... ... ..G ... ..T GTT -G. .-. GC- ..G CGG CGG .G- -TC G.. ...
#Bifurcariopsis_capensis         ... T-G C.A .-- TTG .-- -TG G-T ... ... ... ... ..G ... ..C GA. -G. T-. GC- ..T CGG CGG .G- -AC G.. ...
#Caulocystis_cephalornithos      .C. CGG C.- --- G.G A-- --G GT. G.G ... ... ... ..G ... ..C GTT -G. .-. GC- ..G CGG CGG .G- -TC G.. ...
#Cystoseira_nodicaulis           .C. CGG C.- --- TTC .-- --G GTT G.G G.. ... ... ..G ... ..C GTT -G. .-. GC- ..T CGG CGG .G- -TC G.. ...
```

```
#Notheia_anomala                 ... C.- CG- --- .T. .-- --. G-T G.. ... ... ... C.A ... ..C GT. -G. .-. GC- ..T CGG CGG AG- -AA ... ...
#Cystosphaerae_jacquinotii       ... TG- C.- --- ..A .-- -TG G-T ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..T TGT CGG .G- -GC G.. ...
#Phyllospora_comosa              ... TG- C.- --- ..A .-- -TG G-. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..T TGG CGG .G- -GC G.. ...
#Seirococcus_axillaris           ... TG- C.- --- ..A .-- -TG G-T ... ... ... ... ... ... ..C GA. -G. .-. GC- ..T TGG CGG .G- -GC G.. ...
#Durvillaea_antarctica           ... TG- C.- --- TTC .-- -TG G-. ... ... ... ... ... ... ..C GT. -A. .-. GC- ..T CGG CGA .G- -GC G.. ...
#Durvillaea_potatorum            ... TG- C.A --- TTC T-- -TG G-. ... ... ... ... ..G ... ..C GT. -A. .-. GC- ..T CGG CGA .G- -GC G.. ...
#Taonia_atomaria                 ... ..G C.- --- .TA .-- --G GC. ... ... ... ... ..G ... ..C GA. -G. .-T GC- ... TGT C.G TG- -GC ... ...
#Dictyopteris_polypodioides      ... ..G C.- --- TTC .-- --G GC. ... ... ... ... ..G ... ..C GA. -G. .-T GC- ... TGT C.G CG- -GC ... ...
#Cladostephus_spongiosus         ... TGG C.- --- .TC .-- --G GC. ... ... ... ... ... ... ..C GT. -G. .-. GC- ..G CGA C.G AG- -GC G.. ...
#Halopteris_scoparia             ... TGG C.- --- TTC .-- --G GC. ... ... ... ... ... ... ..C GT. -G. .-. GC- ..G CGA T.G AG- -G. G.. ...
#Syringoderma_phinneyi           ... TGG CT- --- TTC --- -.G GC. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..T TGT C.G .G- -GC G.. ...
#Nemoderma_tingitanum            ... CGC C.T .-- TTC .-- -AG G.T G.. ... ... ... ..G ... ..C GA. -G. .-. GC- ..G CG. TG. .G- -GC G.. ...
#Bachelotia_antillarum           ... TGG CTA G.- T.. .TG TCT GC. G.. ... ... ... ..G ... ..C GA. -G. .-. GC- ..G CGG CGG .G- -G. ... ...
#Haplospora_globosa              ... TGG C.- --- TTC --- --G GC. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..T CGG CGG .G- -GC G.. ...
#Phaeosiphoniella_cryophila      ... TGG C-- --- TTC .-- --- GC. ... ... ... ... ..G ... ..C GT. -A. .-. GC- ..G .GA CGG .G- -GC G.. ...
#Tilopteris_mertensii            ... TGG CT- --- TTC .-- --G GC. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..T CGG CGG .G- -GC G.. ...
#Alaria_esculenta                ... TG- C.- --- TTC .-- --G G-. ... ... ... ... ..G ... ..C G.. -G. .-. GC- ... TG. C.G .G- -GC G.. ...
#Laminaria_ochroleuca            ... TG- C.- --- TTC .-- --G G-. ... ... ... ... ..G ... ..C G.. -G. .-. GC- ..T GG. CGG .G- -GC G.. ...
#Macrocystis_pyrifera            ... TG- C.- --- TTC .-- --G G-. ... ... ... ... ... ... ..C GA. -G. .-. GC- ... GG. CGG .G- -GC G.. ...
#Chorda_filum                    ... TG- C.- --- TTC .-- --G G-. ... ... ... ... ..G ... ..C GT. -A. .-. GC- ..T GGA CGG .G- -GC G.. ...
#Halosiphon_tomentosus           ... TGG CT- --- TTC .-- --G GC. ... ... ... ... ..G ... ..C GA. -G. .-. GC- T.G CGG CGG .G- -GC G.. ...
#Saccorhiza_polyschides          ... AGG CG- --- TTC .-- --. GC. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..T CGG CGG .G- -GC G.. ...
#Cutleria_multifida              ... TGG CT- --- TTC .-- --G GC. ... ... ... ... ..G ... ..C GA. -A. .-. GC- ..G CGG CGG .G- -GC G.. ...
#Ascoseira_mirabilis             ... TGG C-- --- TTC .-- --G GT. ... ... ... ... ..G ... ..C GT. -G. .-. GC- ..T TGG CGG .G- -GC G.. ...
#Arthrocladia_villosa            --- --- --- --- --- --- --- --. -.. .-. ... ... ..G ... ..C GA. -G. .-. GC- ..G CGG CGG .G- -GC G.. ...
#Desmarestia_aculeata            ... TGG C-- --- TTC .-- --- GC. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..G CAG CGG .G- -GC G.. ...
#Desmarestia_ligulata            --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- -.. ...
#Himantothallus_grandifolius     ... TG- C-- --- TTC .-- --- GC. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..G CAG CGG .G- -GC G.. ...
#Phaeurus_antarcticus            ... TGG C-- --- TTG .-- --- GC. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..G CAG CGG .G- -GC G.. ...
#Sporochnus_pedunculatus         ... TGG C.- --- TTC .-- --G GC. ... ... ... ... ..G ... ..C GA. CG. .-. GC- ..T CGG CGG .G- -GC G.. ...
#Scytothamnus_australis          ... TGA C-- --- T.A C-- --- GT. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..G CGG AGG .G- -GC G.. ...
#Stereocladon_rugulosus          ... TGA C-- --- T.A C-- --- GT. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..G CGG CGG .G- -GC G.. ...
#Asteronema_ferruginea           ... TGA C-- --- TTC .-- --G GT. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..G CGG CGG .G- -GC G.. ...
#Asteronema_rhodochortonoides    ... TGG C-- --- TTC .-- --- GC. ... ... ... ... ..G ... ..C GT. -A. .-. GC- ..G .GG TGG .G- -G. G.. ...
#Asterocladon_lobatum            ... TGG C-- --- TTC .-- --- GC. ... ... ... ... ..G ... ..C GT. -A. .-. GC- ..G .GG CGG AG- -GC G.. ...
#Hincksia_granulosa              ... TGA C-- --- TTC .-- --- GT. ... ... ... ... ..G ... ..C G.. -A. .-. GC- T.G .GA CGG .G- -GC -.. ...
#Pylaiella_littoralis            ... TGA C-- --- T.C .-- --- GT. ... ... ... ... ..G ... ..C GT. -A. .-. GC- T.G .G. CGG .G- -GC G.. ...
#Adenocystis_utricularis         ... TGA C-- --- TTC .-- --- GT. ... ... ... ... ..G ... ..C GT. -A. .-. GC- T.G .GT CGG .G- -GC G.. ...
#Utriculidium_durvillei          ... TGA C.T --- TTG .-- --- GT. ... ... ... ... ..G ... ..C GT. -A. .-. GC- T.G .GT CGG .G- -GC G.. ...
#Petalonia_fascia                ... TGA C-- --- TTC .-- --- GT. ... ... ... ... ..G ... ..C GT. -A. .-. GC- T.G .GT CGG .G- -GC G.. ...
#Scytosiphon_lomentaria          ... TGA C-- --- TTC .-- --- GT. ... ... ... ... ..G ... ..C GT. -A. .-. GC- T.G .GT CGG .G- -GC G.. ...
#Chordaria_flagelliformis        ... TGA CT- --- TTC .-- --G GT. ... ... ... ... ..G ... ..C GT. -A. .-. GC- T.G .GA CGG .G- -GC G.. ...
#Punctaria_latifolia             ... TGA CT- --- TTC .-- --G GT. ... ... ... ... ..G ... ..C GT. -A. .-. GC- T.G GGA CGG .G- -GC G.. ...
#Myriotrichia_clavaeformis       ... TGA CT- --- TTC .-- --G GT. ... ... ... ... ..G ... ..C G.. -A. .-. GC- T.G GGA CGG .G- -GC G.. ...
#Dictyosiphon_foeniculaceus      ... TGA CT- --- TTC .-- --G GT. ... ... ... ... ..G ... ..C GA. -A. .-. GC- T.G GGA CGG .G- -GC G.. ...
#Striaria_attenuata              ... TGA CT- --- TTC .-- --G GT. ... ... ... ... ..G ... ..C GT. -A. .-. GC- T.G GGA CGG .G- -GC G.. ...
#Pseudolithoderma_PS5            ... TGG C.- --- TTC .-- --G GC. ... ... ... ... ..G ... ..C GT. -G. .-. GC- ..T CGA C.G AG- -GC G.. ...
#Ralfsia_confusaTH21             ... TGA C.- --- TTC .-- --G GT. ... ... ... ... ..G ... ..C GA. -A. .-. GC- ..G CGG TGG .G- -GC G.. ...
#Ralfsia_expansaPS6              ... TGA CT- --- .TC .-- --G GT. ... ... ... ... ..G ... ..C GA. -G. .-. GC- ..G CGG TGG .G- -GC G.. ...
#Ralfsia_smoothSR6               ... TGA CT- --- .TC .-- --G GT. ... ... ... ... ..G ... ..C GA. -A. .-. GC- ..G CGG TGG .G- -GC G.. ...
#Hapalospongidion_gelatinosumHP4 ... TGA C.C TA- .TC .-- --G GT. ... ... ... ... ..G ... ..C G.. -G. .-. GC- ..G CGG CGG .G- -GC G.. ...
```

```
#Diplura_australisRV16           ... TGG C.C ..- .TC .GG .-G GC. ... ... ... ... ... ... ..C GT. -G. .-. GC- ... CGT C.G AG- -GC G.. ...

