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Taxonomy and systematics of *Rhodophyta* with reference to the Mediterranean taxa

Abstract

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The red algae (*Rhodophyta*) currently comprise some 828 genera and over 4500 species of which some 200 genera and over 550 species are recorded in the Mediterranean region. Molecular data along with ultrastructural characteristics support the subdivision of red algae in the *Bangiophyceae* and the *Florideophyceae*, the latter group distinguished mainly by having cap membranes covering pit-plugs and specialised gametangia (spermatangia and carpogonia the latter provided with trichogynes). The *Florideophyceae* are subdivided in two main lineages: the first includes the *Acrochaetiales*, *Palmariales*, *Nemaliales*, *Corallinales*, *Batrachospermales* and the *Rhodogorgonales*, which are distinguished by having outer cap layers covering their pit-plugs; the second lineage is distinguished by the loss of inner cap layers and includes the *Gigartinales*, *Cryptonemiales*, *Rhodymeniales*, *Gracilariales*, *Bonnemaisoniales*, *Gelidiales*, *Ceramiales*, and the *Ahnfeltiales*. Multicellular carpogonial branches, auxiliary cells, ooblasts, axial or lateral carpogonial branches, and procarpic or non-procarpic conditions have independently developed in both lineages and apparently represent non-homologous structures at this level of phylogenetic resolution. Relationships at infra-ordinal level remain largely speculative and it is here where the above mentioned morphological characters will contribute in the systematics. The Mediterranean marine flora has undergone profound changes since the basin was created in the Palaeozoic and presently has many taxa in common with the neighboring Atlantic, while it has received several alien species in the past 100 years. Most significantly, it includes palaeoendemics and neoendemics and clarifying the systematic position and origin of these unique elements can help us understand the evolution of red algae in general.

Introduction

The post-Kylinian period has been rich in discoveries, not only because Harald Kylin's (1956) magnificent synthesis made a firm basis for further investigations, but also of the new approaches used in the study of algae in general. The application of unialgal cultures under controlled laboratory conditions, the advent of electron and scanning microscopes, and the invention of SCUBA techniques propelled taxonomy to new standards. At the same time, the Linnaean system of classification together with the application of nomenclatural

types, were universally accepted and asked consistently by international journals. The door of 'globalization' for algology and especially for phycology, the study of seaweeds, stood now wide open.

At the same time, Darwin's theory of evolution revived, being exemplified by Hennig's phylogenetic systematics. As Brower (2000) put it, '[t]he process of phylogeny that explains the hierarchical patterns discovered by systematics is one of the most profound empirical theories of modern science.'

It is only unfortunate that the advent of molecular systematics had a negative impact on taxonomy that in the past 10-15 years experienced a retrogression, after forming the main stream of systematic research for more than two centuries.

Since 1982, Michael Melkonian has periodically reviewed the field of algal taxonomy in the book series 'Progress in Botany'. In the following, the major contributions will be summarized giving emphasis to those findings affecting the Mediterranean taxa. The pre-Kylinian period is outlined in Appendix I while the latest changes and additions to the Kylinian classification appear in Appendix II.

Systematics and phylogeny of red algae

Although sexual reproduction remains unknown (or unconfirmed) in several orders and families of the most primitive red algae, the *Bangiophyceae* (Garbary & al. 1980), it is logical (and parsimonious) to assume that the rhodophyte ancestor exhibited sexual reproduction, presumably producing spermatia and forming carpogonia from modified somatic cells (as presently known in several members of the *Bangiophyceae*).

Schmitz (1892), Schmitz & Hauptfleisch (1896), and later Oltmanns (1904) proposed the ordinal classification system that we largely use today, with several modifications suggested by Kylin and later workers (Silva & Johansen 1986). By analogy to the Linnaean system, this classification is based on the structure of the female gametangium (the carpogonium), its post-fertilization stages, and in particular on the existence (or not) of an auxiliary cell that receives the zygote and develops the gonimoblast (that finally forms a cluster of carpospores known as the carposporophyte). Schmitz, Hauptfleisch, and Oltmanns's observations have been confirmed by later morphological investigations, and this classification system is now congruent with ultrastructural characteristics of pit-plugs (Pueschel & Cole 1982; Pueschel & Magne 1987; Pueschel 1987, 1989, 1990, 1994; Pueschel & al. 1992;) (Fig. 1), and the latest molecular (SSU rDNA) data (Choi & al. 2000) (Fig. 2) that collectively and overwhelmingly support : 1) the subdivision of red algae in two main classes (or subclasses), i.e. the *Bangiophyceae* and *Florideophyceae*, with the relationship of the *Cyanidiophyceae* to the other red algae being unresolved (Gross & al. 2001) and 2) the subdivision of the *Florideophyceae* in at least five orders, viz. the *Nemaliales*, *Gigartinales*, *Cryptonemiales*, *Rhodymeniales* and *Ceramiales*. The recognition of two main lineages within the *Florideophyceae* finds presently support by molecular evidence and pit plug characteristics, as we will see below. On the other hand, the elevation of numerous families to ordinal status (i.e. the *Corallinales*, *Batrachospermales*, *Bonnemaisoniales*, *Hildenbrandiales*, *Gelidiales*, *Gracilariales*, *Balbianaes*, *Thoreaes*, *Acrochaetiales*, *Palmariales*, *Ahnfeltiales*, *Rhodogorgonales*,

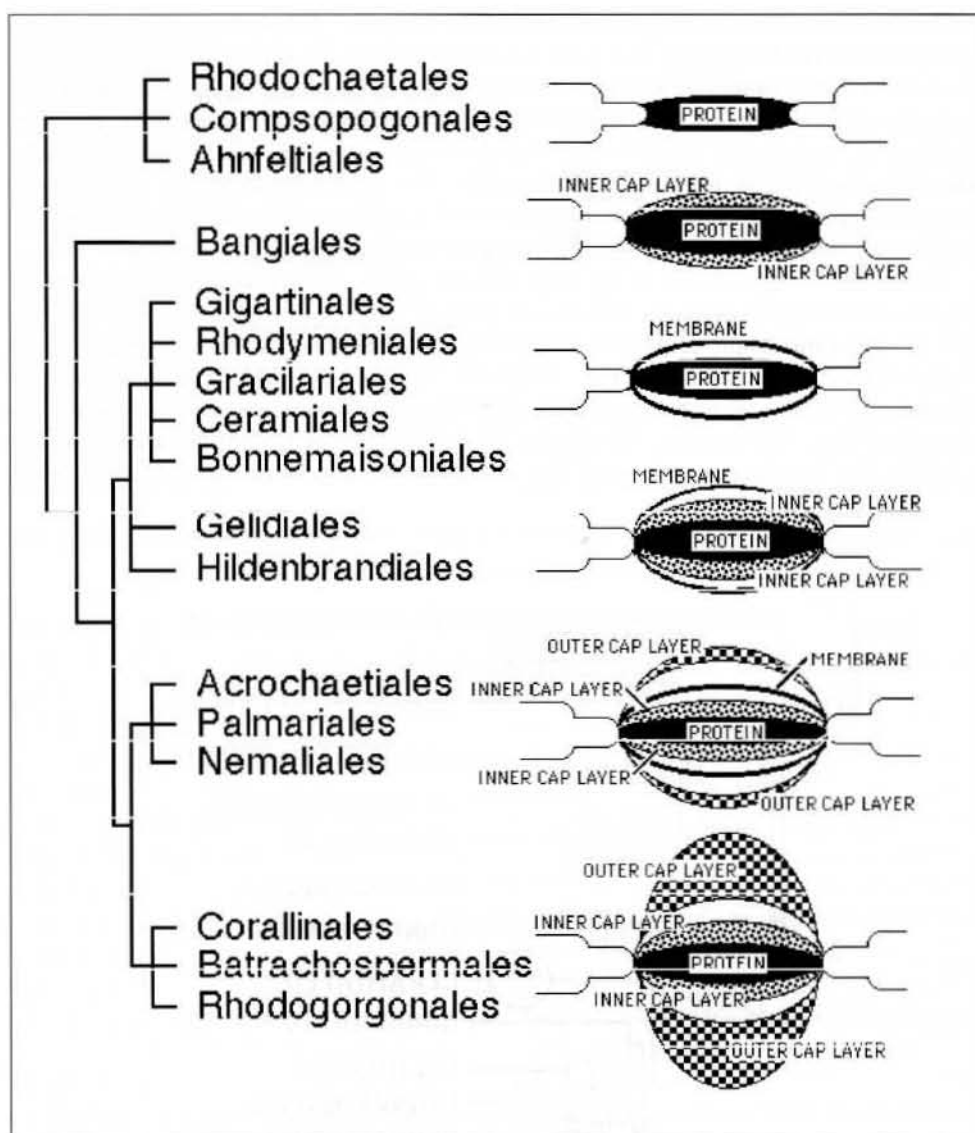


Fig. 1. The six types of rhodophyte pit-plugs and their evolution as indicated by one of the 28 most parsimonious trees based on the assumption that cap membranes and outer cap layers developed once. Cap membranes have been lost secondarily in the *Corallinales-Batrachospermales-Rhodogorgonales* (and almost certainly in the *Ahnfeltiales*). This scenario also suggests that inner cap layers developed once and were lost secondarily in the *Gigartinales-Rhodymeniales-Ceramiales-Bonnemaisoniales-Gracilariales-Ahnfeltiales* (Fig. 2). Pit-plug characters are coded and analysed using the PAUP version 3.1.1, as in Saunders & Bailey (1997) (Table 2) with the following modifications: exclusion of the orders *Porphyridiales*, *Plocamiales* and *Cryptonemiales* (the latter two having identical pit plugs as the *Gigartinales*), inclusion of the *Rhodochaetales*, and coding dome and plate outer cap layers as two independent states of a homologous character (Trick & Poeschel 1991).

Plocamiales, and *Balliales*) (Appendix II) is more in accord with the need to recognize the greater diversity of red algae than what botanical tradition has dictated until now. Surely, most of these new orders are based on monophyletic groups (that are apparently older than any angiosperm group of similar rank), but the relationships between them and to the more 'traditional' *Nemaliales*, *Gigartinales*, *Cryptonemiales*, *Rhodymeniales* and *Ceramiales* are unresolved (or at least not well-founded). The same applies to the relationships between families and tribes within the *Gigartinales* and *Ceramiales*, that together include the vast majority of red algal species. These tasks remain largely unexplored.