[                                111 111 111 111 111 111 111 111 111 111 111 111 111 111 122 222 222 222 222 222 222 222 222 222 222 222 ]
[                                555 666 666 666 677 777 777 778 888 888 888 999 999 999 900 000 000 001 111 111 111 222 222 222 233 333 ]
[                                789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 ]
#Tribonema_aequale               -CC -TT GGA AGA GGG CGC CAG GGA GGG TGA CAG CCC CGT CCA TGG -TT GGC AG- --- -CG TGT --G CGG -AT CGG TCG
#Dictyota_dichotoma              -TG A.. ... .AT .A. .AT ..A ... ... ... ..A T.. ... ... ..C -CG C.G TAC CG- ATC A.C --. ..C GTC ... C.C
#Sphacelaria_cirrosa             -T. -.. ... .A. .A. .AT .GA ... ... ... ..A T.. ... T.T ..C -CC C.G CAG --- --C GCC --. ..C GTA ... C.C
#Fucus_vesiculosus               -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T-- -.A ACA CCG CAA --- -TC GTC --T T.C GTG ... ..C
#Laminaria_digitata              -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA C-- --- -GC C.C --. ..C GTA ... ..C
#Splachnidium_rugosum            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA TC- --- -TC GTC --. ..C GTA ... ..C
#Streblonema_maculans            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA G-- --- -GC CCC --A ..C GTA ... .TC
#Ascophyllum_nodosum             CT. -.. ... ... .A. .AT ..A ... ... ... ..A T.. ... .-- -.A ACA CCG TAA --- -TT GTC --T T.C GTG ... ..C
#Pelvetia_canaliculata           -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T-- -.A ACA CCG CAA --- -TC GTC --T T.C GTG ... ..C
#Xiphophora_chondrophylla        -T. -.. ... .A. .A. .AT ... ... ... ... ..A T.. ... ..- G.C -.. TTG TA- --- -.. ACC A-A G.C GTA ... ..C
#Hormosira_banksii               -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -C. CCG T.- --- -.. ATC ATT G.C GTC G.. ..C
#Himanthallia_elongata           -T. -.. ... .A. .A. .AT ..T ... ... ... A.A T.. ... G.T ..T -CC CCG G-- --- -TC GAC --. ATC GTA AAA C.C
#Anthophycus_longifolius         -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.C G.T -CC CCG C-- --- -TC GTC --. T.C GC. ... .GC
#Sargassum_muticum               -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.C G.T -CC CCG C-- --- -TC GT. --. T.C GTA ... .GC
#Turbinaria_turbinata            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.C G.T -CC CCG C-- --- -TC GTC --. ..C GCA ... .GC
#Axillariella_constricta         -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.C G.T -CC CCG T-- --- -TC G.C --. A.C GCA ... CGC
#Bifurcaria_bifurcata            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.C G.T -CC CCG C-- --- -TC GTC --. A.C GCA ... CGC
#Bifurcaria_brassicaeformis      -T. -.. ... .A. ... .AT ..A ... ... ... ..A T.. ... T.C G.T -CC CCG C-- --- -TC GTC --. T.C GCA ... CGC
#Bifurcariopsis_capensis         -T. -.. ... ... .A. .AT ..A ... ... ... T.A T.. ... TGT ..T -CC CCG C-- --- -GC GAC --. ..C GTC ... C.C
#Caulocystis_cephalornithos      -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... .TC G.T -CC CCG C-- --- -TC G.C --. A.C TTA ... CGC
#Cystoseira_nodicaulis           -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.C G.T -CC CCG C-- --- -TC G.C --. A.C GCA ... CGC
#Notheia_anomala                 -.. -.. ... .A. .A. .AT ..T ... ... ... T.A T.. ... AT. ..T -CC CCG C-- --- -GC GAC --. T.C GTA ... C.C
#Cystosphaerae_jacquinotii       -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.C ..C -CC CCG C-- --- -GC GAC --. ..C GTC ... C.C
#Phyllospora_comosa              -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.C ..C -CC CCG C-- --- -GC GAC --. T.C GTC ... C.C
#Seirococcus_axillaris           -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... ..C ..C -CC CCG C-- --- -TT GAC --. ..C GTC ... ..C
#Durvillaea_antarctica           -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... GAT ..C -CC CCG C-- --- -TT GAC --. ..C GTA T.. ..C
#Durvillaea_potatorum            -T. -.. ... .A. .A. .AT ..T ... ... ... ..A T.. ... .GT ..C -CC CCG C-- --- -GC G.C --. ..C GTA T.. ..C
#Taonia_atomaria                 -TG A.. ... .AT .A. .AT ..T ... ... ... T.A T.. ... T.G ..C -CG C.G TAT CG- ATC A.C --. ..C AGA A.. C.C
#Dictyopteris_polypodioides      -TG A.. ... .AT .A. .AT ..C ... ... ... ..A T.. ... T.. ..C -CG C.G TAT CG- ATC A.C --. ..C G.A A.. C.C
#Cladostephus_spongiosus         -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC C.G CC- --- -.C GCC --. ..C GTA ... ..C
#Halopteris_scoparia             -T. -.. ... .A. .A. .AT ..A ... ... ... T.A T.. ... T.T ..C -CC C.G T-- --- -GC A.. --. ..C GTA ... ..C
#Syringoderma_phinneyi           -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC C.G TAT TGT ATC A.C --. T.C GTA ... C.C
#Nemoderma_tingitanum            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA .-- --- -GC GCC --. ..C GTA ... C.C
#Bachelotia_antillarum           -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.C ..C -CC CCA TCC --- -TT GCC --. ..C GTA ... C.C
#Haplospora_globosa              -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCT GAT T-- -TC G.C --. ..C GTA ... ..C
#Phaeosiphoniella_cryophila      -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA C-- --- -TC .CC --. ..C GTA ... ..C
#Tilopteris_mertensii            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCT GAT T-- -TC G.C --. ..C GTA ... ..C
#Alaria_esculenta                -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC C-A G.- --- -GC G.C --. T.C GTA ... ..C
#Laminaria_ochroleuca            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA C-- --- -GC C.C --. ..C GTA ... ..C
#Macrocystis_pyrifera            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA C-- --- -GC C.. --. ..C GTA ... ..C
#Chorda_filum                    -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA G-- --- -TC C.C --. ..C GTA ... ..C
#Halosiphon_tomentosus           -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCT GAT T-- -TC GTC --. ..C GTA ... C.C
#Saccorhiza_polyschides          -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCG CT- --- -.C .TC --. ..C GTA ... ..C
#Cutleria_multifida              -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCT GAT T-- -TC GTC --. ..C GTA ... ..C
#Ascoseira_mirabilis             -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCG .C- --- -TC .TC --. ..C GTA ... C.C
#Arthrocladia_villosa            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA GTT --- -.C GTC --. ..C GTA ... C.C
```

```
#Desmarestia_aculeata            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA GTT --- -.T GCC --. ..C GTA ... C.C
#Desmarestia_ligulata            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CTA GTT T-- -.T GTC --. ..C GTA ... C.C
#Himantothallus_grandifolius     -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA GCT T-- -.T GCC --. ..C GTA ... C.C
#Phaeurus_antarcticus            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA GC- --- -.T GCC --. ..C GTA ... C.C
#Sporochnus_pedunculatus         -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.C ..C -CC CCT CC- --- -.C GTC --. ..C GTA ... C.C
#Scytothamnus_australis          -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA T.- --- -TT GTC --. ..C GTA ... C.C
#Stereocladon_rugulosus          -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA TC- --- -TC GTC --. ..C GTA ... C.C
#Asteronema_ferruginea           -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA TC- --- -TC GTC --. ..C GTA ... ..C
#Asteronema_rhodochortonoides    -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCG C-- --- -TC GCC --. ..C GTA ... ..C
#Asterocladon_lobatum            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCG C-- --- -TA ACC --. ..C GTA ... ..C
#Hincksia_granulosa              -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCG C-- --- -.C .CC --A ..C GTA ... ..C
#Pylaiella_littoralis            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCG .-- --- -TC .CC --A ..C GTA ... ..C
#Adenocystis_utricularis         -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCG C-- --- -GC .CC --A ..C GTA ... ..C
#Utriculidium_durvillei          -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCG C-- --- -GC .CC --A ..C GTA ... ..C
#Petalonia_fascia                -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -C. CCG C-- --- -GC .CC --A ..C GTA ... ..C
#Scytosiphon_lomentaria          -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -C. CCG C-- --- -GC .CC --A ..C GTA ... ..C
#Chordaria_flagelliformis        -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA C-- --- -TC .CC --A ..C GTA ... ..C
#Punctaria_latifolia             -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CTA G-- --- -TC CCC --A ..C GTA ... ..C
#Myriotrichia_clavaeformis       -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA C-- --- -TC CCC --A ..C GTA ... ..C
#Dictyosiphon_foeniculaceus      -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA C-- --- -TC CCC --A ..C GTA ... ..C
#Striaria_attenuata              -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCA C-- --- -TC CCC --A ..C GTA ... ..C
#Pseudolithoderma_PS5            -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC C.G .T- --- -.C GAC --. ..C GTA ... C.C
#Ralfsia_confusaTH21             -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCG .CT T-- -.C GTC --. T.C GTA ... ..C
#Ralfsia_expansaPS6              -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CTA ..T T-- -.C GTC --. ..C GTA ... C.C
#Ralfsia_smoothSR6               -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC CCG .CT T-- -.C GTC --. T.C GTA ... ..C
#Hapalospongidion_gelatinosumHP4 -T. -.. ... .A. .A. .AT .GA ... ... ... ..A T.. ... T.T ..C -CC CCG .CT TAC TTT C.. -C. ..C GTA ... C.C
#Diplura_australisRV16           -T. -.. ... .A. .A. .AT ..A ... ... ... ..A T.. ... T.T ..C -CC C.G .T- --- -.C G.C --. ..C GCA ... C.C

[                                222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 222 223 333 333 333 333 ]
[                                333 334 444 444 444 555 555 555 566 666 666 667 777 777 777 888 888 888 899 999 999 990 000 000 000 111 ]
[                                567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 ]
#Tribonema_aequale               GGC CTC GAC GAG TCG AGT TGC TTG GGA TTG CAG CTC AAA GCG GGT GGT AAA TTC CAT CCA AGG CTA AAT ATG GGT GGG
#Dictyota_dichotoma              .CT T.. ... ... ... ... ... ... ... ... ... ... ... .A. ... ... ... C.. ... ... .A. ... ..C .C. ..G ...
#Sphacelaria_cirrosa             .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ..G ...
#Fucus_vesiculosus               .CT T.. T.T ... ... ... ... ... ... ... ... ... ... .T. ... ... ... ... ... .T. .A. ... ... .C. C.. ...
#Laminaria_digitata              .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Splachnidium_rugosum            .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Streblonema_maculans            .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Ascophyllum_nodosum             .CT T.. T.T ... ... ... ... ... ... ... ... ... ... .T. ... ... ... ... ... .T. .A. ... ... .C. C.. ...
#Pelvetia_canaliculata           .CT T.. T.T ... ... ... ... ... ... ... ... ... ... .T. ... ... ... ... ... .T. .A. ... ... .C. C.. ...
#Xiphophora_chondrophylla        .CT T.. T.. ... ... ... ... ... ... ... ... ... ... .T. ... ... ... ... ... .T. .A. ... ..C .C. C.G ...
#Hormosira_banksii               .CT T.. ... ... ... ... ... ... ... ... ... ... ... .T. ... ... ... ... ... .T. .A. ... ..C .C. C.. ...
#Himanthallia_elongata           .TT T.. T.A ... ... ... ... ... ... ... ... ... ... .T. ... ... ... ... ... .T. .A. ... ..C .C. C.. A..
#Anthophycus_longifolius         .CT T.. T.. ... ... ... ... ... ... ... ... ... ... .T. ... ... ... ... ... .T. .A. ... ... .CC ... ...
#Sargassum_muticum               .CT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ... .CC ... ...
#Turbinaria_turbinata            .CT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ... .CC ... ...
#Axillariella_constricta         .CT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ... .C. ... ...
#Bifurcaria_bifurcata            .CT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ... .C. ... ...
#Bifurcaria_brassicaeformis      .CT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ... .GA ... ...
#Bifurcariopsis_capensis         .TT T.. .T. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. C.. ...
#Caulocystis_cephalornithos      .CT T.T T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ... .C. ... ...
```

```
#Cystoseira_nodicaulis           .CT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ... .C. ... ...
#Notheia_anomala                 .CT T.. ... ... ... ... ... ... ... ... ... ... .T. ... ... ... ... ... .T. .A. ... ..C .C. A.. ...
#Cystosphaerae_jacquinotii       .TT T.. ..A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ... .C. A.. ...
#Phyllospora_comosa              .TT T.. ..A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. A.. ...
#Seirococcus_axillaris           .TT T.. TT. ... ... ... ... ... ... ... ... ... ... ... ... ... ... .C. ... .T. .A. ... ..C .C. A.. .A.
#Durvillaea_antarctica           .TT T.. A.. ... ... ... ... ... ... ... ... ... ... .T. ... ... ... ... ... .T. .A. ... ..C .C. C.. ...
#Durvillaea_potatorum            .TT T.. ... ... ... ... ... ... ... ... ... ... ... .T. ... ... ... ... ... .T. .A. ... ..C .C. C.. ...
#Taonia_atomaria                 .TT T.. ... ... ... ... ... ... ... ... ... ... ... TG. ... ... ... C.. ... ... .A. ... ..C .C. ..G ...
#Dictyopteris_polypodioides      .TT T.. ... ... ... ... ... ... ... ... ... ... ... TG. ... ... ... C.. ... ... .A. ... ..C .C. ..G ...
#Cladostephus_spongiosus         .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ..G ...
#Halopteris_scoparia             .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ..G ...
#Syringoderma_phinneyi           .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... .A. ... .T. .A. ... ... ..T ... ...
#Nemoderma_tingitanum            .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Bachelotia_antillarum           .TT T.. ..A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Haplospora_globosa              .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Phaeosiphoniella_cryophila      .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Tilopteris_mertensii            .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Alaria_esculenta                .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Laminaria_ochroleuca            .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... .C. ... .T. .A. ... ..C .C. ... ...
#Macrocystis_pyrifera            .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Chorda_filum                    .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Halosiphon_tomentosus           .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Saccorhiza_polyschides          .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Cutleria_multifida              .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Ascoseira_mirabilis             .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Arthrocladia_villosa            .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Desmarestia_aculeata            .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Desmarestia_ligulata            .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Himantothallus_grandifolius     .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Phaeurus_antarcticus            .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .-- --- ---
#Sporochnus_pedunculatus         .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Scytothamnus_australis          .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Stereocladon_rugulosus          .TT T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Asteronema_ferruginea           .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Asteronema_rhodochortonoides    .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Asterocladon_lobatum            .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... .A.
#Hincksia_granulosa              .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Pylaiella_littoralis            .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Adenocystis_utricularis         .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Utriculidium_durvillei          .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Petalonia_fascia                .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Scytosiphon_lomentaria          .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Chordaria_flagelliformis        .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Punctaria_latifolia             .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Myriotrichia_clavaeformis       .TT T.. T.. ... ... ... ... ... ... ... ... ... ...  -. ... ... ... ... .T. .A. ... ..C .C. ... ...
#Dictyosiphon_foeniculaceus      .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Striaria_attenuata              .TT T.. T.. ... ... ... ... ... ... ... ... ... ...  -. ... ... ... ... .T. .A. ... ..C .C. ... ...
#Pseudolithoderma_PS5            .TT T.. C.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ... .C. ..A ...
#Ralfsia_confusaTH21             .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Ralfsia_expansaPS6              .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Ralfsia_smoothSR6               .TT T.. T.. ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
```

```
#Hapalospongidion_gelatinosumHP4 .TT T.. T.A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ... ...
#Diplura_australisRV16           .TT T.. ..A ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... .T. .A. ... ..C .C. ..A ...

[                                333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 333 ]
[                                111 111 122 222 222 223 333 333 333 444 444 444 455 555 555 556 666 666 666 777 777 777 788 888 888 889 ]
[                                345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 ]
#Tribonema_aequale               AGA CCG ATA GCG AAC AAG TAC CGT GAG GGA AAG ATG AAA AGA ACT TTG GAA AGA GAG TTA AA- AGT GCT TGA AAT TGC
#Dictyota_dichotoma              ... ... ... ... ... ... ... ... ... .-. ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C .T. ... ...
#Sphacelaria_cirrosa             ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Fucus_vesiculosus               ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... .G. ..G ... ..C ... ... ...
#Laminaria_digitata              ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Splachnidium_rugosum            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Streblonema_maculans            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Ascophyllum_nodosum             ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... .G. ..A ... ..C ... ... ...
#Pelvetia_canaliculata           ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... .G. ..G ... ..C ... ... ...
#Xiphophora_chondrophylla        ... ... ... ... ... ... ... ... ... .A. ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... G..
#Hormosira_banksii               ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Himanthallia_elongata           ... ... ... ... ... ... ... ... ... ... ... ... G.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Anthophycus_longifolius         ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Sargassum_muticum               ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Turbinaria_turbinata            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Axillariella_constricta         ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Bifurcaria_bifurcata            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Bifurcaria_brassicaeformis      ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Bifurcariopsis_capensis         ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... .C. ..G ... ..C ... ... ...
#Caulocystis_cephalornithos      ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Cystoseira_nodicaulis           ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Notheia_anomala                 ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Cystosphaerae_jacquinotii       ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Phyllospora_comosa              ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Seirococcus_axillaris           ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Durvillaea_antarctica           ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Durvillaea_potatorum            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Taonia_atomaria                 ... ... ... ... ... ... ... ... ... .-. ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Dictyopteris_polypodioides      ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Cladostephus_spongiosus         ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... .G. ..G ... ..C ... ... ...
#Halopteris_scoparia             ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Syringoderma_phinneyi           ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Nemoderma_tingitanum            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Bachelotia_antillarum           ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Haplospora_globosa              ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Phaeosiphoniella_cryophila      ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Tilopteris_mertensii            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Alaria_esculenta                ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Laminaria_ochroleuca            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Macrocystis_pyrifera            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Chorda_filum                    ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Halosiphon_tomentosus           ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Saccorhiza_polyschides          ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Cutleria_multifida              ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Ascoseira_mirabilis             ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
```

```
#Arthrocladia_villosa            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Desmarestia_aculeata            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Desmarestia_ligulata            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Himantothallus_grandifolius     ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Phaeurus_antarcticus            --- --- -.. ... ... ... .-- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- ---
#Sporochnus_pedunculatus         ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Scytothamnus_australis          ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Stereocladon_rugulosus          ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Asteronema_ferruginea           ... ... ... ... ... ... ... T.. ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Asteronema_rhodochortonoides    ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Asterocladon_lobatum            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Hincksia_granulosa              ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Pylaiella_littoralis            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Adenocystis_utricularis         ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Utriculidium_durvillei          ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Petalonia_fascia                ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Scytosiphon_lomentaria          ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Chordaria_flagelliformis        ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Punctaria_latifolia             ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Myriotrichia_clavaeformis       ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Dictyosiphon_foeniculaceus      ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Striaria_attenuata              ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Pseudolithoderma_PS5            ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Ralfsia_confusaTH21             ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Ralfsia_expansaPS6              ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Ralfsia_smoothSR6               ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Hapalospongidion_gelatinosumHP4 ... ... ... .T. ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...
#Diplura_australisRV16           ... ... ... ... ... ... ... ... ... ... ... ... C.. ... ... ... A.. ... ... ... ..G ... ..C ... ... ...

[                                333 333 333 444 444 444 444 444 444 444 444 444 444 444 444 444 444 444 444 444 444 444 444 444 444 444 ]
[                                999 999 999 000 000 000 011 111 111 112 222 222 222 333 333 333 344 444 444 445 555 555 555 666 666 666 ]
[                                123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 ]
#Tribonema_aequale               TGA AAG GGA ACC GAA GGG -AG GCA GTG -CT GG- --- TTC AGT G-C GTC TT- GCC CCT G-G GC- --- -CT CG- GCC CCG
#Dictyota_dichotoma              ..G ... ... .G. ... ..A -.A .AG ... TGC ..T TGC CCG G.C --G CCA AC- -.. .TA C-C TG- --- -T. ..- CAG GT.
#Sphacelaria_cirrosa             ... ... ... .G. ... ..A -.A ... ... T.. ..- --- CGG .T. --. .CT .A- T.. GAG A-. C.- --- -.. ..- .G. T.C
#Fucus_vesiculosus               ... ... ... .G. ... ..A TTA T.. ... T.. ..- --- CGG TTC --. .CT .C- T.. TGC .-T T.- --- -.. ..- .AA .GC
#Laminaria_digitata              ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGT C.A --A .CT ..- C.. T.C .-C C.- --- -T. ..- .GG .TC
#Splachnidium_rugosum            ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGT TT. --. .CT .A- C.T TT. .-C C.- --- -.. ..- .GG .AT
#Streblonema_maculans            ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CAG TC. --T .CT .C- T.. T.. .-C C.- --- -.. ..- .GG .TC
#Ascophyllum_nodosum             ... ... ... .G. ... ..A T.A C.. ... T.. ..- --- CGG TTC --. .CT .C- T.. TGC .-T T.- --- -.. ..- .AA .GC
#Pelvetia_canaliculata           ... ... ... .G. ... ..A T.A T.. ... T.. ..- --- CGG TTC --. .CT .C- T.. TGC .-T T.- --- -.. ..- .AA .GC
#Xiphophora_chondrophylla        ... ... ... .G. ... ..A A.A T.. ... T.. ..- --- CGT TTC --. .CT .C- T.. TTC .-T T.- --- -.. ..- .AA .GT
#Hormosira_banksii               ... ... ... .G. ... ..A AGA T.. ... T.. .T- --- CGG TCC --. .CT .C- T.. .GC .-C T.- --- -.. ..- .AG .TT
#Himanthallia_elongata           ... ... A.. .G. ... ..A -.A T.. ... T.. .T- --- CGG TTC --. .CT .C- TTT GGC .-T T.- --- -.. ..- .AG .GC
#Anthophycus_longifolius         ... ... ... .G. ... ..A -.. C.. ... T.. ..- --- CGG TTC --T .CT .C- T.. GAC .-. T.- --- -.C ..- .A. .GT
#Sargassum_muticum               ... ... ... .G. ... ..A -.. C.. ... T.. ..- --- CGG TTC --T .CT .C- T.. GAC .-. T.- --- -TC ..- .A. .GT
#Turbinaria_turbinata            ... ... ... .G. ... ..A -.. C.. ... T.. ..- --- CGG TTC --T .CT .C- T.. GAC .-. T.- --- -.C ..- .A. .GT
#Axillariella_constricta         ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGG TTC --T .CT .C- T.. GAC .-. T.- --- -T. G.- .A. .GT
#Bifurcaria_bifurcata            ... ... ... .G. ... ..A -.. C.. ... T.. ..- --- CGG TTG --T .CT .C- T.. GAC .-. T.- --- -T. ..- .A. .GT
#Bifurcaria_brassicaeformis      ... ... ... .G. ... ..A -.. C.. ... T.. ..- --- CGG TTC --T .CT .C- T.. GA. .-. T.- --- -.. ..- .A. .GT
#Bifurcariopsis_capensis         ... ... ... .G. ... ..A -.A T.. ... T.. ..- --- CGG TTC --. .CT .C- T.. .GC C-T T.- --- -.. ..- .AA GGC
```