The information provided by pit-plug structures (Fig. 1), in combination to the most recent molecular data (Fig. 2), specifically defines: 1) that cap membranes mark the origin of the *Florideophyceae* and independently disappear in the *Ahnfeltiales*, the *Batrachospermales*, and in the common ancestor of the *Corallinales* and *Rhodogorgonales*, 2) that outer cap layers (OCLs) are so far unique to six orders; i.e. the *Acrochaetiales*, *Palmariales*, *Nemaliales* (that have the plate-like type), and to the *Corallinales*, *Rhodogorgonales*, and *Batrachospermales* (that have the dome-like type),

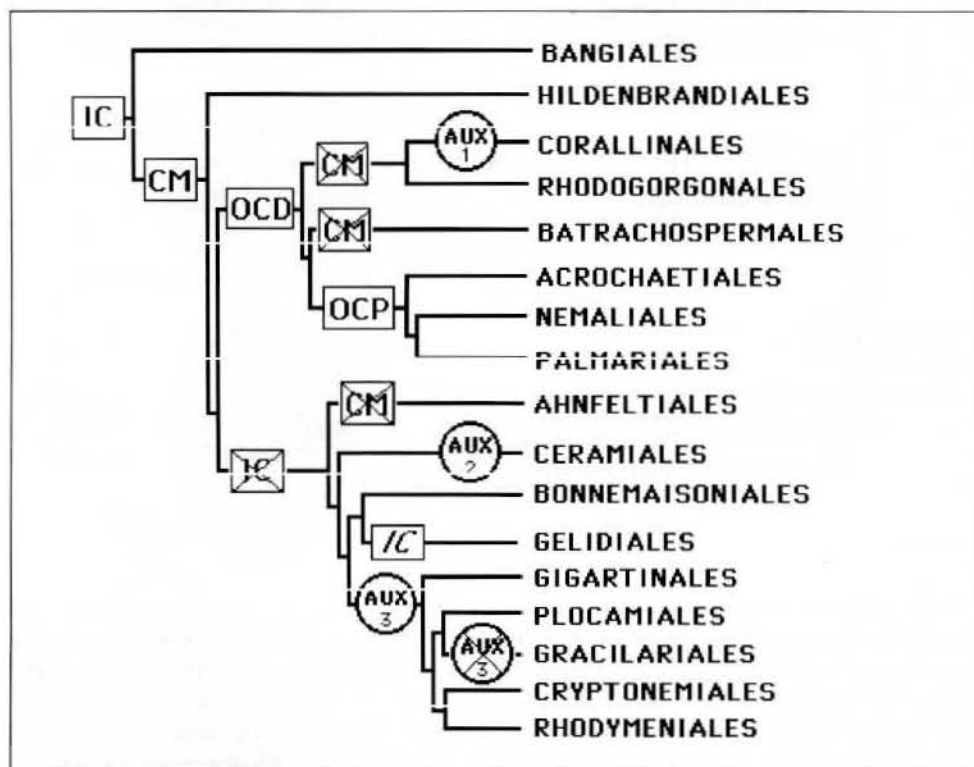


Fig. 2. Relationships between 17 rhodophyte orders, as indicated by a phylogenetic analysis of SSu rDNA sequences based on parsimony (modified after Choi & al. 2000, fig. 2). The origin (or loss) of IC (inner cap layers), CM (cap membranes), OCD (dome outer cap layers), OCP (plate outer cap layers), as also the development of 3 non-homologous types of auxiliary cells (AUX) are marked. For further explanation see in the text.

and 3) that inner cap layers (ICLs) appear before cap membranes and secondarily disappear in the common ancestor of the *Ahnfeltiales*, *Ceramiales*, *Bonnemaisoniales*, *Gigartinales*, *Cryptonemiales*, *Gracilariales*, and *Rhodymeniales*. The re-occurrence of ICLs in the *Gelidiales* could be interpreted as a reversal or as a non-homologous new type.

If pit-plug characteristics seem to be congruent with the latest SSU rDNA data, the evolution of the carpogonium and auxiliary cell systems still present mysteries to be discovered and guide us in the understanding of the ordinal and infra-ordinal classifications. As regards the carpogonium, it is clear that after being a modified somatic cell in the *Bangiophyceae*, it marks its unique function first in the Florideophyceean ancestor by developing terminally on a branched thallus (cfr. the unbranched thallus in *Erythrotrichia* Areschoug; Magne 1990, fig. 2) and forming a distinctive trichogyne (cfr. protrichogyne in *Bangia* C. Agardh; see Gargiulo & al. 2001, fig. 29). At the same time, in the vast majority of the *Florideophyceae*, spermatia are released singly from spermatangia which are generally specialised (accessory) diminutive cells and not modified somatic cells as in certain *Bangiophyceae* (cf. Magne 1989). The current topology (Fig. 2) also suggests that the development of single carpogonia (i.e. lacking carpogonial branches) persisted in certain members of the *Rhodogorgonales*, certain primitive *Corallinales* (Townsend & al. 1994), in the *Acrochaetiales*, *Thoreales* (Yoshizaki 1986; *Thoreales* is included in the *Batrachospermales* in fig. 2), and in the *Palmariales*. Multicellular carpogonial branches evolved in most members of the *Corallinales*, *Batrachospermales*, and *Nemaliales* (in all cases apparently independently), and generally in all orders of the second lineage (except the *Gelidiales*). In the *Ahnfeltiales* (the most primitive order of the second lineage), the carpogonial branch is 2-celled and develops on lateral (cortical) filaments. In the second most primitive order, the *Ceramiales*, the carpogonial branch is 4-celled, while a 2-celled carpogonial branch exists again in certain members of the *Gigartinales* (e.g. in *Predaea* De Toni fil.) suggesting that 3- or more-celled carpogonial branches developed independently several times along this lineage. The single carpogonia of the *Gelidiales* can be interpreted either as a reversal or as a neoteny (assuming that single carpogonia are rare or have been secondarily lost in all other orders of this lineage). Neither the evolution of the position of the carpogonial branch is a straightforward event in the present cladogram (Fig. 2), if we assume that the most primitive type is exemplified by carpogonia (or carpogonial branches) borne on filaments of unlimited growth (i.e., medullary filaments or axes). This is the type that is recorded in the *Acrochaetiales*, *Rhodogorgonales* (Ogden 1992), and also present in a few *Ceramiales* (i.e., *Warrenia* Harvey, *Balliella* Itono & Tanaka and also rarely in some other genera; Athanasiadis 1996a). It has been suggested that the transfer of the carpogonial branch to a periaxial position occurred in connection to the production of the periaxial cell itself (the axial carpogonial branch following the part of the cell wall forming the lateral periaxial cell), and this has been documented in *Balliella* as regards carpogonial branches and gland cells (Athanasiadis 1996a). In all other orders the carpogonial branch is generally localized on a lateral filament of the outer cortex (i.e. a filament of limited growth), and whether this is because axial carpogonia in these groups have gone extinct (or remain to be discovered) is uncertain.

The development of an auxiliary cell system in the *Florideophyceae* has apparently occurred several times, as previously suggested by Drew (1954) who distinguished between different types of auxiliary cells. In the *Nemaliales*, *Palmariales*, *Acrochaetiales*,

and *Batrachospermales* auxiliary cells are lacking and the carpo- or tetra-sporophyte develops either from the fertilized carpogonium (*Acrochaetiales* and *Palmariales*) or from the fusion of the carpogonium with hypogenous/supporting cells. However, auxiliary cells are present in the primitive *Corallinales* (Lebednik 1977).

In the second lineage, auxiliary cells are lacking in the *Ahnfeltiales*, *Bonnemaisoniales* and *Gelidiales*, while in the *Ceramiales* they appear only after fertilization. In the more advanced orders, auxiliary cells are generally present as supporting cells of carpogonial branches (*Gigartinales* and *Plocamiales*), while in the *Rhodymeniales*, *Cryptonemiales*, and certain genera of the *Gigartinales* auxiliary cells are located on accessory filaments. The present molecular and ultrastructural data suggest that auxiliary cells developed independently at least three times in the *Florideophyceae* (Fig. 2).

The present topology also suggests that gonimoblast development from the carpogonium itself, or from a fusion cell that includes the carpogonium, is a plesiomorphy that has persisted in orders lacking auxiliary cells (e.g. *Acrochaetiales* and *Palmariales*). In those groups that regularly form auxiliary cells, it has been either modified to procarpy, or to a non-procarpic development exemplified by the occurrence of an ooblast linking several auxiliary cells. The present molecular and ultrastructural data suggest that these modifications have been achieved independently (i.e. non-procarpy in the *Cryptonemiales* and certain *Gigartinales*, and procarpy in the *Plocamiales*, *Ceramiales*, *Rhodymeniales*, *Corallinales*, and certain *Gigartinales*; in all cases apparently independently).

As mentioned previously, the infra-ordinal systematics remain largely unexplored and in particular the relationships between genera and species that for more than two centuries have been in the focus of traditional taxonomic research. This is also the field that directly affects our knowledge of the Mediterranean taxa, since we have no endemics above the level of tribe. On the other hand, several Mediterranean species are types of genera, which typify families and orders, and therefore the status of these species directly affects the ordinal and infra-ordinal classification in general.

The origins of the mediterranean flora

The geological and climatic events that have marked the species composition of the Mediterranean Sea started at the Palaeozoic. The splitting of Pangea at about 300 MYA created the Palaeotethys and the earliest algal fossils we know from that time belong to coralline red algae of the genus *Archaeolithophyllum* Johnson [several species are described from southern and central Europe, dated back to Carbon and Permian (363-245 MYA; Lemoine 1977), and certain bryopsidalean algae recorded from the eastern Mediterranean and dated back to the Triassic (225 MYA; Dragastan & al. 1997).

Palaeotethys was replaced by the shallow and warm Tethys, c. 65-135 MYA, that extended as a girdle from the east to the west, at about the same latitude of the present-day Mediterranean, and connected the present-day Caribbean with the Indo-Pacific. From this period we know several extant coralline genera, presently having a pantropical or more widespread distribution, such as *Sporolithon* Heydrich, *Lithophyllum* Philippi, *Lithothamnion* Heydrich, and *Mesophyllum* Lemoine (Lemoine 1977). *Titanoderma* Nägeli appears at about 38 MYA, and *Neogoniolithon* Setchell & Mason at about 10 MYA

(Wray 1977), while *Spongites* Kützing at about 5-23 MYA (from Malta; Braga & al. 1993). Other calcified fossils from this period belong to *Solenoporaceae*, *Dasycladaceae*, and *Codiaceae* (Wray 1977).

The genesis of the proper Mediterranean started at about Mid-Miocene (13-16 MYA) with the closure of the passages to the Indian Ocean, and was fulfilled with the isolation from the Atlantic at the start of the Messinian period (about 7 MYA; closure of the Gibraltar Straits; Por 1978).

It is widely accepted that during the Messinian period (4-7 MYA), a salinity crisis took place that probably wiped out most of the marine life, but it is also postulated that some biota survived within euryhaline lakes (Por 1978, 1989; Basso & al. 1996; Athanasiadis 1999a). Until today, we do not have clear evidence of Tethyan (or Palaeotethyan) relics in the Mediterranean, although the number of putative candidates is increasing. Obviously, taxa with broader distribution in the Atlantic could have easily survived and later recolonize the Mediterranean, and such a species could be *Lithophyllum racemus* (Lamarck) Foslie known from deposits in Europe since the Burdigalian (16-22 MYA; Basso & al. 1996). Other putative Tethyan relics are the South Aegean endemic *Beckerella mediterranea* Huvé (with congeners restricted to the Indo-Pacific; Silva & al. 1996), *Peyssonnelia immersa* Maggs & Irvine (known only from the North Aegean and the southern British Isles; Athanasiadis 1987), several species of *Areschouggiaceae* (see below), and two species of *Mesophyllum* Lemoine, viz. *M. macroblastum* (Foslie) Adey (known only from the western Mediterranean and southern Australia; Woelkerling & Harvey 1993) and *M. macedonis* Athanasiadis (known from the North Aegean and most closely related to *M. ornatum* (Foslie & Howe) Athanasiadis from the Caribbean and the Pacific; Athanasiadis 1999a).