```
#Caulocystis_cephalornithos      ... ... ... .G. ... ..A -.. C.. ... T.. .A- --- CGG TTG --T .CT .C- T.. GAC .-. T.- --- -T. G.- .G. .GC
#Cystoseira_nodicaulis           ... ... ... .G. ... ..A -.. C.. ... T.. ..- --- CGG TTG --T .CT .C- T.. GAC .-. T.- --- -T. ..- .A. .GT
#Notheia_anomala                 ... ... ... .G. ... ..A -.A T.. ... T.. ..- --- .GT TT. --T .CT .C- T.. GAC .-. T.- --- -T. ..- .AT .GC
#Cystosphaerae_jacquinotii       ... ... ... .G. ... ..A -.A T.. ... T.. ..- --- CGG T.. ACT .GT .C- T.. GGC .-C C.- --- -TC ..- .GA .GT
#Phyllospora_comosa              ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGG TC. ACT TG. .C- T.. GGC .-C C.- --- -T. ..- .GG .GC
#Seirococcus_axillaris           ... ... ... .G. ... ..A -.A TG. ... T.. ..- --- CGG T.. ACT .G. A.G T.A GGC .-C C.- --- -TC ..- .GA .GC
#Durvillaea_antarctica           ... ... ... .G. ... ..A -.A T.. ... T.. .T- --- CGG TT. --T .CT .C- T.. GTG T-. T.- --T TT. G.- .A. GTT
#Durvillaea_potatorum            ... ... ... .G. ... ..A -.A T.. ... T.. .T- --- CGG TC. --T .CT .C- T.. GT. C-. T.- --- -T. ..- .G. GTT
#Taonia_atomaria                 ..G ... ... .G. ... ..A -.A .AG ... TGC ..T CGC CGG ..C --G CCA AC- T.. .A. T-. C.- --- -.. ..T .GT GT.
#Dictyopteris_polypodioides      ..G ... ... .G. ... ..A -.A .AG ... TGC ..A CGC CGG ..C --G CCA AC- C.. .A. T-T TTT TGC C.. ..T .GT GT.
#Cladostephus_spongiosus         ... ... ... .G. ... ..A -.A ... ... T.. ..- --- .GG GT. --. .CT .A- T.. GGA .-A C.- --- -T. ..- .GT ..C
#Halopteris_scoparia             ... ... ... .G. ... ..A -.A ... ... T.. ..- --- CGG TT. --. .CT .C- T.. GGG ATA C.- --- -T. ..- .GT T.T
#Syringoderma_phinneyi           ... ... ... .G. ... ..A -.A ... ... T.. ..- --- .AG TC. --. .CT .C- T.. T.. A-C C.- --- -T. ..- .GG TGT
#Nemoderma_tingitanum            ... ... ... .G. ... ..A -.A C.. ... T.. .T- --- CGG TTC --. .CT .C- T.. T.C .-C C.- --- -TC ..- .GG .GT
#Bachelotia_antillarum           ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGG GTC --. .C. .C- C.. GTC .-C C.- --- -.C ..- .GG .G.
#Haplospora_globosa              ... ... ... .G. ... ..A -.A C.. ... T.. .T- --- CAG .TC --. .CT .C- C.. T.C .-C C.- --- -T. ..- .GG .GT
#Phaeosiphoniella_cryophila      ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAG TT. --. .CT .C- T.. T.. .-C C.- --- -.. ..- .GG .TC
#Tilopteris_mertensii            ... ... ... .G. ... ..A -.A C.. ... T.. .T- --- CAG .TC --. .CT .C- T.. T.C .-C C.- --- -T. ..- .GG .GT
#Alaria_esculenta                ... ... ... .G. ... ..A -.A C.. ... TA. ..- --- CGT C.A --A .CT ..- C.. T.C .-C C.- --- -.. ..- .GG .TC
#Laminaria_ochroleuca            ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CCT C.A --A .CT ..- C.. T.C .-C C.- --- -T. ..- .GG .TC
#Macrocystis_pyrifera            ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGT C.A --A .CT ..- C.. A.C .-C C.- --- -.. ..- .GG .T.
#Chorda_filum                    ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- .AG TT. --. .CT .C- T.. G.C .-C C.- --- -.. ..- .GG .A.
#Halosiphon_tomentosus           ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAG TTC --. .CT .C- T.. T.C .-C C.- --- -.. ..- .GG .GT
#Saccorhiza_polyschides          ... ... ... .G. ... ..A -.A C.. ... T.. .T- --- CGG TC. --. .CT .C- T.. T.C .-C C.- --- -.. ..- .GG .GT
#Cutleria_multifida              ... ... ... .G. ... ..A -.A C.. ... T.. .T- --- CA. GTC --. .CT .C- T.. T.. .-C C.- --- -.. ..- .GG .TC
#Ascoseira_mirabilis             ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAG TTC --. .CT .C- ... TTC .-C C.- --- -.C ..- .GG .GT
#Arthrocladia_villosa            ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAG TT. --. .CT .C- T.. T.. .-C C.- --- -.. ..- .GG .GT
#Desmarestia_aculeata            ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- C.. .TC --. .CT .C- T.. TTC .-C C.- --- -.. ..- --- --T
#Desmarestia_ligulata            ... ... ... .G. ... ..A -.A C.. ... TG. .A- --- CAT .TC --. .CT .C- T.. TT. .-C C.- --- -.. ..- --- --T
#Himantothallus_grandifolius     ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAT CTC --. .CT .C- T.. T.. .-C C.- --- -T. ..- .GG .GT
#Phaeurus_antarcticus            --- --- --- --- --- --- --A C.. ... T.. .A- --- C-T CAA --. -CT .C- T.. T.. .-C C.- --- -.. ..- .G- -GT
#Sporochnus_pedunculatus         ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGG T.A --A .CT .C- T.. T.C .-C C.- --- -.. ..- .GG .GT
#Scytothamnus_australis          ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGG CTC --. .CT .C- CT. ATG .-C C.- --- -.. ..- .GG ..T
#Stereocladon_rugulosus          ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- .CG TT. --. .CT .C- CT. AT. .-C C.- --- -T. ..- .G- ..T
#Asteronema_ferruginea           ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAG TTC --. .CT .C- C.. TT. .-C C.- --- -.. ..- .GG .TT
#Asteronema_rhodochortonoides    ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CGT TTA --A .CT .C- T.. TT. .-C C.- --- -.. ..- .G- .GC
#Asterocladon_lobatum            ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAG TTA --T .CT .C- T.. TT. .-C C.- --- -.. ..- .GG .GC
#Hincksia_granulosa              ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGG GTC --. .CT .C- T.. T.C .-C C.- --- -.. ..- .GG .GT
#Pylaiella_littoralis            ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAG TC. --T .CT .C- T.. T.C .-C C.- --- -.. ..- .GG .GT
#Adenocystis_utricularis         ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGG TTC --. .CT .C- T.. TTG .-C C.- --- -.. ..- .GG ..T
#Utriculidium_durvillei          ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGG TTC --. .CT .C- T.. TTG .-C C.- --- -.. ..- .GG ..T
#Petalonia_fascia                ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGG TTC --. .CT .C- T.. TTG .-C C.- --- -.. ..- .GG ..T
#Scytosiphon_lomentaria          ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CGG TTC --. .CT .C- T.. TTG .-C C.- --- -.. ..- .GG ..T
#Chordaria_flagelliformis        ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAG TTC --. .CT .C- ... .T. .-C C.- --- -T. ..- .G- .GT
#Punctaria_latifolia             ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAG TT. --. .CT .C- T.. .TC .-C C.- --- -T. ..- .GG .TT
#Myriotrichia_clavaeformis       ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CGG GT. --. .YT .C- T.. .TC --C C.- --- -T. ..- .GG .TT
#Dictyosiphon_foeniculaceus      ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CAG TT. --. ..T .C- C.. A.C .-T C.- --- -T. ..- .GG TT.
#Striaria_attenuata              ... ... ... .G. ... ..A -.A C.. ... T.. .A- --- CGG GT. --. .CT .C- T.. .TC --C C.- --- -T. ..- .GG .TT
#Pseudolithoderma_PS5            ... ... ... .G. ... ..A -.A ... ... T.. ..- --- CGG TC. --. .CT .C- T.. -T. .AT C.- --- -.. ..- .GG T.T
#Ralfsia_confusaTH21             ... ... ... .G. ... ..A -.A C.. ... T.A ..- --- CCG TTC --. .CT ..- T.. ... .-C TT- --- -T. ..- AAG .AT
#Ralfsia_expansaPS6              ... ... ... .G. ... ..A -.A C.. ... T.. ..- --- CCG TTC --. .CT .C- T.. T.C .-C TT- --- -.. ..- AAG .GT
```

```
#Ralfsia_smoothSR6                ... ... ... .G. ... ..A -.A C.. ... T.A ..- --- CCG TTC --. .CT .C- C.. ..C .-C TT- --- -T. ..- AAG .A.
#Hapalospongidion_gelatinosumHP4 ... ... ... .G. ... ..A -.A T.. ... T.. ..- --- CCG TTA --. .CT .C- T.. T.C .-C CT- -GC -TA ..C AAG .GT
#Diplura_australisRV16            ... ... ... .G. ... ..A -.A ... ... T.. ..- --- CGG TT. --. .CT .C- T.. TTG A-C T.T --- -.. .T- --. ..T