A large number of Atlantic species (presumably of Tethyan origin) colonized (or recolonized) the Mediterranean Sea after the end of the Messinian period (about 4 MYA), and presently the representation of Atlantic-Mediterranean species is 78 % in the Aegean Sea (Athanasiadis 1987).

Lessepsian species are recorded in the eastern Mediterranean after the opening of the Suez Canal in 1869 (Por 1975, 1978, 1989). *Caulerpa taxifolia* (Vahl) C. Agardh and numerous other alien species are introduced in the western and eastern Mediterranean in the last century (Verlaque 1994, 2001; Ribera & Boudouresque 1995). One of these species, *Womersleyella setacea* (Hollenberg) R. E. Norris, shows a remarkable ability to disperse, colonizing areas in both the eastern and western basin within less than five years (Athanasiadis 1997b).

While the introduction of alien species has attracted the interest of many taxonomists, the origin of the Mediterranean endemics that some reports estimate to be 40 % of the Mediterranean flora (and about 20 % in the Aegean Sea) remains unexplored. Three scenarios seem plausible:

- 1) these 'endemics' include species with presently unknown distributions outside the Mediterranean,
- 2) there are true endemics that evolved after the Messinian period, and these should be called neoendemics, or
- 3) there are relics from the Tethyan period and these should be named palaeoendemics (Fig. 3).

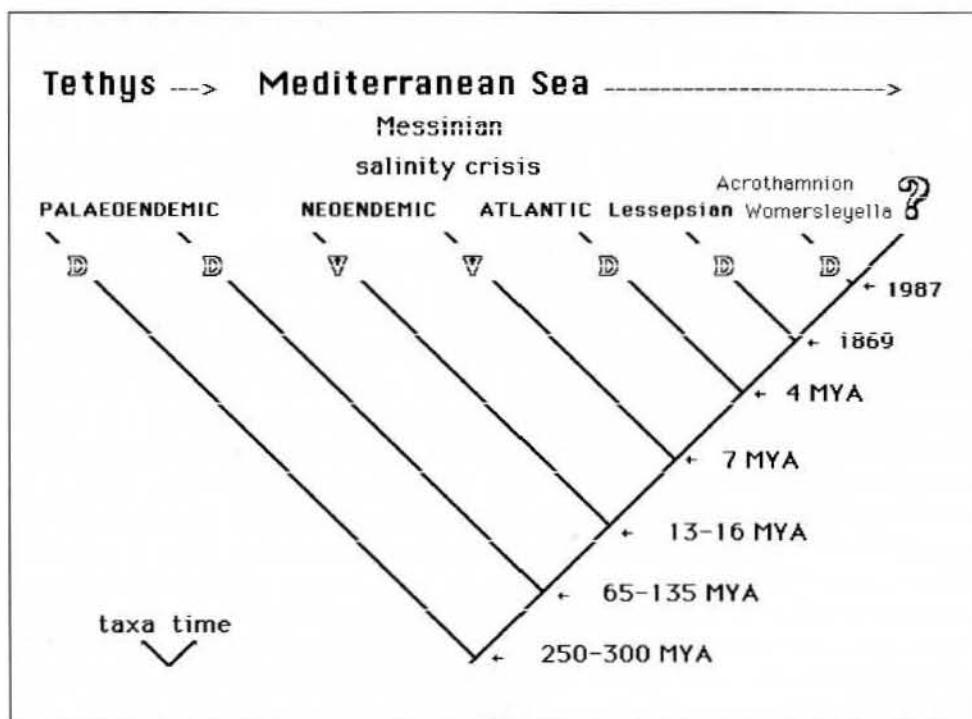


Fig. 3. Hypothetical illustration of the origins of the Mediterranean seaweeds. The letters D and V indicate dispersal or vicariance events that probably resulted (or will result) in the genesis of new taxa.

The taxonomy of species

To a great extent, our knowledge of the Mediterranean species is based on pre-Kylinian studies or on investigations of material from the northern Atlantic, since this adjoining region has a large number of taxa in common with the Mediterranean. For example, the life histories of *Scinaia* Bivona-Bernardi (Boillot 1968, 1969a), *Halarachnion* Kützinger (Boillot 1972), *Halymenia floresii* Kützinger (Maggs & Guiry 1982a), *Naccaria wiggii* (Turner) Endlicher (Boillot 1967), *Meredithia* J. Agardh (Guiry & Maggs 1985), *Schizymenia* J. Agardh (Ardré 1977, 1980) and *Helminthora divaricata* (C. Agardh) J. Agardh (Cunningham & al. 1993) have been elucidated using isolates from Atlantic France or the British Isles. Such data, however, need to be confirmed for Mediterranean plants since in some cases deviations have been reported (Maggs & Guiry 1982a). On the other hand, a great number of older Mediterranean records remain unclarified because comparative studies with types or new topotype material have been limited. Some of these problems will be outlined in discussing the current situation in each group.

BANGIOPHYCEAE

The taxonomy of this group was reviewed by Garbary & al. (1980), and further nomenclatural comments within the five currently accepted orders are discussed by Silva & al.

(1996). The latest comparative study between selected genera and orders is given by Zuccarello & al. (2000), who combined both traditional and molecular/ultrastructural data.

PORPHYRIDIALES

Cyanidium Geitler, previously included in the *Phragmonemataceae* (Garbary & al. 1980), has been transferred to the new class *Cyanidiophyceae*, together with two other genera whose relationships to the other red algae remain enigmatic (Muravenko & al. 2001, Gross & al. 2001). A revision of the cosmopolitan genus *Rhodella* Evans gave evidence to establish the new genus *Dixoniella* Scott & al. (1992) on the basis of several ultrastructural characteristics. A second unicellular genus, *Rhodosorus* Geitler, has recently received a new species, *R. magnei* Fresnel & Billard (1995), from the West Indies. In the same publication, the authors reported the presence of *Rhodosorus marinus* Geitler from Corsica and Syria. Magne (1995) cultured *Goniotrichopsis sublittoralis* Smith from material collected at Mallorca and Roscoff, noting the apparent similarity to *Stylonema alsidii* (Zanardini) Drew.

ERYTHROPELTIDALES

Members of this group have been included in the classical studies of Berthold (1882a, 1882b) from Naples, but have received less attention in the Mediterranean since then. Using material from Roscoff, Magne (1990) described the asexual and sexual life histories of *Erythrotrichia carnea* (Dillwyn) J. Agardh, where apical cells of 3-celled gametophytes first function as spermatangia (cutting off single spermatia) and then become carpogonia to receive the liberated spermatia. In the genus *Porphyrostromium* Trevisan 1848 [typified by the Mediterranean *P. boryanum* (Montagne) Silva in Silva & al. (1996) and including *Erythrotrichopeltis* Kornmann 1984 and *Erythropeltis* Schmitz 1896 as taxonomic synonyms], Kornmann (1984) described a heteromorphic life history between a peltoid and a filamentous phase in material from Helgoland that he synonymized with *Erythrotrichia discigera* Berthold (type locality: Naples). He also observed peltoid plants interspersed among the filamentous ones, the latter producing spermatia, and suggested that the peltoid ones were the product of carpospores. He later synonymized *E. discigera* with several other European taxa under *Porphyrostromium obscurum* (Berthold) Kornmann (1987). *Erythrocladia subintegra* Rosenvinge, characterized by a discoid thallus with marginal growth and previously accommodated in *Erythropeltis*, has been recognized as the distinct genus *Sahlingia* Kornmann (1989). The vegetative and reproductive morphology of Sicilian isolates of *Erythrocladia irregularis* Rosenvinge have been investigated in culture by Gargiulo & al. (1987b) who observed both colonial and discoidal thallus formation.

COMPSOPOGONALES

The single family of this order is widely distributed in tropical and subtropical freshwaters (Necchi Júnior & al. 2001). Since the first finding of the genus *Compsopogon* in southern Europe (Pisa) by Meneghini (1840, as *Lemanea corinaldii* Meneghini), Boillot (1958) reported *Compsopogon coeruleus* (Balbis) Montagne from the Banyuls area. Subsequent records of *Compsopogon coeruleus* and *C. chalybeus* Kützinger have been made from a freshwater canal in Malta and an aquarium in Catania (Sicily) respectively (Battiato & al. 1979), while *C. lusitanicus* Reiss was described from Portugal. All these species have now been synonymized and referred to *C. coeruleus* by Vis & al. (1992). A second

Mediterranean species, *Compsopogon aegyptiacus* Aleem (1981) has been described from the brackish lake Manzala at the Nile Delta.

BANGIALES

Karyological studies by Gargiulo & al. (1991) have shown that Mediterranean plants of *Bangia atropurpurea* (Roth) C. Agardh include populations with two different karyotypes, $n = 3$ and $n = 4$. In subsequent studies, they investigated the karyology and ecology of Sicilian populations of *Bangia* (Gargiulo & al. 1996, 2001) and *Porphyra leucosticta* Thuret (Gargiulo & al. 1994) and found that in the former species temperature (15–18°C) was the main factor controlling monospore and conchospore productions. They described spermatia and carpogonia (similar to those illustrated by Berthold 1882b, figs. 12–14) and confirmed the typical heteromorphic, sexual life cycle of *Bangia atropurpurea* ($n = 3$, $2n = 6$), although the site of meiosis was not investigated. This remains a controversial issue for those members of the order having sexual reproduction, and particularly in *Porphyra* since recent observations indicate that meiosis takes place during the first division of conchospores (and not during their formation; Griffin & al. 1999). A catalogue of the known species of *Porphyra* was prepared by Yoshida & al. (1997). In this work, synonymies between some taxa are given while eleven species appear to be described from the Mediterranean alone.

RHODOCHAETALES

The sexual reproduction of the single species of this order, *Rhodochaete parvula* Thuret, was studied in culture by Magne (1960), who reported monoecious gametophytes releasing laterally spermatia from (modified) axial cells and subsequent fusion between spermatia and single axial cells (i.e. carpogonia) the latter producing single carpospores. Karyological observations indicated that gametophytes were haploid ($n = 4$) and the fertilized carpogonia diploid ($2n = 8$). The possible site of meiosis was later investigated by Boillot (1969b, 1975, 1978) who also demonstrated the presence of isomorphic sporophytes. She also investigated the pit connections of the species, reporting a unique type of non well-defined pit-plugs (Boillot 1978). Pueschel & Magne (1987) later showed that pit-plugs lacked both cap layers and a membrane, and therefore were of the most simple type known for red algae (Fig. 1).

Apart from a spurious record from Victoria, *Rhodochaete parvula* is only known from the Mediterranean and the Caribbean Seas. The Australian record differed markedly in vegetative characteristics (i.e. cell size, branching pattern, basal system) and reproductive features (i.e. absence of gametangial cells and presence of monospores), as also in habitat (growing on the green alga *Palmophyllum* Kützinger), while its SSU rDNA sequence was closely similar to members of the *Erythropeltidales* (Zuccarello & al. 2000).