[                                444 444 444 444 444 444 444 444 444 444 455 555 555 555 555 555 555 555 555 555 555 555 555 555 555 555 ]
[                                677 777 777 778 888 888 888 999 999 999 900 000 000 001 111 111 111 222 222 222 233 333 333 334 444 444 ]
[                                901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 ]
#Tribonema_aequale               GGT G-C T-- --G C-- --- --- --- --- -TC GCT GAG CCT TG- TCA G-G GCG G-- GTT CTC TGT --C CGC GGG --- --A
#Dictyota_dichotoma              ..- .GT A-- --. G-- --- --- --- --- -C. ..C CG. ..G C.G ... .-. .GT AGC .CC G-- G.C --T ..G ... AAG AGC
#Sphacelaria_cirrosa             C.- .CT C-- --. .-- --- --- --- --- --G CT. CC. ..G .AG C.. .-C ..C .-- .G. .-- C.G --. ... ... ATG CTT
#Fucus_vesiculosus               T.- .AT C-- --. .-- --- --- --- --- --G TT. CC. T.G ..G ... .-T ..C .-- .C. A-- GC. --T T.. ... AGC CTG
#Laminaria_digitata              T.- .GT C-- --. .-- --- --- --- --- --G T.. TC. ..G ..G C.. .-. .TC .-- .G. A-- ..G --T T.. ... AGC CTG
#Splachnidium_rugosum            T.- .AT .-- --. .-- --- --- --- --- --G TT. AT. T.G ..G C.. .-. ..C .-- .G. A-- GAG --T T.. ... AGC CTG
#Streblonema_maculans            T.- .TT .-- --. .-- --- --- --- --- --G CT. CT. ..G ..G C.. .-. ..C .-- .G. G-- .CG --T T.. ... AGT CTG
#Ascophyllum_nodosum             T.- .AT C-- --. .-- --- --- --- --- --G TT. CC. T.G ..G ... .-T ..C .-- .C. A-- GCG --T ... .A. AGC CTG
#Pelvetia_canaliculata           T.- .AT C-- --. .-- --- --- --- --- --G TT. CC. T.G ..G ... .-T ..C .-- .C. A-- GCG --T ... ... AGC CTG
#Xiphophora_chondrophylla        T.- .AT C-- --. .-- --- --- --- --- --G TT. CC. T.G ..G C.. .-. ..T .-- .G. A-- .TG --T ... ... AGC CTG
#Hormosira_banksii               ..- .AT .-- --. .-- --- --- --- --- --G .T. CC. T.G ..G C.. .-. ..C .-- ... A-- GT. TGT T.. ... AGG CT.
#Himanthallia_elongata           CT- TAT .-- --. .-- --- --- --- --- --G TT. CC. T.G ..G C.. .-. .TC .-- .G. A-- GTA --T T.. ... AGC CTG
#Anthophycus_longifolius         C.- .G. .-- --. .-- --- --- --- --- --G CT. CC. ..G ..G C.. .-. ..C .-- .G. .-- G.G --. ... ... AAT CGG
#Sargassum_muticum               C.- .GT .-- --. .-- --- --- --- --- --G CT. CC. .TG .TG C.. .-. ..C .-- .G. .-- G.G --. ... ... AAT CGG
#Turbinaria_turbinata            C.- .G. .-- --. .-- --- --- --- --- --G CT. CC. ..G ..G C.. .-. ..C .-- .G. .-- G.G --. ... ... AAC CGG
#Axillariella_constricta         C.- .G. .-- --. .-- --- --- --- --- --G CT. CC. ..G ..G C.. .-. .TC .-- .G. T-- G.G --. ... ... ATC CCG
#Bifurcaria_bifurcata            C.- .-. .-- --. .-- --- --- --- --- --G C.. CC. ..G ..G C.. .-. .TC .-- .G. .-- G.G --. ... ... ATC CC.
#Bifurcaria_brassicaeformis      C.- .GT .-- --. .-- --- --- --- --- --G CT. CC. ..G ..G C.. .-. .TC .-- .G. T-- G.G --. ..T ... AAC CGG
#Bifurcariopsis_capensis         A.- .AT C-- --. .-- --- --- --- --- --G TT. CC. T.G ..G C.. .-. .GC .-- .G. A-- GCG --T T.. ... AGT CTG
#Caulocystis_cephalornithos      C.- .G. G-- --. .-- --- --- --- --- --G CT. CC. T.G ..G C.. .-. ..C .-- .G. T-- G.G --. ... ... ATC TCG
#Cystoseira_nodicaulis           C.- .G. .-- --. .-- --- --- --- --- --G CT. CC. ..G ..G C.. .-. .TC .-- .G. T-- G.G --. ... ... ATC CCG
#Notheia_anomala                 C.- .G. C-- --. .-- --- --- --- --- --G TT. .C. ..G ..G ... .-. ..C .-- .G. A-- CT. TGA T.. ... ATC CTT
#Cystosphaerae_jacquinotii       C.- .A. .G- -AA .-- --- --- --- --- -AG AT. CC. ..G ..G C.. .-. ..C .-- .G. G-- ACG --T T.. ... AGA CTG
#Phyllospora_comosa              C.- .T. .G- -AA A-- --- --- --- --- -CG AT. CC. ..G ..G C.. .-. ..C .-- .G. G-- ACG --T ... ... AGA CTG
#Seirococcus_axillaris           A.- .A. CC- -AA .-- --- --- --- --- -AG .T. CC. ..G ..G ... .-. ..C .-- .G. G-- ACG --T ... ... AGA CTG
#Durvillaea_antarctica           C.- .AT .-- --. .-- --- --- --- --- --G TT. CC. T.G ..G C.. T-A ..C .-- .G. G-- .C. --T T.. ... AGC CTG
#Durvillaea_potatorum            C.- .AT C-- --. .-- --- --- --- --- --G .T. CC. G.G ..G C.. .-. ..C .-- .G. G-- .C. --T T.. ... AGC CTG
#Taonia_atomaria                 ..- .GT A-- --. G-- --- --- --- --- -C. ... CC. ..G CTG ... .C. .TT .-C .CC G-- G.C --T ... ... AGG CCC
#Dictyopteris_polypodioides      ..- .GT A-- --. G-- --- --- --- --- -C. ... CC. ..G CTG ... .C. .TC .-C .CC G-- G.C --T ... ... AGG CTC
#Cladostephus_spongiosus         C.- .CT C-- --. .-- --- --- --- --- --G CTC CC. ..G ..G C.. .-C ..C .-- .G. T-- C.G --T T.. ... ATG CTT
#Halopteris_scoparia             C.- .T. .-- --. .-- --- --- --- --- --G TT. CC. ..G ..G C.. .-C ..C .-- .G. .-- .T. --T ... ... AAG CTT
#Syringoderma_phinneyi           T.- .T. .-- --. .-- --- --- --- --- --G TT. TTA ..G ..G C.. .-. ..C .-- .G. A-- ..G --T T.. .CC AAG CG.
#Nemoderma_tingitanum            T.- .TT .-- --. .-- --- --- --- --- --G TT. CC. T.G ..G C.. .-. ..C .-- .G. A-- GC. --T T.. ... AGT CGG
#Bachelotia_antillarum           C.- .AT C-- --. .-- --- --- --- --- --G TTC CC. ..G ..G C.. .-. ..C .-- .A. G-- C.G --. ... ... ACC CCG
#Haplospora_globosa              T.- .CT .-- --. .-- --- --- --- --- --G TT. TT. T.G ..G C.. .-. ..C .-- .G. A-- GTG --T T.. ... AGT CTG
#Phaeosiphoniella_cryophila      T.- .AT .-- --. .-- --- --- --- --- --G TT. CT. T.G ..G C.. .-. ..C .-- .G. A-- GAA --T T.. ... AGT CTG
#Tilopteris_mertensii            T.- .CT .-- --. .-- --- --- --- --- --G TT. TT. T.G ..G C.. .-. ..C .-- .G. A-- GCG --T T.. ... AGT CTG
#Alaria_esculenta                T.- .GT C-- --. .-- --- --- --- --- --G T.. TC. ... ..G C.. .-. .TC .-- .G. A-- ..G --T T.. ... AGT CTG
#Laminaria_ochroleuca            T.- .GT C-- --. .-- --- --- --- --- --G T.. TG. ..G ..G C.. .-. ..C .-- .G. A-- ..G --T T.. ... AGC CTG
#Macrocystis_pyrifera            C.- .GT C-- --. .-- --- --- --- --- --G T.. TC. ..G ..G C.. .-. ..C .-- .G. A-- C.G --T T.. ... AGC CTG
#Chorda_filum                    C.- .TT .-- --. .-- --- --- --- --- --G TT. CT. T.G ..G C.. .-. ..C .-- .G. A-- CCG --T T.. ... AGC CTG
#Halosiphon_tomentosus           T.- .TT .-- --. .-- --- --- --- --- --G TT. CT. T.G ..G C.. .-. ..C .-- .G. A-- G.G --T T.. ... AGT CTG
#Saccorhiza_polyschides          T.- .T. .-- --. .-- --- --- --- --- --G TT. CC. ..G ..G C.. .-. ..C .-- .G. A-- GCG --T T.. ... AGT CTG
#Cutleria_multifida              T.- .AT .-- --. .-- --- --- --- --- --G TT. CT. G.G ..G C.. .-. A.C .-- .G. A-- GTG --T T.. ... AGT CTG
```

```
#Ascoseira_mirabilis             T.- .TT .-- --. .-- --- --- --- --- --G TT. CT. T.G ..G C.. .-. ..C .-- .G. A-- G.G --T T.. ... AGT CTG
#Arthrocladia_villosa            T.- .TT .-- --. .-- --- --- --- --- --G .T. CT. ..G ..G C.. .-. ..C .-- .G. G-- GAG --T ... ... AGC CTG
#Desmarestia_aculeata            T.- .TT .-- --. .-- --- --- --- --- --G TT. ... T.G ..G C.. .-. ..C .-- .G. .-- GAG --T T.. .?. AGC CTG
#Desmarestia_ligulata            T.- .TT .-- --- .-- --- --- --- --- --G C.. AT. T.G ..G C.. .-. ..C .-- .G. .-- GAG --T T.. ... AGC CTG
#Himantothallus_grandifolius     T.- .TT .-- --. .-- --- --- --- --- --G TT. TT. T.G ..G C.. .-. ..C .-- .G. G-- GAG --T T.. ... AGC CTG
#Phaeurus_antarcticus            T.- .TT .-- --. .-- --- --- --- --- --G TT. TT. T.G ..G C.. .-. ..C .-- .G. G-- GAG --T T.. ... AGT CTG
#Sporochnus_pedunculatus         T.- .TG .-- --. .-- --- --- --- --- --G T.. CC. ..G ..G C.. .-. ..C .-- .GC A-- G.G --T T.T ... AGT CTG
#Scytothamnus_australis          T.- AAT C-- --. .-- --- --- --- --- --G TTG CC. T.G ..G C.. .-. ..T .-- .G. A-- GAG --T ... ... AGC CTG
#Stereocladon_rugulosus          T.- AAT .-- --. .-- --- --- --- --- --G TTG CGA T.G ..G C.. .-. ... A-- .G. .-- GAG --T ... ... AGC CTG
#Asteronema_ferruginea           T.- .AT C-- --. .-- --- --- --- --- --G TTC CT. T.G ..G C.. .-. ..T .-- .G. A-- GCG --T T.. ... AGC CTG
#Asteronema_rhodochortonoides    T.- .T. .-- --. .-- --- --- --- --- --T TT. CT. T.G .AG C.. .-. ..C .-- .G. G-- .TG --. ... ... AGC CTG
#Asterocladon_lobatum            T.- .TT .-- --. .-- --- --- --- --- --G T.. CT. T.G ..G C.. .-. ..C .-- .G. G-- GTG --. T.. .A. ATC CTG
#Hincksia_granulosa              T.- .TT .-- --. .-- --- --- --- --- --G TT. CC. ..G ..G C.. .-. ..C .-- .G. A-- GC. --T T.. ... AGG CTG
#Pylaiella_littoralis            T.- .TT .-- --. .-- --- --- --- --- --G TT. CT. T.G ..G C.. .-. ..C .-- .G. A-- GCG --T T.. ... AGT CTG
#Adenocystis_utricularis         T.- .TT .-- --. .-- --- --- --- --- --G TT. CC. ..G ..G C.. .-. ..C .-- .G. A-- GTG --T T.. ... AGC CTG
#Utriculidium_durvillei          T.- .TT .-- --. .-- --- --- --- --- --G TT. CC. ..G ..G C.. .-. ..C .-- .G. A-- GTG --T T.. ... AGC CTG
#Petalonia_fascia                C.- .TT .-- --. .-- --- --- --- --- --G TT. CC. ..G ..G C.. .-. ..C .-- .G. A-- GCG --T T.. ... AGG CTG
#Scytosiphon_lomentaria          T.- .TT .-- --. .-- --- --- --- --- --G TT. CC. ..G ..G C.. .-. ..C .-- .G. A-- GCG --T T.. ... AGG CTG
#Chordaria_flagelliformis        T.- .TT .-- --. .-- --- --- --- --- --G TTC CT. T.G ..G C.. .-. ..C .-- .G. G-- GCG --T T.. .-. AGC CTG
#Punctaria_latifolia             T.- .TT .-- --. .-- --- --- --- --- --G TTC CT. T.G ..G C.. .-. ..C .-- .G. G-- GCG --T T.. ... AGC CTG
#Myriotrichia_clavaeformis       T.- .TT .-- --. .-- --- --- --- --- --G TTC CC. T.G ..G C.. .-. ..C .-- .G. A-- GCG --T T.. .T. AGC CTG
#Dictyosiphon_foeniculaceus      T.- .CT .-- --. .-- --- --- --- --- --G TTC CT. T.G ..G C.. .-. ..C .-- .G. A-- GCG --T T.. .T. AGC CTG
#Striaria_attenuata              T.- .TT .-- --. .-- --- --- --- --- --G TTC CT. T.G ..G C.. .-. ..C .-- .G. A-- GCG --T T.. .H. AGC CTG
#Pseudolithoderma_PS5            C.- .T. C-- --. .-- --- --- --- --- --G TT. CC. ..G .AG C.. .-C ..C .-- .G. T-- G.G --T T.. ... ACG CTT
#Ralfsia_confusaTH21             ..- .C. .-- --. .-- --- --- --- --- --G TT. CG. ..G ..G C.. .-. ..C .-- .G. G-- GTG --T T.. ... ATG CCG
#Ralfsia_expansaPS6              T.- .TT .-- --. .-- --- --- --- --- --G TT. CG. ..G ..G C.. .-. ..C .-- .G. G-- .TG --T T.. ... ATG CTG
#Ralfsia_smoothSR6               ..- .T. .-- --. .-- --- --- --- --- --G TT. C.. ..G ..G C.. .-. ..C .-- .G. G-- GTG --T T.. ... ATG CCG
#Hapalospongidion_gelatinosumHP4 ..- .T. ATT T-. .-- --- --- --- --- --G TT. CG. ..G ..G C.. .-. ..C .-- .G. G-- .TG --T T.. ... AAA GTG
#Diplura_australisRV16           T.- .TT GGG G-. .GG GGG TCT TGG CCT GCG T.. CC. ..G ..G C.. .-C ..C .-- .G. T-- ..G --T T.. ... ATG CTG

[                                555 555 555 555 555 555 555 555 555 555 555 555 555 555 555 555 555 556 666 666 666 666 666 666 666 666 ]
[                                444 555 555 555 566 666 666 667 777 777 777 888 888 888 899 999 999 990 000 000 000 111 111 111 122 222 ]
[                                789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 ]
#Tribonema_aequale               TCT GT- -CG T-- -CG TCG GAG GTA --- --- -GG GTG CT- --- --- --- -TG CAT CTG A-- --A ACG -TC GTC GT- --C
#Dictyota_dichotoma              CG. CG- -G. GAT CG. .A. .C. AGC --- --- C.C T.C GGT G-- --- --- -GT GCG ... TCA -GG C.C -CG ..- .G- TTG
#Sphacelaria_cirrosa             CGC C.- -.. GGA -G. .A. CGY C.C --- --- -.T C.C GGC --- --- --- -GA G-C G.. .AT --. C.. -.G .C- ..- --T
#Fucus_vesiculosus               CG. CA- -.. GGA -G. .AC .T- C.C --- --- --- C.C G-- --- --- --- -GA G-A TG. .AT --G C.. -.G .C- ..- --G
#Laminaria_digitata              CG. CG- -T. GAA -G. .A. CCT C.C --- --- --- C.C G-- --- --- --- -GA G-G G.. .AT --. C.. -CG .C- ..- --G
#Splachnidium_rugosum            CGC C.- -.. GAA -G. .A. CTC ..C --- --- --- C.C G-- --- --- --- -GA .-G G.. .AT --. C.. -.G ..- ..- --G
#Streblonema_maculans            CGC T.- -T. GGA -G. .A. C.T C.C --- --- --- T.C G-- --- --- --- -GA G-. G.. .AG --. C.T -.G .C- ..- --G
#Ascophyllum_nodosum             CG. TA- -.. GGA -G. .AC .T- C.C --- --- --- C.C G-- --- --- --- -GA G-A TG. .AT --G C.. -.G .C- ..- --G
#Pelvetia_canaliculata           CG. CA- -.. GGA -G. .AC .T- C.C --- --- --- C.C G-- --- --- --- -GA G-A TG. .AT --G C.. -.G .C- ..- --G
#Xiphophora_chondrophylla        CG. AA- -T. GGA -G. .AC .T- C.C --- --- --- T.C G-- --- --- --- -GA G-A GG. .AT --G C.A -.G AC- ..- --T
#Hormosira_banksii               CG. CG- -.. GGA -G. .AC .T- C.C --- --C TCC T.A G.G GG- --- --- -GA G-A GG. .AT --G C.. -.G .C- .A- --A
#Himanthallia_elongata           CGC TG- T.. GGA -G. .AC .T- C.C --- --- --C T.T G-- --- --- --- -GA G-A TG. .AT --G C.. -.G .C- ..- --G
#Anthophycus_longifolius         CG. CC- CT. GGA -G. .AC .C- C.C --- --- --- T.C G-- --- --- --- -GA G-G TG. .AT --G C.T -GG .A- .C- -T.
#Sargassum_muticum               CG. CC- CT. GGA -G. .AC .C- C.C --- --- --- T.C G-- --- --- --- -GA G-G TG. .AT --G C.. -GG ..- .C- -T.
#Turbinaria_turbinata            CG. CC- C.. GGA -G. .AC .C- C.C --- --- --- T.C G-- --- --- --- -GA G-G TG. .AT --G C.. -GG ..- .C- -T.
#Axillariella_constricta         CG. CC- T.. GGA -G. .AC .T- C.C --- --- --- T.C G-- --- --- --- -GA G-A GG. .AT --G C.. -GG .C- .C- -TT
#Bifurcaria_bifurcata            CG. CC- C.. GGA -G. .AC .T- C.C --- --- --- T.C G-- --- --- --- -GA G-A GG. ?AT --G C.. -GG .C- .C- -T.
#Bifurcaria_brassicaeformis      CG. CC- T.. GGA -G. .AC .T- C.C --- --- --- T.C G-- --- --- --- -GA G-A TG. .AT --. C.. -GG AC- .CT CT.
```