FLORIDEOPHYCEAE

HILDENBRANDIALES

Early molecular investigations (Freshwater & al. 1994; Ragan & al. 1994) confirmed Schmitz & Hauptfleisch (1897) original placement of *Hildenbrandia* Nardo next to the Corallinaceae, an opinion also held by Kylin (1956). However, Pueschel & Cole (1982) found that *Hildenbrandia* shared the same type of pit-plugs with the *Gelidiales* (Fig. 1) and

proposed the new order *Hildenbrandiales*. Originally described from Venice, *Hildenbrandia* presently accommodates about 20 species. Eight marine species have been studied by Denizot (1968) and their distributions along the European coast are reassessed by Maggs (1990a). After studying marine and freshwater members from Europe and North America, Sherwood & Sheath (2000a) reported partly conflicting taxon-relationships, as mirrored by rbcL vs. 18S rRNA gene phylogenies. They concluded that freshwater *H. crouanii* J. Agardh probably derives from the marine *H. rubra* (Sommerfelt) Meneghini. The relationships of the marine representatives in the Mediterranean remain to be investigated. Denizot (1968) included the genus *Apophlaea* Hooker & Harvey from New Zealand in the family *Hildenbrandiaceae*, and this was confirmed by later molecular studies (Pueschel 1989; Saunders & Bailey 1999). It should be added that the basal, isolated position of the order as indicated by SSU rDNA sequence data (Fig. 2) is not convincing, while a position near the OCL-free lineage of the *Florideophyceae* is in accord with the morphological similarity between *Hildenbrandia* and the sporophyte stage of *Ahnfeltia* Fries.

CORALLINALES

Preliminary molecular investigations (Freshwater & al. 1994; Ragan & al. 1994) have pointed to the *Hildenbrandiales* as the potential sister taxon of the *Corallinales*, but this aimed to change with the discovery of the *Rhodogorgonales* (Fredericq & Norris 1995) and the close relationship found between this new order and the coralline algae (Saunders & Bailey 1997). Unlike the *Rhodogorgonales*, whose two genera are restricted to the tropics of the Caribbean and the Pacific (Ogden 1992), the *Corallinales* are one of the most successfully dispersed and rich in species groups in marine waters. Their fossil record is also impressive and numerous extinct species and genera have been described from deposits dated since the Cambrian (Woelkerling 1988). In the most recent phylogenetic studies (Bailey & Chapman 1998; Bailey 1999), geniculate and non-geniculate members were brought together and two families were recognized: the *Sporolithaceae* and the *Corallinaceae*; the latter including the subfamilies, *Corallinoideae* (geniculate), *Lithophylloideae* (non-geniculate and including the geniculate *Amphiroideae*), *Metagoniolithoideae* (geniculate and closely related to the *Lithophylloideae*), *Mastophoroideae* (non-geniculate and related to *Metagoniolithoideae*), and *Melobesioideae* (non-geniculate). The single genus *Choreonema* Schmitz placed in the subfamily *Choreonematoideae* has been recently considered to be a member of the *Melobesioideae* (Broadwater & al. 1988). All families, except the recently established *Austrolithaceae* [but see Babbini & Bressan (1997) regarding older records], and subfamilies (except the *Metagoniolithoideae*) have Mediterranean representatives. Detailed inventories of species and genera recorded in the Mediterranean Sea have been published by Bressan & Babbini-Benussi (1995) and Babbini & Bressan (1997).

Since the classical study of Hamel & Lemoine (1953), Woelkerling (1983a, 1983b, 1985, 1993), Woelkerling & Verheij (1995), and Woelkerling & Lamy (1998) have studied historical collections in several herbaria and also re-examined the types of Mediterranean species described by Kützinger, Hauck, and Philippi. These studies provided the foundations for the correct application of names. In some cases the lack of data of new topotype collections precluded the establishment of unequivocal conclusions. The problematic cases will be here listed within each group. Parallel to that, an attempt has been made to abolish

the classical terms hypothallium (or hypothallus) and perithallium (or perithallus), introducing synonymous terms (see Woelkerling 1988). This has added to the difficulty of interpreting and comparing information, and therefore many workers have continued to use the classical terminology, following Cabioch (1972, 1988). On the other hand, the concept of dimerous vs. monomerous growth (Woelkerling 1988) has been more widely accepted, particularly as each type mirrors a specialized hypothallial organization (*viz.* monostromatic and polystromatic arrangement of filaments, respectively).

SPOROLITHACEAE

This family is represented by at least one species in the Mediterranean Sea, *viz.* *Sporolithon ptychoides* Heydrich (formerly placed in the genus *Archeolithothamnion auctorum* by Hamel & Lemoine 1953; Alongi & al. 1996). Recent Mediterranean records of *S. mediterraneum* (Heydrich) Foslie and *S. molle* (Heydrich) Heydrich remain uncertain (Alongi & al. 1996).

CORALLINACEAE

CORALLINOIDEAE

SEM studies of *Corallina* Linné and *Halimtilon* (Decaisne) Lindley resulted in the recognition of different types of surface morphologies (Garbary & Johansen 1982), and several taxa were transferred to an emended *Halimtilon* [among them the Mediterranean *Halimtilon virgatum* (Zanardini) Garbary & Johansen]. A morphometric analysis of eastern Mediterranean members of *Corallina*, *Jania* Lamouroux and *Amphiroa* Lamouroux was made by Economou-Amilli & al. (1990). It should be mentioned that analogous studies in the Melobesioideae have resulted in the recognition of at least two surface types (*Leptophytum*- and *Phymatolithon*-type; Chamberlain & Irvine 1994).

LITHOPHYLLOIDEAE

Within the Lithophylloideae that presently includes the Ampiroideae (Bailey 1999), the recognition of *Amphiroa rubra* (Philippi) Woelkerling (1983b) based solely on a study of its type from Sicily created uncertainty, since some authors considered this species to be a synonym of *A. cryptarthrodia* Zanardini (Athanasiadis 1987: 30, Furnari & al. 1999: 9), while others kept the two taxa distinct (Sartoni & de Biasi 1999). Previously, Hamel & Lemoine (1953: 42, following Weber van Bosse) considered *A. verruculosa* Kützinger to be a synonym of *A. cryptarthrodia*, while Cabioch (1972: 206) used the name *A. verruculosa* for the species growing partly endophytically in *Lithophyllum stictaeforme* (Areschoug) Hauck (= *Pseudolithophyllum expansum sensu* Lemoine; Athanasiadis 1999b). Other nomenclatural changes have affected the names of common lithophylloids such as, the 'trottoir-alga' *Lithophyllum byssoides* (Lamarck) Foslie [= *L. lichenoides* Philippi (Chamberlain 1997) and *L. tortuosum sensu* Huvé; Woelkerling 1983a, Woelkerling in Woelkerling & Lamy 1998] and the eastern Mediterranean endemic *Tenarea tortuosa* (Esper) Lemoine (= *T. undulosa* Bory; see Woelkerling & al. 1985). The genus *Titanoderma* Nägeli now accommodates species previously placed in the genus *Dermatolithon* Foslie (Woelkerling 1988). A later proposal by Woelkerling and his co-workers to merge *Titanoderma* with *Lithophyllum* Philippi was not accepted and recent

molecular studies have confirmed that these two genera are distantly related (Bailey 1999). Whether the Mediterranean endemics *Goniolithon* Foslie and *Tenarea* are generically distinct from *Titanoderma* remains unclear, but if this is the case it would indicate that *Goniolithon* and *Tenarea* are Tethyan relics (*Titanoderma* being widely distributed, with fossils dated at least since Eocene, 38 MYA; Wray 1977). The alternative hypothesis is that *Titanoderma* is paraphyletic and that the Mediterranean species of *Tenarea* and *Goniolithon* represent advanced lineages within *Titanoderma*. *Lithophyllum yessoense* Foslie has been recently recorded as an adventive on the French Mediterranean coast (Verlaque 2001).

MASTOPHOROIDEAE

The re-appraisal of the genus *Spongites* Kützinger, originally described from the Mediterranean (see Woelkerling 1985), created uncertainty because none of the species included in this genus by Kützinger could be unequivocally identified with known Mediterranean taxa (Cabioch 1988). Athanasiadis (1987) suggested a potential relationship between *Neogoniolithon mamillosum sensu* Hamel & Lemoine (1953) and *Spongites ramulosus* (Philippi) Kützinger but this was not accepted by Ballesteros (1990) who kept the two species distinct. A second attempt to establish the presence of *Spongites* in the Mediterranean was made by introducing the combination *Spongites notarisi* (Dufour) Athanasiadis (1987), but even this proposal was abandoned (Athanasiadis 1997a) in light of Solm-Laubach's 100 year old illustration showing the development of carposporangia across the entire fusion cell. It should be remembered that a modern study of the type of *Neogoniolithon* Setchell & Mason from the Red Sea remains to be made and that the current generic circumscriptions of both *Neogoniolithon* and *Spongites* are based on southern Australian plants (Penrose 1991, 1992). At the species level, the situation in *Neogoniolithon* is also complicated as some authors advocate the existence of cosmopolitan species while others maintain a species status for entities that are morphologically and geographically separated (see Athanasiadis 1997a). Denizot & al. (1981) described a remarkable reef-formation in Tunisia, largely composed of a sterile form of *N. notarisi*, and since then this form was also observed in West and South Crete and in the North Aegean (Athanasiadis unpublished data). A new species of *Fosliella* Howe was described from the North Adriatic (Bressan & al. 1977) and later recorded as far north as southern Scandinavia and also in southern Australia (Chamberlain 1994, as *Hydrolithon*). Spore germination patterns in several species of *Fosliella* and other corallines were analyzed by Bressan (1980), and his results were evaluated by Chamberlain (1984) who distinguished between a 4-celled central element in *Fosliella* and an 8-celled element in *Pneophyllum* Kützinger. The merging of *Fosliella* with *Hydrolithon* Foslie was not accepted by Athanasiadis (1996b).

MELOBESIOIDEAE

Basso (1995b) described several species of *Lithothamnion* Heydrich from the soft bottoms of the Tyrrhenian Sea. One of these species was *Lithothamnion minervae* Basso to replace the misapplied name *L. fruticosum* auctorum (now *Spongites fruticosus* Kützinger). Whether more distinct species of *Lithothamnion* have been confused under the

name *L. fruticosum* remains to be investigated. The genus *Mesophyllum* Lemoine has received particular attention (Basso 1995a; Cabioch & Mendoza 1998; Athanasiadis 1999a) and a study is currently made to extend our knowledge to members in other parts of the world (Athanasiadis 2001), which could also clarify the relationships and origins of the Mediterranean species.

BATRACHOSPERMALES & THOREALES

Our knowledge of the taxonomy, systematics and phylogeny of these orders in the Northern Hemisphere has greatly improved in light of the morphological and molecular investigations by Vis & al. (1998), Sheath & Müller (1999), Sheath & al. (2000) and collaborators. Entwistle (1999) updated the European *Batrachospermaceae* records in the PC herbarium. The first record of *Paralemanea* from South Italy (Aspromonte) was reported by Mannino & al. (2001).