```
#Bifurcariopsis_capensis         CGC C.- -.. GGA -G. .AC .T- C.C --- --- -TC C.T G.G G-- --- --- -GA G-A TG. .AT --G C.. -.G .C- ..- --G
#Caulocystis_cephalornithos      CG. CC- T.. GGA -G. .AC .T- C.C --- --- --- T.C G-- --- --- --- -GA G-A GG. .AT --G C.. -GG .C- .C- -T.
#Cystoseira_nodicaulis           CG. CC- C.. GGA -G. .AC .T- C.C --- --- --- T.C G-- --- --- --- -GA G-A GG. .AT --G C.. -GG .C- .C- -T.
#Notheia_anomala                 .G. C.- -T. GGA -G. .AC .T- C.C --- --- --- T.C G-- --- --- --- -GA G-A GG. .AT --G C.T -AG A.- ..- --G
#Cystosphaerae_jacquinotii       CGC AAG G.. GGA -G. .AC .T- C.C --- --- C.T ACT T.C G-- --- --- -GA G-A GG. .TT AC. ... -.G .C- ..- --G
#Phyllospora_comosa              CGC AAG G.. GAA -G. .AC .T- C.C CGT GCC T-C TC. GAG CGC TCG --- -GA G-A GG. .AT AGG C.. -.G .C- ..- --G
#Seirococcus_axillaris           CGC AAG G.. .GA -G. .AC .T- C.C --- --- -CA TAA G.T TTC G-- --- -GA G-A GG. .CT AC. ... -.G .C- ..- --G
#Durvillaea_antarctica           CG. CG- -G. GGA -G. .AC .T- C.C --- --- --- T.C G-- --- --- --- -GA G-A AG. .AT --G C.C -.T .C- ..- --G
#Durvillaea_potatorum            CGC .G- -G. GGA -G. .AC .T- C.C --- --- --- T.C G-- --- --- --- -GA G-A GG. .AT --G C.T -.. .C- ..- --G
#Taonia_atomaria                 CGC .C- -.. GAT CG. .G. CC- C.C --- --- -CC C.C GGG --- --- --- -GA G-G G.. TCA -GG C.. -G. ..- ..- GCG
#Dictyopteris_polypodioides      CGC .C- -G. GAT CG. .A. CCC ..C CCC GTC CCC ..C AAA CCG GGA TGG AGA G-G G.. TCA -GG C.C -G. ... .G- -TG
#Cladostephus_spongiosus         CGC C.- -.. GGA -G. .A. CGC C.C --- --- --A T.C G.- --- --- --- -GA G-C G.. .AG --. C.. -.G .C- ..- --T
#Halopteris_scoparia             CGC C.- -.. GGA -G. .A. CGT T.C --- --A TTC T.T T.G GT- --- --- -GA A-C G.. .AT --. C.. -.G .C- ..- --T
#Syringoderma_phinneyi           ATG T.- -.. GGA AG. .A. TC- T.- --- --- --- T.T --- --- --- --- --A A-G A.. .AT --. C.C -GG AC- ..- --T
#Nemoderma_tingitanum            CGC C.- -.. GGA -G. .AC .T- C.C --- --- --- T.C G-- --- --- --- -GA G-A GG. .AT --. C.. -.G .C- ..- --T
#Bachelotia_antillarum           CGC CA- -G. GAA -G. .A. CTT A.C --- --- C.. TCT .CG --- --- --- -GA G-G G.. .AT --. C.C -.G .C- .CC TCT
#Haplospora_globosa              CGC C.- -.. GAA -G. .G. CCT A.C --- --- --- C.C G-- --- --- --- -GA T-G G.. .AT --. C.. -.G .C- ..- --T
#Phaeosiphoniella_cryophila      CAC C.- -.. GAA -G. .G. CCT --- --- --- --- TC. --- --- --- --- --- --G G.. .AT --. C.. -.G ..- ..- --G
#Tilopteris_mertensii            CGC C.- -.. GAA -G. .A. CCT A.C --- --- --- C.C G-- --- --- --- -GA T-G G.. .AT --. C.. -.G ..- ..- --T
#Alaria_esculenta                CG. CG- -G. GAA -G. .A. CCT C.C --- --- --- T.C G-- --- --- --- -GA G-G G.. .AG --. C.C -CG .C- ..- --G
#Laminaria_ochroleuca            CG. CG- -T. GAA -G. .A. CCT C.C --- --- --- C.C G-- --- --- --- -GA G-G G.. .AT --. C.. -CG .C- ..- --G
#Macrocystis_pyrifera            CGC CG- -.. GGA -G. .A. CC- T.C --- --- --C C.C G-- --- --- -G- -GA A-G G.. .AT --G C.. -CG .C- ..- --G
#Chorda_filum                    CGC C.- -.. GAA -G. .A. CCT C.C --- --- --- C.C G-- --- --- --- -GA G-G G.. .AT --. C.. -.G .C- ..- --A
#Halosiphon_tomentosus           CGC T.- -.. GAA -G. .A. CTT C.C --- --- --- C.C G-- --- --- --- -GA G-A G.. .AT --. C.. -GG .C- ..- --G
#Saccorhiza_polyschides          CGC C.- -.. GAA -G. .A. CCT C.C --- --- --- C.C G-- --- --- --- -GA A-G G.. .AT --. C.. -.G .C- ..- --T
#Cutleria_multifida              CGC C.- -.. GAA -G. .A. CTC C.C --- --- --- C.C G-- --- --- --- -GA G-G G.. .AT --. C.. -.G .C- ..- --T
#Ascoseira_mirabilis             CGC C.- -.. GAA -G. .A. CCT C.C --- --- --- T.C G-- --- --- --- -GA G-G G.. .AT --. C.. -.G .C- ..- --G
#Arthrocladia_villosa            CAC C.- -.. GAA -G. .A. CC- C.C --- --- --- T.C G-- --- --- --- -GA A-G G.. .AT --. C.. -.G ..- ..- --G
#Desmarestia_aculeata            CAC C.- -.. GA- -G. .A. CCT C.C --- --- --- T.C G-- --- --- --- -GA G-G G.. .AT --. C.. -.G ..- ..- --G
#Desmarestia_ligulata            CAC T.- -.. GAA -G. .A. CCT C.C --- --- --- C.C G-- --- --- --- -GA G-G G.. .AT --. C.. -.G ..- ..- --G
#Himantothallus_grandifolius     CAC C.- -.. GAA -G. .A. CCT C.C --- --- --- C.C G-- --- --- --- -GA G-G G.. .AT --. C.. -.G ..- ..- --G
#Phaeurus_antarcticus            CAC C.- -.. GA- -G. .A. CT- C.C --- --- --- TC. --- --- --- --- --A G-G G.. .AG --. C.. -.G ..- ..- --G
#Sporochnus_pedunculatus         CGC CC- -.. GGA -G. .A. CCT C.C --- --- --- C.C G-- --- --- --- -GA G-G G.. .AT --. C.. CGG .C- ..- --g
#Scytothamnus_australis          CGC C.- -.. GAA -G. .A. .CA ..C --- --- --- C.C G-- --- --- --- -GA .-G ... .AT --. C.. -.G .C- ..- --G
#Stereocladon_rugulosus          CGC C.- -.. GAA -G. .A. CTT ..C --- --- --- T.C G-- --- --- --- -GA .-A G.. .AG --. C.. -.G .C- ..- --G
#Asteronema_ferruginea           CGC C.- -.. GAA -G. .A. CTT AAC --- --- --- C.C G-- --- --- --- -GT T-A GC. .AT --. C.. -.G .C- ..- --G
#Asteronema_rhodochortonoides    CGC C.- -.. GAA -G. .A. CTT A.C --- --- --- T.C G-- --- --- --- -GA T-A G.. .AT --. C.. -.G .C- ..- --G
#Asterocladon_lobatum            CGC C.- -.. GAA -G. .A. CTT C.C --- --- --- TGC G-- --- --- --- -GA G-A G.. .AT --. C.. -.G .C- ..- --G
#Hincksia_granulosa              CGC T.- -.. GGA -G. .A. C.T C.C --- --- --- T.C G-- --- --- --- -GA A-. G.. .AT --. C.. -.G .C- ..- -TT
#Pylaiella_littoralis            CGC T.- -.. GAA -G. .A. CGT C.C --- --- --T C.T T.- --- --- --- -GA G-C G.. .AG --. C.. -.G .C- ..- --G
#Adenocystis_utricularis         CGC T.- -.. GAA -G. .A. C.T C.C --- --- --- T.C G-- --- --- --- -GA G-. G.. .AG --. C.. -.G .C- ..- --G
#Utriculidium_durvillei          CGC T.- -.. GAA -G. .A. C.T C.C --- --- --- T.C G-- --- --- --- -GA G-. G.. .AG --. C.. -.G .C- ..- --G
#Petalonia_fascia                CGC T.- -.. GAA -G. .A. CGT C.C --- --- -.A C.C G.C --- --- --- -GA G-C G.. .AG --. C.. -.G .C- ..- --T
#Scytosiphon_lomentaria          CGC C.- -.. GAA -G. .A. CGC C.C --- --- -.A C.T G.C --- --- --- -GA G-C G.. .AT --. C.. -.G .C- ..- --T
#Chordaria_flagelliformis        CGC CG- -T. GGA -G. .A. C.T C.C --- --- --- T.C G-- --- --- --- -GA G-. G.. .AG --. C.T -CG .C- ..- --G
#Punctaria_latifolia             CGC C.- -.. GGA -G. .A. C.T C.C --- --- --- T.C G-- --- --- --- -GA G-. G.. .AG --. C.T -GG .C- ..- --G
#Myriotrichia_clavaeformis       CGC CC- -G. GAA -G. .A. C.T C.C --- --- --- T.C G-- --- --- --- -GA G-. G.. .AT --. C.T -GG .C- ..- --G
#Dictyosiphon_foeniculaceus      CGC CG- -T. GGA -G. .A. C.T C.C --- --- --- T.C G-- --- --- --- -GA G-. G.. .AG --. C.T -CG .C- ..- --G
#Striaria_attenuata              CGC C.- -T. GAA -G. .A. C.T C.C --- --- --- T.C G-- --- --- --- -GA G-. G.. .AG --. C.T -CG .C- ..- --G
#Pseudolithoderma_PS5            CGC C.- -.. GAA -G. .A. CCT ..C --- --- --- T.C G-- --- --- --- -GA A-G G.. .AT --. C.T -.G .C- ..- -TT
#Ralfsia_confusaTH21             C.. CG- -G. GAA -G. .A. CTC TC- --- --- --- T.. .-- --- --- --- --A G-A G.. .AT --. C.C -CG T.- .C- --T
```

```
#Ralfsia_expansaPS6              CGC C.- -.. GAA -G. .A. TCC TCT CT- --- --- C.C G-- --- --- -GG -AT AGG A.. .AT --. C.. -.G .C- ..- --T
#Ralfsia_smoothSR6               C.. CG- -G. GAA -G. .A. CTC TC- --- --- --- T.. .-- --- --- --- --A G-A G.. .AT --. C.C -CG T.- .C- --T
#Hapalospongidion_gelatinosumHP4 CGC C.- -T. GAA -G. .A. TCC TC- --- --- --- T.. ..C GAG AGA ACG AGA .GG A.. .AT --. C.T -CG .C- ..- --G
#Diplura_australisRV16           CGC C.- -.. GAA -G. .G. CCC A.C --- --- --- T.C G-- --- --- --- -GA G-G G.. .AT --. C.. -.G .C- ..- -TT

[                                666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 666 777 ]
[                                222 223 333 333 333 444 444 444 455 555 555 556 666 666 666 777 777 777 788 888 888 889 999 999 999 000 ]
[                                567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 345 678 901 234 567 890 123 456 789 012 ]
#Tribonema_aequale               TT- --- -GT CGC GG- --- GCT -GG ACC --G AGG CAG GGG AGT GGT ATT TAT TTT GCT GCT TCC TCC GG- C-- CCT GTC
#Dictyota_dichotoma              ..- --- -.C .CT .A- --- ..C -C. G.. C-C --- --- --- --- --- --- --- --- --- --- --- --- --- .G- T.. .G.
#Sphacelaria_cirrosa             ..- --- -.. ..- ..- --- C.G -.. G.. GC. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- G.. .A.
#Fucus_vesiculosus               .C- --- -.. ... .A- --- .GC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Laminaria_digitata              .C- --- -.. ... .A- --- CTG -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- T.. .A.
#Splachnidium_rugosum            .C- --- -.. ... .A- --- TTC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Streblonema_maculans            .C- --- -.. ... .A- --- CGG -C. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Ascophyllum_nodosum             .C- --- -.. ... .A- --- .GC -T. T.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- G-- ... .A.
#Pelvetia_canaliculata           .C- --- -.. ... .A- --- .GG -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ... .A.
#Xiphophora_chondrophylla        ..- --- -.. ... .A- --- TG. -T. G.T G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Hormosira_banksii               .CT AT- -.. ..T .A- --- .GC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Himanthallia_elongata           .C- --- -.. ... .A- --- TGG -T. G.. G-A --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ... .A.
#Anthophycus_longifolius         .CC --- -.. ... ..- --- C.. T.. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Sargassum_muticum               .CC --- -.. ... ..- --- C.. T.. G.T G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Turbinaria_turbinata            ..C --- -.C ... ..- --- C.. C.. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ... .A.
#Axillariella_constricta         .CC --- -.. ... ..- --- T.G T.. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ..C .A.
#Bifurcaria_bifurcata            ..T --- -.. ... ..- --- T.. T.. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ..C .A.
#Bifurcaria_brassicaeformis      .CC A-- -.. ... ..- --- C.. T.. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Bifurcariopsis_capensis         .C- --- -.. ... .A- --- TGG -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ... .A.
#Caulocystis_cephalornithos      .CC --- -.. ... ..- --- T.G -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ..C .A.
#Cystoseira_nodicaulis           .CC --- -.. ... ..- --- T.. T.. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ... .A.
#Notheia_anomala                 AC- --- -.. ... .T- --- TTG -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ... .A.
#Cystosphaerae_jacquinotii       .C- --- -.. ... .A- --- CGC -C. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Phyllospora_comosa              .C- --- -.C ... .A- --- CGC -C. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Seirococcus_axillaris           .G- --- -.. ... .A- --- CGG -C. GG. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Durvillaea_antarctica           .C- --- -.. ... .A- --- .GA --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- ---
#Durvillaea_potatorum            .C- --- -.. ... .A- --- .GA -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- --- -.. .A.
#Taonia_atomaria                 GC- --- -.C ... .AG ACG A.. -C. G.. C-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- T.. .G.
#Dictyopteris_polypodioides      GC- --- -.C ... .AG TT- ..C -C. G.. C-. --- --- --- --- --- --- --- --- --- --- --- --- --C .-- T.. .G.
#Cladostephus_spongiosus         ..- --- -.. ... .A- --- C.G -.. G.. GC. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- G.. .A.
#Halopteris_scoparia             ..- --- -.. ... .A- --- .AG -.. G.. GC. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- G.- -A.
#Syringoderma_phinneyi           CA- --- -.. ... .A- --- CTG -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Nemoderma_tingitanum            ..T T-- -.. ... .A- --- .GC -T. G.T G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Bachelotia_antillarum           ..T CCC C.. ... ..- --- C.G -C. ... G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Haplospora_globosa              .C- --- -.. ... .A- --- CGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Phaeosiphoniella_cryophila      .C- --- -.. ... .A- --- TTC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- T.. .A.
#Tilopteris_mertensii            .C- --- -.. ... .A- --- CGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Alaria_esculenta                .C- --- -.. ... .A- --- CTG -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- T.. .A.
#Laminaria_ochroleuca            .C- --- -.. ... .A- --- C.G -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- T.. .A.
#Macrocystis_pyrifera            .C- --- -.. ... .A- --- CTG -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- T.. .A.
#Chorda_filum                    .C- --- -.. ... .A- --- TGG -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Halosiphon_tomentosus           .C- --- -.. ... .A- --- CTC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Saccorhiza_polyschides          .C- --- -.. ... .A- --- CGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
```