ACROCHAETIALES

The monogeneric system followed by some authors has not added anything to our knowledge of the acrochaetioid algae (Silva & al. 1996) and therefore Papenfuss's (1945, 1947) classification, as critically evaluated by Stegenga (1977), Stegenga & Mulder (1979), and Stegenga (1985), is strongly recommended. According to the latter findings and the latest Mediterranean check-lists (Gallardo & al. 1985; Giaccone & al. 1985), four genera should be recognized in the Mediterranean, viz. *Acrochaetium* Nägeli [having cells with a stellate, axile chromatophore with one pyrenoid, e.g. *Acrochaetium mediterraneum* (Levring) nov. comb.¹], *Colaconema* Batters (having cells with a laminate, parietal chromatophore with one pyrenoid), *Audouinella* Bory (having cells with several band-shaped, spiral chromatophores without pyrenoids), and *Rhodochorton* Nägeli (having cells with several discoid chromatophores without pyrenoids). A fifth genus, *Rhodothamniella* J. Feldmann, was originally placed in the *Acrochaetiaceae* to distinguish species having several parietal chromatophores, each with one pyrenoid, but recent molecular studies of its generitype have indicated a position in the *Palmariales* (Saunders & al. 1995). Feldmann included two more species in *Rhodothamniella*, two of which [*R. codicola* (Børgesen) Bidoux & Magne and *R. codii* (Crouan frat.) J. Feldmann in Bidoux & Magne (1989)] are also recorded in the western Mediterranean (Verlaque 2001). Molecular studies have now confirmed that certain acrochaetioid species represent the diploid sporophyte stage of species of *Batrachospermales* (Pueschel & al. 2000), while the term 'acrochaetioid filament' has frequently been used in the past century to describe the heteromorphic sporophytes of certain members of *Nemaliales* and *Gigartinales* showing a *Bonnemaisonia*-type of life history (e.g. *Predaea*; Athanasiadis 1988). *Acrochaetium polyides* (Rosenvinge) Bø

¹ Basionym: *Chantransia mediterranea* Levring (1942: 6, fig. 1 A-G; type locality: Mondello, Sicily; type: in GB). Note: according to the original description the species exhibits stellate chromatophores with a single central pyrenoid and therefore its position in *Acrochaetium* is justified. The combination *Acrochaetium mediterraneum* Levring appeared first in Boudouresque (1969) and later in Boudouresque & Perret (1977), while the combination *Acrochaetium mediterraneum* (Levring) Boudouresque appeared in Coppejans & Boudouresque (1976), Boudouresque & Perret-Boudouresque (1987), and in Perret-Boudouresque & Seridi (1989); in all cases without a reference to the basionym.

rgesen has been linked with the sporophyte phase of *Helminthora divaricata* (C. Agardh) J. Agardh (Magne & Abdel-Rahman 1983).

NEMALIALES

Early investigations of various species of this order (formerly including members of the *Bonnemaisoniales*, *Batrachospermales*, *Thoreales* and *Acrochaetiales*) claimed the absence of tetrasporophytes and the presence of meiosis during carpospore formation ('zygotic meiosis'). This view was substantially changed after life history and karyological studies by Magne (1965) and later authors (Ramus 1969), who showed that carpospores in most members of these orders were diploid giving rise usually to a filamentous diploid tetrasporophyte. Yet, the so called 'zygotic meiosis' (first proposed by Svedelius in 1915) aimed to be demonstrated for at least few species of the *Nemaliales* presently assigned to the family *Liagoraceae*.

GALAXAURACEAE

Mediterranean records of the three known Mediterranean-Atlantic species of the genus *Scinaia* Bivona-Bernardi were studied by Cinelli & Codomier (1973). Previously, van den Hoek & Cortel-Breeman (1970b) investigated the life history of *S. complanata* (Collins) Cotton from material collected at Banyuls and found that even in this species the sporophyte is a reduced acrochaetioid plant, as reported for *S. furcellata* (Turner) J. Agardh by Boillot (1968, 1969a). The third species, *S. turgida* Chemin, is presently known as *S. interrupta* (DC) Wynne (1989).

The genus *Tricleocarpa* Huisman & Borowitzka (1990) presently accommodates *T. fragilis* (Linné) Huisman & Townsend (1993) that is synonymized with *Galaxaura oblongata* (Ellis & Solander) Lamouroux, widely reported from the tropics and the subtropics including the Mediterranean Sea. Yet, the types of *G. oblongata* and *T. fragilis* are from the Caribbean and 'American Ocean' respectively, and a comparison with plants described from the Mediterranean (i. e. *Galaxaura adriatica* Zanardini) remains to be made in a modern context. Magruder (1984) cultured carpospores of *T. fragilis* (as *G. oblongata*) from Hawaii and observed the development of diminutive acrochaetioid sporophytes producing cruciately divided tetraspores. Tetraspores gave rise to gametophytes indicating that the species exhibits a *Bonnemaisonia*-type of life history like most members of *Nemaliales*. It should be mentioned that in at least one member of this family (i.e. *Nothogenia* Parkinson) the sporophyte is crustose resembling the genus *Cruoriopsis* Dufour.

LIAGORACEAE

Since the classical study of Stosch (1965) who demonstrated a *Bonnemaisonia*-type of life history in *Liagora farinosa* Lamouroux (using material from the Liparian Islands), a second type of life history involving the formation of meiotic carpotetraspores (and hence the absence of a tetrasporophyte) was confirmed in *Liagora tetrasporifera* Børgesen by Couté (1971, 1976; material from Banyuls). Previously, Børgesen had described the unusual carpotetrasporangia in *L. tetrasporifera* from the Canary Isles and Bodard (1971) had observed meiosis in carpotetrasporangia of another *Liagoraceae*, *Helminthocladia senegalensis* Bodard. Hence, the *Liagora tetrasporifera*-type of life history was founded by Dixon (Guiry 1990). It should be noted that carpotetrasporangia are also known in *Rhodochorton* (*Acrochaetiaceae*), in two genera of the *Phyllophoraceae* and also in

Capreolia Guiry & Womersley of the *Gelidiaceae*. Guiry (1990) was critical to the limited evidence of meiosis in the carpotetrasporangia of the *Liagoraceae* and called for further investigations, because in *Liagora harveyana* Zeh he observed carpotetrasporangia that eventually produced filamentous tetrasporophytes and coined the term 'quadripartite carposporangia' to notify the difference. Couté (1971, 1976) also studied the life history of *Liagora distenta* (Mertens) Lamouroux from Banyuls and reported a *Bonnemaïsonia*-type of life history as previously observed in *L. farinosa* by von Stosch (1965).

Liagora farinosa was selected as the type of the new genus *Ganonema* Fan & Wang (1974), which was not immediately recognized (Abbott 1984, 1990a; Guiry 1990). Yet, *Ganonema* gained later support by Huisman & Kraft (1994), Kvaternik & Afonso-Carrillo (1995) and more recently by Kvaternik & al. (1996) who reported *G. farinosum* (Lamouroux) Fan & Wang from the Canary Isles. The types of several species of *Liagora* and *Ganonema* originally described by Lamouroux and other authorities were re-examined by Abbott (1990a, 1990b). Only *Liagora viscida* (Forsskål) C. Agardh appears to be based on Mediterranean material.

Helminthocladia agardhiana Dixon, considered to be 'restricted to a small area of Morocco and adjacent parts of North Africa' (Dixon & Irvine 1977), is apparently also known from Messina (Giaccone & Bressan 1973, as *H. hudsonii*) and this unusual disjunct distribution remains enigmatic since the species is unknown in other parts of the Mediterranean. Feldmann (1939) reported the occurrence of carpotetrasporangia, which was recently confirmed (O'Dwyer & Afonso-Carrillo 2001) although the nature of these spores and the life history of the species remain unknown. Cremades Ugarte (1993) considered *Fucus stackhousei* Clemente to be an earlier synonym of *H. agardhiana* but the discovery of a new species of *Helminthocladia* from the Canary Isles (O'Dwyer & Afonso-Carrillo 2001) makes this synonymy uncertain. Cunningham & al. (1993, as *H. stackhousei*) reported a *Bonnemaïsonia*-type of life history in *Helminthora divaricata* (C. Agardh) J. Agardh from Ireland, and pointed out the need of re-investigations of Mediterranean records of this species.

After Magne's (1961) finding that carpospores of *Nemalion helminthoides* (Velley) Batters from Roscoff are diploid, a *Bonnemaïsonia*-type of life history has been demonstrated in this and other species of the genus (Chen & al. 1978, Masuda & Horiuchi 1988). One of the questions that remain unclear is the relation between the poorly branched *N. helminthoides* (commonly known in the Mediterranean; e.g. Hamel 1930) and the well-branched dark-colored *N. multifidum* (Weber & Mohr) Endlicher (originally described from Scandinavia; Söderström 1970).

NACCARIACEAE

Only the type species of the genus *Naccaria* Endlicher, *N. wiggii* (Turner) Endlicher, is known in the Mediterranean-NE Atlantic, since according to Dixon & Irvine (1977) the recognition of slender Mediterranean plants as belonging to separate species (i.e. *N. vidovichii* Meneghini and *N. gelatinosa* J. Agardh) is not justified. Chemin (1927) and Boillot (1967) cultured carpospores of Atlantic plants and reported the development of acrochaetioid filaments. Boillot even observed erect gametophytes developing from these filaments, while Jones & Smith (1970) established the presence of tetrasporangia-like structures on these presumed tetrasporophytes. The other species of the genus are distrib-

uted in the Caribbean, southern Australia and Hawaii (Abbott 1985) and knowledge of their life histories is unknown.

CERAMIALES

CERAMIACEAE

Athanasiadis (1996a) monographed several tribes of the former antithamnoid-heterothamnoid complex and divided the family into the subfamilies Callithamnioideae (= Compsothamnioideae) and Ceramioideae. The Ceramioideae are distinguished by several synapomorphies including the presence of lateral filaments of determinate growth (whorl-branches) and the development of adventitious axes from whorl-branch cells. This subfamily now includes about half of the ceramiaceous tribes and is probably paraphyletic with regard to the families *Rhodomelaceae*, *Dasyaceae*, and *Delesseriaceae*. In the Callithamnioideae, the study of the Mediterranean-Azorean *Balliella cladoderma* (Zanardini) Athanasiadis showed that gland cells are initiated on axial cells and are later transferred to periaxial cells following the part of cell wall that is displaced laterally to form the periaxial (daughter) cell. A similar pattern in the evolution of the carpogonial branch was postulated, since axial procarps were also found for the first time in *Balliella* and in certain species of the tribes Pterothamnioideae, Scagelioideae, and Perithamnioideae. The family includes the poorly known Mediterranean genera: *Pterocladopsis* Ercegovic, *Ptilocladopsis* Berthold (placed in the Ptilocladopseae by Schmitz & Hauptfleisch), and *Pseudospora* Schiffner (tentatively placed in the Callithamnioideae).

CALLITHAMNIOIDEAE

With the removal of the Southern Hemisphere genus *Ballia* Harvey to its own order (Choi & al. 2000), the most primitive ceramialean tribe Warrenioideae comprises only the southern Australian genus *Warrenia* Harvey, where carpogonial branches develop on filaments of unlimited growth. Next to the Warrenioideae, the tribe Delesseriopseae includes one of the most primitive ceramialean members, viz. *Balliella* Itono & Tanaka, with wide distribution in the tropics and the subtropics.

The monogeneric tribe Halosioideae was erected by Cormaci & Furnari (1994) for the Mediterranean endemic *Halosia elisae* Cormaci & Furnari. *Halosia* Cormaci & Furnari develops periaxial carpogonial branches where the supporting filaments are of reduced growth. In addition, the genus shows some advanced features such as spherical involucre tetrasporangia.

The tribe Callithamnioideae has received considerable attention worldwide starting with a thorough revision of species of *Callithamnion* Lyngbye, *Seirospora* Harvey, and *Aglaothamnion* Feldmann-Mazoyer in the British Isles (Maggs & Hommersand 1993). Furnari & al. (1998) showed that Mediterranean isolates of *Aglaothamnion tenuissimum* (Bonnemaison) Feldmann-Mazoyer are interfertile with plants of *A. byssoides* Harvey from the Atlantic and proposed their merging at species level, recognizing two varieties to accommodate each of the two geographically isolated entities.

The remaining Mediterranean species of this subfamily are currently spread within five tribes and have not received major attention since the classical study of Feldmann-Mazoyer (1941). *Spermothamnion feldmanniae* Huvé (1970), originally described from

the Gulf of Marseilles, has been transferred to the genus *Tiffaniella* Doty & Meñez (see Gómez Garreta & al. 2001).

CERAMIOIDEAE

The most primitive member of this subfamily is the monogeneric tribe Pterothamniceae which comprises twenty-six species. Two species and one subspecies are known in the Mediterranean Sea. The generitype *Pterothamnion plumula* (Ellis) Nägeli (previously widely reported from various parts of the world) is restricted to the North Atlantic-Mediterranean region and is represented by the subspecies *haplokladion* Athanasiadis in the Adriatic & Ionian Seas. Records of *P. plumula* from the western basin have been referred to *P. polyacanthum* Kützinger, originally described from Ireland. *Pterothamnion crispum* (Ducluzeau) Nägeli was shown to belong to the exclusively Pacific section *Tetrakladion*, and its extra-European origin is supported by a record from South Africa.

The tribe Dohrnielleae has expanded to accommodate, apart from its type *Dohrniella* Funk, *Callithamniella* Feldmann-Mazoyer, *Antithamnionella* Lyle and two more genera from the Southern Hemisphere (Athanasiadis 1996a). *Callithamniella* shares several characteristics with *Antithamnion* and *Antithamnionella* and a possible hybrid origin has been hypothesized (Athanasiadis 1996a). *Callithamniella tingitana* (Bornet) Feldmann-Mazoyer is the only member of the genus having a Mediterranean distribution. In contrast, *Dohrniella* appears to be an exclusively Mediterranean-C. Atlantic genus having two rare endemics (i.e. *D. nana* Mayhoub, *D. neapolitana* Funk) in the Mediterranean Sea. The largest genus in the tribe, *Antithamnionella*, is represented by five species in the Mediterranean none of which is endemic [i.e., *A. boergesenii* (Cormaci & Furnari) Athanasiadis, *A. elegans* (Berthold) Price & John, *A. spirographidis* (Schiffner) Wollaston, and *A. sublittoralis* (Setchell & Gardner) Athanasiadis]. Despite the recognition of several new taxonomic characteristics (such as gland cell and spermatangial ontogeny), and the transfer of some species to a new genus, a cladistic analysis has shown that *Antithamnionella* is paraphyletic (Athanasiadis 1996a). Perestenko segregated certain boreal species (including *A. spirographidis*) in the new genus *Irtugovia* Perestenko, while the discovery of the bizarre Caribbean genus *Liagorothamnion* Huisman & al. (2001), placed in its own tribe but considered to be related to the Dohrnielleae, has emphasized the uncertain relationships between members in these tribes.

The tribe Antithamniceae presently comprises five genera, of which *Antithamnion* Nägeli accommodates thirty-one species worldwide. Three subdivisions have been recognized, each including Mediterranean (indigenous or adventive) representatives. Subgenus *Pteroton* (originally restricted to the Indo-Pacific) is now represented in the Mediterranean by two introduced species, viz. *A. pectinatum* (Montagne) Athanasiadis & Tittley and *A. amphigeneum* Millar (= *A. algeriense* Verlaque & Seridi). The subgenus *Antithamnion* comprises the sections *Enallassomena* and *Pedicellata*. In the Mediterranean, the former is represented by *A. decipiens* (J. Agardh) Athanasiadis (originally described from Nice and also occurring in the Central Atlantic) and *A. piliferum* Cormaci & Furnari (a Sicilian endemic), and the latter is represented by *A. tenuissimum* (Hauck) Schiffner (a Mediterranean endemic) and *A. heterocladum* Funk (also known from the Azores and the Scilly Isles). The generitype *Antithamnion cruciatum* (C. Agardh) Nägeli, also known from the Black Sea and the North Atlantic (and recently recorded in southern Australia;

Womersley 1998), has been postulated to be a hybrid resulted from the crossing of *A. decipiens* and a member of the section *Pedicellata* (i.e. *A. tenuissimum*, *A. villosum*, or *A. heterocladum*). Of the remaining 4 genera in the tribe Antithamnieceae, *Acrothamnion* J. Agardh is represented in the Mediterranean by the adventive *A. preissii* (Sonder) Wollaston (Cinelli & Sartoni 1969).

The tribe Ceramieae has expanded to receive two Southern Hemisphere genera (previously placed in the Heterothamnieceae), and the resurrected *Corallophila* Weber van Bosse that includes the cosmopolitan *C. cinnabarina* (Bory) R. E. Norris, also known in the Mediterranean Sea. The genus *Ceramium* Roth has received two more Mediterranean species, viz. *C. greacum* Lazaridou & Boudouresque (1992) described from the Aegean and later recorded also from the Gulf of Taranto (see Floristics), and *C. giacconeii* Cormaci & Furnari (1991) based on previous Mediterranean records of *C. cingulatum* Weber van Bosse. *Ceramium inconspicuum* Zanardini was resurrected by Cormaci & al. (1994) to join congeners producing limited cortication (*C. codii*-complex).

In the Griffithsieae, Cormaci & al. (1994) clarified the distinction between *Anotrichium tenue* (C. Agardh) Nägeli and *A. secundum* (J. Agardh) Furnari. The former species develops terminal tetrasporangia on 5-8 whorl-branches while in the latter species tetrasporangia develop subterminally (and adaxially) on 8-50 whorl-branches.

DELESSERIAEAE

Wynne (1996) updated his generic key that now accommodates eighty-nine genera. He also provided pertinent literature data of the currently accepted genera and their types. In a recent molecular investigation (Lin & al. 2001), three main groups were distinguished, viz. the Delesserioideae, the Nitophylloideae and a third assemblage comprising certain members of the Nitophylloideae referred to the new subfamily Phycodryioideae. The taxonomy of several Mediterranean species described by Ardissone, Rodriguez, Zanardini, and Borzi (Appendix II) and currently referred to *Nitophyllum* Greville, *Arachnophyllum* Zanardini, and *Myriogramme* Kylin remains unclarified (Gómez Garreta & al. 2001). The recent records of *Apoglossum gregarium* (Dawson) Wynne from the western Mediterranean have been considered to represent introductions (see Floristics).

DASYACEAE

The little known members of the genera *Dasyella* Falkenberg and *Eupogodon* Kützinger have been studied by Coppejans & Boudouresque (1984), Jong (1997), and Jong & al. (1997). Jong & al. (1998) published a cladistic analysis of the family and put forward the first phylogenetic hypothesis that points to the *Dasya-Eupogodon* group as being the most advanced. This group includes most of the Mediterranean dasyaceous species. The adventive *Dasyisiphonia* Lee & West has been reported also from Mediterranean France (Verlaque 2001).

RHODOMELACEAE

Within the tribe Laurencieae, which is well-represented in the Mediterranean, the genus *Laurencia* Lamouroux has received major attention worldwide. Garbary & Harper (1998) attempted a phylogenetic analysis of twenty-nine species (of about 150 recognized) and proposed the division of *Laurencia* in three genera to accommodate: 1) species with tetrasporangia and spermatangial structures cut off from outer cortical cells and secondary

pit-plugs present or not in outer cortical cells (within the genus *Osmundea* Stackhouse), 2) species with tetrasporangia borne periclinally on the growing frond and secondary pit-plugs absent in outer cortical cells [within *Chondrophycus* (Tokida & Saito) Garbary & Harper], and 3) species with tetrasporangia borne anticlinally to the growing frond and secondary pit-plugs present in outer cortical cells (within *Laurencia sensu stricto*). In addition, *Osmundea* and *Chondrophycus* have two periaxial cells from each axial cell, while *Laurencia* has four, and in *Laurencia* and *Chondrophycus* spermatangia develop on trichoblasts (Nam & al. 2000 and references therein). Mediterranean representatives of these three genera currently comprise at least eighteen species (Boisset & al. 2000, Gómez Garreta & al. 2001, Furnari & al. 2001). The reproductive morphology of the symbiotic alga *Erythrocytis montagnei* (Derbès & Solier) Silva, commonly found on species of *Laurencia* and *Chondrophycus*, has been studied by De Masi & Gargiulo (1982).

The next rich in species rhodomelaceous tribe in the Mediterranean is the Polysiphonieae where *Polysiphonia* Greville has about forty-five species alone (Gómez Garreta & al. 2001). A key to the majority of these species was posthumously published by Feldmann (1981), while a thorough account of the genus from the French coast was previously published by Lauret (1967, 1970). Recent additions to the genus are *P. banyulensis* Copejans (1975, 1978) and *P. perforans* Cormaci & al. (1998). Verlaque (2001) synonymized the Mediterranean endemic *P. mottei* Lauret (1967) with *P. harveyi* Bailey (originally described in 1848 from Connecticut), and also reported the Pacific adventives *P. morrowii* Harvey and *Herposiphonia parca* Setchell together with an unidentified species of *Pterosiphonia* Falkenberg from Thau Lagoon on the Mediterranean France. New observations on other little known species have been published by Pizzuto & al. (1996) and Gómez Garreta & al. (2001). Mc Ivor & al. (2000) analysed rbcL sequences from twenty-three species and reported the presence of four groups within the complex *Polysiphonia*, *Boergesenella* Kylin and *Leptosiphonia* Kylin, that were more distantly related to *Herposiphonia* Nägeli, *Pterosiphonia* Falkenberg and *Lophosiphonia* Falkenberg. Kim & al. (2000) re-examined the taxonomic status of the generitype *Polysiphonia urceolata* (Dillwyn) Greville [= *P. stricta* (Dillwyn) Greville]. The morphology, reproduction and geographical distribution of *Womersleyella* (*Polysiphonia*) *setacea* have been studied in a series of papers (see Verlaque 1989, Airoidi & al. 1995, Athanasiadis 1997b). Experimental culture tests have been made by Rindi & al. (1999), but despite all these independent investigations we still do not know the origin of this species or fully explain its rapid spread and massive local occurrence in the Mediterranean.