```
#Cutleria_multifida              AC- --- -.. ... .A- --- CGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ... .A.
#Ascoseira_mirabilis             .C- --- -.. ... .A- --- CTC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Arthrocladia_villosa            .C- --- -.. ... .A- --- TTC -C. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Desmarestia_aculeata            .C- --- -.. -.. .A- --- TTC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Desmarestia_ligulata            .C- --- -.. ... .A- --- TTC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Himantothallus_grandifolius     .C- --- -.. ... .A- --- TTC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Phaeurus_antarcticus            .C- --- -.. ... .A- --- TTC -T. G.. G-- --- --- --- --- --- --- --- --- --- --- --- --- --- --- -.. .A.
#Sporochnus_pedunculatus         .C- --- -.C ... .A- --- ..C -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ..- -A.
#Scytothamnus_australis          .C- --- -.. ... .A- --- .TC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Stereocladon_rugulosus          .C- --- -.. ... .A- --- TTC -T. G.T G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Asteronema_ferruginea           .C- --- -.. ... .A- --- TGC -T. G.T G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Asteronema_rhodochortonoides    AC- --- -.. ... ..- --- CGG -C. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Asterocladon_lobatum            .C- --- -.. ... ..- --- CGG -C. G.. G-T --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ... .A.
#Hincksia_granulosa              .C- --- -.. ... TA- --- .GC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Pylaiella_littoralis            .C- --- -.. ... .A- --- TGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- TAC ... .A.
#Adenocystis_utricularis         .C- --- -.. ... .A- --- CGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Utriculidium_durvillei          .C- --- -.. ... .A- --- CGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Petalonia_fascia                .C- --- -.. ... .A- --- TGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Scytosiphon_lomentaria          .C- --- -.. ... .A- --- TGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Chordaria_flagelliformis        .C- --- -.. ... .A- --- TGC -C. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Punctaria_latifolia             .C- --- -.. ... .A- --- CGG -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Myriotrichia_clavaeformis       .C- --- -.. ... .A- --- CGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Dictyosiphon_foeniculaceus      .CC --- -.. ... .A- --- CGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Striaria_attenuata              .C- --- -.. ... .A- --- CGC -T. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- T.. .A.
#Pseudolithoderma_PS5            .-- --- -.. ... .A- --- C.C -.. G.. GC. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- G.. .A.
#Ralfsia_confusaTH21             .C- --- -.. ... .A- --- CGC -C. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Ralfsia_expansaPS6              AC- --- -.. ... .A- --- CGG -C. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Ralfsia_smoothSR6               .C- --- -.. ... .A- --- CGC -C. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- T-- ... .A.
#Hapalospongidion_gelatinosumHP4 ..C --- -.. ... .A- --- TGG -C. G.. G-. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- ... .A.
#Diplura_australisRV16           .-- --- -.. ... .A- --- C.C -.. G.. GC. --- --- --- --- --- --- --- --- --- --- --- --- --- .-- G.. .A.

[                                777 777 777 777 777 777 7]
[                                000 000 011 111 111 112 2]
[                                345 678 901 234 567 890 1]
#Tribonema_aequale               GAA A-- TGC TTC CCT TTA C
#Dictyota_dichotoma              .GT CGC G.. ..T T.. .C. .
#Sphacelaria_cirrosa             ... .-- ..c ..T T.. ... .
#Fucus_vesiculosus               ... .-- ..G .AT T.. .C. .
#Laminaria_digitata              ... .-- ..G ..T T.. ... .
#Splachnidium_rugosum            ... .-- ..G ..T T.. .C. .
#Streblonema_maculans            ... .-- ..G ..T T.. ... .
#Ascophyllum_nodosum             ... .-- ..G ..T T.. .C. .
#Pelvetia_canaliculata           ... .-- ..G ..T T.. .C. .
#Xiphophora_chondrophylla        ... .-- ..G ..T T.. .C. .
#Hormosira_banksii               ... .-- ..G ..T T.. .C. .
#Himanthallia_elongata           ... .-- ..G ..T T.. .C. .
#Anthophycus_longifolius         ... .-- ..G C.T T.. .C. .
#Sargassum_muticum               A.. .-- ..G C.T T.. .C. .
#Turbinaria_turbinata            ... .-- ..G ..T T.. .C. .
#Axillariella_constricta         ... .-- ..G ..T T.. .C. .
#Bifurcaria_bifurcata            ... .-- ..G ..T T.. .C. .
```

```
#Bifurcaria_brassicaeformis      ... .-- ..G A.T T.. .C. .
#Bifurcariopsis_capensis         ... .-- ..G ..T T.. .C. .
#Caulocystis_cephalornithos      ... .-- ..G ..T T.. .C. .
#Cystoseira_nodicaulis           ... .-- ..G A.T T.. .C. .
#Notheia_anomala                 ... .-- ..G ..T T.. ... .
#Cystosphaerae_jacquinotii       ... .-- ..G ..T T.. .C. .
#Phyllospora_comosa              ... .-- ..G ..T T.. .C. .
#Seirococcus_axillaris           ... .-- ..G ..T T.. .C. .
#Durvillaea_antarctica           --- --- --- --- --- --- -
#Durvillaea_potatorum            ... .-- ..G ..T T.. .C. .
#Taonia_atomaria                 ... CGC C.. ..T T.. .C. .
#Dictyopteris_polypodioides      ... C-- GC. GCT TT. --- -
#Cladostephus_spongiosus         ... .-- ..- --- --- --- -
#Halopteris_scoparia             ... .-- .-- --- --- --- -
#Syringoderma_phinneyi           ... .-- ... ..T T.. ... .
#Nemoderma_tingitanum            ... .-- ..G ..T T.. .C. .
#Bachelotia_antillarum           ... .-- ..G ..T T.. .C. .
#Haplospora_globosa              ... .-- ..G ..T T.. ... .
#Phaeosiphoniella_cryophila      ... .-- ..G ..T T.. ... .
#Tilopteris_mertensii            ... .-- ..G ..T T.. ... .
#Alaria_esculenta                ... .-- ..G ..T T.. ... .
#Laminaria_ochroleuca            ... .-- ..G ..T T.. .C. .
#Macrocystis_pyrifera            ... .-- ..G ..T T.. ... .
#Chorda_filum                    ... .-- ..G ..T T.. ... .
#Halosiphon_tomentosus           ... .-- ..G ..T T.. ... .
#Saccorhiza_polyschides          ... .-- ..G ..T T.. ... .
#Cutleria_multifida              ... .-- ..G ..T T.. ... .
#Ascoseira_mirabilis             ... .-- ..G ..T T.. ... .
#Arthrocladia_villosa            ... .-- ..G ..T T.. ... .
#Desmarestia_aculeata            ... .-- ..G ..T T.. ... .
#Desmarestia_ligulata            ... .-- ..G ..T T.. ... .
#Himantothallus_grandifolius     ... .-- ..G ..T T.. ... .
#Phaeurus_antarcticus            ... .-- ..G ..T T.. ... .
#Sporochnus_pedunculatus         ... .-- ..G ..T T.. ... .
#Scytothamnus_australis          ... .-- -.G ..T T.. .-. .
#Stereocladon_rugulosus          ... .-- ..G ..T T.. ... .
#Asteronema_ferruginea           ... .-- ..G ..T T.. ... .
#Asteronema_rhodochortonoides    ... .-- ..G ..T T.. ... .
#Asterocladon_lobatum            ... .-- ..G ..T T.. ... .
#Hincksia_granulosa              ... .-- ..G ..T T.. ... .
#Pylaiella_littoralis            ... .-- ..G ..T T.. ... .
#Adenocystis_utricularis         ... .-- ..G ..T T.. ... .
#Utriculidium_durvillei          ... .-- ..G ..T T.. ... .
#Petalonia_fascia                ... .-- ..G ..T --- --- -
#Scytosiphon_lomentaria          ... .-- ..G ..T T.. ... .
#Chordaria_flagelliformis        ... .-- ..G ..T T.. ... .
#Punctaria_latifolia             ... .-- ..G ..T T.. ... .
#Myriotrichia_clavaeformis       ... .-- ..G ..T T.. ... .
#Dictyosiphon_foeniculaceus      ... .-- ..G ..T T.. ... .
#Striaria_attenuata              ... .-- ..G ..T T.. ... .

#Pseudolithoderma_PS5             ... .-- ..T ..T T.. ... .
#Ralfsia_confusaTH21              ... .-- ..G ..T T.. ... .
#Ralfsia_expansaPS6               ... .-- ..G ..T T.. .C. .
#Ralfsia_smoothSR6                ... .-- ..G ..T T.. ... .
#Hapalospongidion_gelatinosumHP4 ... .-- ..G ..T T.. ... .
#Diplura_australisRV16            ... .-- ..T ..T T.. ... .
```