Sicilian isolates of *Lophocladia lallemandii* (Montagne) Schmitz were studied in culture by Cormaci & Motta (1985), who completed the sexual life history of the species. They also reported a remarkable ability of trichoblasts to generate new thalli and suggested that the species propagates mainly vegetatively in the field.

BONNEMAISONIALES

The presence of filamentous or crustose tetrasporophytes in the life history of *Bonnemaisonia* C. Agardh and *Asparagopsis* Harvey were originally demonstrated by Feldmann & Mazoyer (1937) and Feldmann & Feldmann (1939, 1942) and subsequently confirmed by other authors (Chihara 1960, 1961; Chen & al. 1969; Rueness & Åsen 1982).

The presence of meiotic tetrasporangia in the life history of *Bonnemaisonia* was disputed by Kylin (1945) who maintained that in *B. asparagoides* (Woodward) C. Agardh gametophytes developed from somatic cells of the crustose (*Hymenoclonium serpens*-like) phase. Starting from cultures of *Hymenoclonium*-like plants from Banyuls, Cortel-Breeman (1975) obtained erect gametophytes, but she could not link indisputably their development from tetraspores or from somatic cells. On the other hand, Rueness & Åsen (1982) confirmed Kylin's findings, and Chen & al. (1970) reported the same phenomenon in *B. hamifera* Hariot. Similar cases of direct development of gametophytes are also known in the *Gigartinales*, e.g. in *Calosiphonia* (Mayhoub 1973, 1975) and in members of the *Nemaliales* (Boillot 1967).

In *Asparagopsis* Harvey, there is a long-standing controversy regarding the identity of the Mediterranean sporophytes (that are usually sterile), in view of the occurrence of a second indigenous (?) species, *A. taxiformis* (Delile) Trevisan, believed to have a morphologically identical sporophyte phase. Dixon (1964) and Guiry & Dawes (1992) drew attention to the first description of *Polysiphonia hillebrandii* Bornet from Elba in 1883, which might either belong to the sporophyte phase of *A. armata* (indicating an earlier introduction in the Mediterranean than in the 1920's; Verlaque 1994) or to *A. taxiformis* (originally described from Alexandria in 1813 and now also reported from the Balearic Islands and Sicily; Barone & al. 2001). Guiry & Dawes also demonstrated the presence of environmentally distinct strains of *A. armata* from Messina, Australia and Ireland and suggested that the species may have been introduced several times in the Northern Hemisphere.

GELIDIALES

Molecular investigations in this group have included few species so far and therefore hypotheses of taxon relationships remain speculative (Freshwater & al. 1995, Thomas & Freshwater 2001). For example, in the genus *Gelidiella* Feldmann & Hamel only the type has so far been sequenced, while at least four other species are known in the Mediterranean alone. In the genus *Ptilophora* Kützinger only three species have been analysed of the twelve recognized by Norris (1987). It could be added that some workers recognize *Beckerella* Kylin as distinct from *Ptilophora*, because the latter genus is associated symbiotically (?) with sponges and produces proliferations from the entire thallus (while *Beckerella* develops only marginal ramifications). The South Aegean endemic, *Beckerella mediterranea* Huvé, lacks sponges on its thallus and develops marginal proliferations which supports its original generic position. Of the twelve species of *Gelidium* recorded in Europe (Gallardo & al. 1985), seven have been included in the molecular studies of Freshwater & Rueness (1994), who found a close relationship between *G. latifolium* (Greville) Bornet & Thuret and *G. attenuatum* (Turner) Thuret, and a more remote relationship between these two taxa and *G. pulchellum* (Turner) Kützinger, *G. canariensis* (Grunow) Seoane-Camba, *G. sesquipedale* (Clemente) Thuret, and an undescribed species from Mallorca. The molecular studies of Freshwater & al. (1995) and Thomas & Freshwater (2001) also supported the recognition of the new genus *Pterocladia* Santelices & Hommersand (1997) to accommodate the pantropical *P. capillacea* (Gmelin) Santelices & Hommersand (Felicini & Perrone 1994), the Mediterranean-Atlantic *P. melanoidea* (Bornet) Santelices & Hommersand, and other species from southern Australia, Costa Rica and New Caledonia.

GIGARTINALES

With the recognition of the orders *Corallinales* and *Hildenbrandiales* (both previously included in the *Cryptonemiales sensu* Kylin), *Ahnfeltiales*, *Plocamiales* and *Gracilariales* (all three previously included in the *Gigartinales sensu* Kylin), and the emendation of the *Cryptonemiales* to include the families *Halymeniaceae* and *Sebdeniaceae* (Saunders & Kraft 1996, as *Halymeniales*), the remaining forty-two cryptonemialean-gigartinean families form an unresolved complex. Representatives of twelve of these families have so far been molecularly examined (Saunders & Kraft 1996, 1997). Twenty-one families and one subfamily have Mediterranean representatives.

ACROSYMPHYTACEAE

The life history of *Acrosymphyton purpuriferum* (J. Agardh) Sjöstedt was originally investigated by Genevieve Feldmann (1955) who observed that carpospores produced crustose plants. The complete life history was elucidated by Cortel-Breeman & van den Hoek (1970) who cultured carpospores and obtained tetrasporophytes similar to *Hymenoclonium serpens* (Crouan *frat.*) Batters. Released tetraspores gave rise to erect gametophytes of *A. purpuriferum* morphology. Subsequent culture experiments of crustose plants of *Hymenoclonium serpens* from Banyuls-sur-mer confirmed the heteromorphic life history (Cortel-Breeman 1975). Of the five known species of *Acrosymphyton*, four are endemic to the Mediterranean, Caribbean, New Zealand and northern N. S. W., respectively (the fifth and presumably most primitive species is known from the Hawaiian Islands and southern Australia; Womersley 1994).

ARESCHOUGIACEAE

This is a family of twenty-five genera widely distributed in the tropics and the subtropics, but without true (?) Mediterranean representatives. The family is also poorly represented on the Atlantic coast of Europe. The first Mediterranean finding refers to *Solieria chordalis* (C. Agardh) J. Agardh (1842: 157 'specimina ex mari Nicaensi perhibita in collectione Rissoana vidi'), but this early record was never confirmed and remains doubtful in the absence of vouchers in Herbarium Agardh in Lund (Gabrielson & Hommersand 1982). The species was reported again in 1977 on the coast of Albères (Verlaque 1994) and the Bay of Naples (De Masi & Gargiulo 1982b), but at least the first record has now been referred to *Agardhiella subulata* (C. Agardh) Kraft & Wynne (Verlaque 2001). Perrone & Cecere (1994) reported from Mar Piccolo the massive occurrence of *Solieria filiformis* (Kützinger) Gabrielson and *Agardhiella subulata* (the former species identified in local herbarium collections dated since 1922). These three species are known from the Atlantic, and whether the Mediterranean records are recent introductions, post-Messinian colonizers or Tethyan relics is uncertain. In the eastern Mediterranean, *Sarconema filiforme* (Sonder) Kylin has been reported twice from the Levant Sea (Rayss 1963; Mayhoub 1976) and once from Greece (Verlaque 1994). Ribera & Boudouresque (1995) have considered even these records as probable recent migrations, in which case dispersals to nearby areas is to be expected in the near future.

CALOSIPHONIACEAE

The heteromorphic life history of *Calosiphonia vermicularis* (J. Agardh) Schmitz was clarified by Mayhoub (1973) who observed carpospores to develop a crustose plant

resembling *Hymenoclonium serpens*. He originally reported erect gametophytes borne directly from the crustose phase and suggested that meiosis took place during somatic growth in the gametophyte, as known to occur in the *Batrachospermales*. He subsequently observed the production of zonately divided tetrasporangia on the crustose phase (Mayhoub 1975), as presently known in a member of the second genus of this family, *Schmitzia hiscockiana* Maggs & Guiry (1985). Karyological investigations remain to confirm the supposed alternation of ploidy and the site of meiosis. The life history of the generitype *Schmitzia neapolitana* (Berthold) Silva, originally described from Naples, remains unclarified.

CAULACANTHACEAE

Three species and genera are reported in the Mediterranean, viz. the cosmopolitan *Catenella caespitosa* (Withering) Irvine, the pantropical *Caulacanthus ustulatus* (Turner) Kützinger, and the rare endemic *Feldmannophycus rayssiae* Augier & Boudouresque (1971). Their taxonomy rests upon studies from the late 60's and 70's (Searles 1968; Kraft 1981; Rueness 1997, 1999; Rueness & Rueness 2000).

CRUORACEAE

Cruoria cruoriaeformis (Crouan frat.) Denizot (1968) is the only species of this genus reported in the Mediterranean, since *Crouoria rosea* (Crouan frat.) Crouan frat. has been associated with the tetrasporophyte phase of members of the *Furcellariaceae* (*Halarachnion* Kützinger and *Neurocaulon* Zanardini). Taxonomic and biogeographic data of the monotypic *Cruoriaceae* have been updated by Maggs (1990a).

CYSTOCLONIACEAE

Three species are presently known in the Mediterranean, viz. the Atlantic-Mediterranean *Calliblepharis jubata* (Goodenough & Woodward) Kützinger and *Rhodophyllis divaricata* (Stackhouse) Papenfuss, and the little known endemic *Rhodophyllis strafforelli* Ardissonne.

DUMONTIACEAE

This is a large cold water family whose taxonomy, systematics and biogeography have been thoroughly studied by Sandra Lindstrom and more recently by Tai & al. (2001). In the Mediterranean, the family is represented by the generitype of *Dudresnaya* Crouan frat., *D. coccinea* (C. Agardh) Crouan frat. [= *D. verticillata* (Withering) Le Jolis], originally described from southern England and Atlantic France (Sjöstedt 1926; Robins & Kraft 1985).

FURCELLARIACEAE

The heteromorphic life history of *Halarachnion* was elucidated by Boillot (1965, 1972) using material from Bretagne. The genus *Neurocaulon* has been included in the Cryptonemialean studies of Codomier (1967, 1969b, 1972), who also elucidated its heteromorphic life history using material from Banyuls and showing that the sporophyte is crustose, resembling *Crouoria rosea* and producing zonately divided tetraspores (Codomier 1969b).

GIGARTINACEAE

In the Mediterranean, the genus *Chondracanthus* Kützinger accommodates the

Mediterranean-Atlantic species *C. teedei* (Roth) Kützinger and *C. acicularis* (Roth) Fredericq, previously placed in *Gigartina* (Hommersand & al. 1993). The life history and temperature responses of strains of *C. teedii* from Sicily and several places in the Atlantic have been comparatively studied by Guiry & al. (1987). As typical for the family, species of *Chondracanthus* exhibit a *Polysiphonia*-type of life history. *Chondrus* Stackhouse is now also represented on the Mediterranean French coast by the Asiatic adventive *C. giganteus* Yendo (Verlaque & Latala 1996; Verlaque 2001).

GLOIOSIPHONACEAE

The record of *Gloiosiphonia capillaris* (Hudson) Carmichael from Sicily (Giaccone & al. 1985) is the only known in the Mediterranean and needs to be confirmed. The other known members of this family in the Mediterranean, *Schimmelmanna schousboei* (J. Agardh) J. Agardh and *Thuretella schousboei* (Thuret) Schmitz are also rarely reported. While the sporophyte phase of *G. capillaris* has been associated with *Cruoriopsis hauckii* Batters from the British Isles (Maggs 1983), tetrasporophytes have never been reported in the other genera (Chihara 1972) and attempts to clarify their life history in culture (see Battiatto & Duro 1979) have been fruitless. The status of *Cruoriopsis* Dufour, based on *C. crucialis* from the Ligurian Sea remains unclarified (Denizot 1968; Irvine & Farnham 1983).

HYPNEACEAE

The pantropical *Hypnea musciformis* (Wulfen) Lamouroux, originally described from the Adriatic, is considered to be the only indigenous member of this family in the Mediterranean. Five other species have been reported and are considered to be probable Lessepsian adventives (see Verlaque 1994; Ribera & Boudouresque 1995): viz. *Hypnea cervicornis* J. Agardh [now placed in synonymy with *H. spinella* (C. Agardh) Kützinger], *Hypnea esperi* auctorum (of uncertain taxonomic status), *H. harveyi* Kützinger [now placed in synonymy with *H. spicifera* (Suhr) Harvey], and *H. hamulosa* (Esper) Lamouroux (of uncertain taxonomic status) (see Silva & al. 1996). The first Mediterranean record of *H. valentiae* (Turner) Montagne from Rhodes Island was also attributed to Lessepsian migration by Reinbold (Athanasiadis 1987), but it remains unconfirmed. Yet, the latter species has now been reported also from Thau Lagoon (Verlaque 2001). The taxonomy of the genus *Hypnea* Lamouroux rests upon regional monographs (Bodard 1968, Womersley 1994, Mshigeni 1974, 1976).

KALLYMENIACEAE

The genera *Kallymenia* J. Agardh and *Meredithia* J. Agardh from the Banyuls area have been studied by Codomier (1968, 1969a, 1971, 1972, 1973b, 1973c) and Huvé & Passelaigue (1970), who totally recognized seven species. The close similarity between the filamentous/crustose sporophyte of *Meredithia microphylla* (J. Agardh) J. Agardh and *Rhodochorton hauckii* (Schiffner) Hamel was pointed out by Codomier (1973b), while Guiry & Maggs (1985) elucidated the heteromorphic life history of *M. microphylla* using material from Ireland.

NEMASTOMACEAE

The elevation of Schizymenieae to the level of family left four genera in the

Nemastomataceae, with *Nemastoma* J. Agardh being the only Mediterranean representative. In the generitype *Nemastoma dichotomum* J. Agardh, only carpogonial and carposporic plants are sufficiently described. Berthold (1884, pl. VI figs 9-15, as *Gymnophlaea*) illustrated the presence of carpogonial branches and auxiliary cells borne on separate filaments of the outer cortex (Oltmanns 1904, fig. 433), and the development of gonimoblasts from the contact between the auxiliary cell and the ooblast. However, in a study of Aegean and type specimens from the Adriatic, Athanasiadis (1988) found that carpogonial branches and auxiliary cells were located on accessory (rhizoidal) filaments (a condition previously known for auxiliary cells only in the Australian genus *Adelophycus* Kraft), and that development of gonimoblasts could occur from unfertilized auxiliary cells supporting carpogonial branches (a clear procarpic condition). Previously, Cortel-Breeman & van den Hoek (1970) and van den Hoek & al. (1972) cultured carpospores of *N. dichotomum* and obtained achrochaetoid filaments reproducing by monospores. Three other Mediterranean species of *Nemastoma*, viz. *N. dumontioides* J. Agardh, *N. inconspicuum* Reinsch and *N. constrictum* Ercegovic remain poorly known. The presence of zonately divided tetrasporangia in *N. inconspicuum* is the only reference of such structures in the genus, and family, since *Predaea* has recently been transferred to the *Schizymeniaceae* (Saunders & Kraft 2000).

PEYSSONNELIACEAE

This family includes encrusting genera and has been taxonomically revised by Denizot (1968). The largest genus, *Peyssonnelia* Decaisne, accommodates some fourteen species in the Mediterranean Sea (Boudouresque & Denizot 1975, Verlaque 1978, Marcot & Boudouresque 1977, Marcot 1980, Athanasiadis 1985a). The originally monotypic *Metapeysonnelia* Boudouresque & al. (1976) was originally described from material collected on the Mediterranean coast of France and was later reported from the Aegean Sea. A second species has been recently described from Florida and Belize (Verlaque & al. 2000). The biogeography of the *Peyssonneliaceae* has been discussed by Maggs (1990a) who postulated a Tethyan origin for the genus *Peyssonnelia*. The family is also represented in the Mediterranean by the little known endemic *Polystrata compacta* (Foslie) Denizot, the recently recorded *Polystrata fosliei* (Weber van Bosse) Denizot (Cecere & al. 1996) previously known from the Pacific, the Caribbean and Cape Verde Islands, and the generitype of *Cruoriella* Crouan *frat.* that is included in the genus *Peyssonnelia* by some authors (Maggs 1990a). Several European fossils referred to the *Peyssonneliaceae* have been described by Massieux & Denizot (1964) and Denizot & Massieux (1965).

PHYLLOPHORACEAE

Of the three genera recorded in the Mediterranean, *Schottera* Guiry & Hollenberg (1975) is based on the Mediterranean-Atlantic *S. nicaeensis* (Duby) Guiry & Hollenberg previously accommodated in *Petroglossum* Hollenberg. Schotter's (1952, 1960, 1968) extensive studies on this family have raised numerous questions regarding the taxonomy of Mediterranean members of the genera *Phyllophora* Greville and *Gymnogongrus* Martius. *Gymnogongrus* presently includes species having a *Liagora tetrasporifera*-type of life history, since species with a *Bonnemaisonia*-type of life history have been segregated in the genus *Ahnfeltiopsis* Silva & DeCew (1992) recently been reported from

Mediterranean France (Verlaque 2001). Similarly, with the re-appraisal of *Coccotylus* Kützinger to accommodate *C. truncatus* (Pallas) Wynne & Heine, *Phyllophora* now includes species with a *Polysiphonia*-type of life history only (Maggs 1989, 1990b). The single record of *Phyllophora traillii* Batters [now *Erythrodermis traillii* (Batters) Guiry & Garbary (1990)] from the Spanish Mediterranean coast (Gallardo & al. 1985) requires confirmation.

RHIZOPHYLLIDACEAE

This family is represented by two crustose endemic species in the Mediterranean, viz. *Rhizophyllis squamariae* (Meneghini) Kützinger and *Contarinia peyssonneliaeformis* Zanardini. They have been united under the genus *Contarinia* Zanardini by Denizot (1968), but differ at least in the type of division of their tetrasporangia (irregularly zonate in *R. squamariae* but cruciate in *C. peyssonneliaeformis*).

RISSOELLACEAE

The single species *Rissoella verrucosa* (Bertoloni) J. Agardh of this monotypic family is restricted to the western Mediterranean and parts of the warm E. Atlantic (Sansón & al. 1991). Male plants were recorded for the first time by Schotter (1964), who also described the ontogeny of the spermatangia.

SARCODIACEAE

This family includes tentatively the rare endemic *Chondrymenia lobata* (Meneghini) Zanardini, originally described from the Adriatic and later reported from the western Mediterranean basin (see Boudouresque & Huvé 1969). Boudouresque & al. (1990) summarized later records of the species whose reproductive morphology remains poorly studied and its life history unknown.

SCHIZYMENIACEAE

This family presently includes four genera of which *Predaea*, *Schizymenia* J. Agardh and *Platoma* (J. Agardh) Schmitz are known in the Mediterranean. The taxonomy of the endemic *Predaea ollivieri* J. Feldmann and *P. pusilla* (Berthold) J. Feldmann has been reassessed studying populations in the western basin and the Adriatic Sea and comparing them with congeneric species (Verlaque 1990a). In a previous investigation of Aegean plants of *P. ollivieri*, Athanasiadis (1988) cultured carpospores and reported the development of acrochaetoid filaments bearing tetrasporangia-like structures, eventually producing diminutive filamentous males, in agreement with previous findings in the genus. The new forma *P. pusilla* f. *alboranensis* Conde & al. (1998) was described on the basis of material from the Alboran Island. This new taxon differs in producing terminal bi-cellular propagules, a feature analogous to what has been reported in *P. bisporifera* Kajimura (1987) from Japan. Several independent studies (Ardre 1977, 1980, DeCew & al. 1992; Alongi & Cormaci 1993; Masuda & Guiry 1994) have linked the sporophyte phase of species of *Schizymenia* and *Platoma* with species of *Haematocelis* J. Agardh or *Haematocelis*-like crusts. The family now includes genera having a heteromorphic life history, although tetrasporophytes of the fourth genus in the family, *Titanophora* (J. Agardh) J. Feldmann, remain unrecorded.

SCHMITZIELLOIDEAE

This monotypic subfamily is represented by the single species *Schmitziella endophrasea* Bornet & Batters that was originally placed in the *Corallinales* and later considered to be related to the *Acrochaetiales* (Woelkerling 1988). A study of its pit-plugs has, however, precluded a position in these orders indicating an affiliation with the *Gigartinales* (Pueschel 1989).

SPHAEROCOCCACEAE

Two species of this monotypic family are known in the Mediterranean, viz. the little known *Sphaerococcus rhizophylloides* Rodriguez and the generitype *S. coronopifolius* Stackhouse that exhibits a heteromorphic life history with a crustose tetrasporophyte phase similar to *Haematocelis fissurata* Crouan *frat.* (Maggs & Guiry 1982b). Yet, *H. fissurata* has not been reported within the entire known distribution of *S. coronopifolius* (i.e. eastern Mediterranean to southern Scandinavia; see Athanasiadis 1996b), while in the North Aegean an undescribed crust referred to *Haematocelis* has been identified (Athanasiadis 1987).

WURDEMANNIACEAE

This monotypic family is represented in the Mediterranean by the generitype *Wurdemannia miniata* (Sprengel) J. Feldmann & Hamel, widely reported in the tropics and the subtropics. Its previous inclusion in the *Gelidiales* or *Gigartinales* has been speculative, but a recent study of its pit-plugs has indicated an affiliation with the *Gigartinales* (Pueschel 1989). Most Mediterranean records are based on sterile material, but there is a description of tetrasporic and cystocarpic plants from the Adriatic (Schiffner 1933, as *Pseudogelidium*).

PLOCAMIALES

Only two species of this group have been sequenced so far (Saunders & Kraft 1994) but these show a remote relationship to the rest of the *Gigartinales* and a close affinity to the *Rhodymeniales-Gracilariales-Cryptonemiales* complex (Choi & al. 2000). Apart from the cosmopolitan *Plocamium cartilagineum* (Linné) Dixon, the Southern Hemisphere species *P. secundatum* (Kützinger) Kützinger has recently been reported from Sicily (Cormaci & al. 1991).

GRACILARIALES

Fredericq & Hommersand (1990) proposed discrete character combinations to segregate between several gracilarioid genera. In particular, gonimoblasts are connected to pericarps via nutritive cells/filaments in *Gracilaria* and *Hydropuntia* Montagne, but not in *Gracilariopsis* Dawson. Moreover in *Gracilaria* nutritive cells occur all over the pericarp while in *Hydropuntia* they are restricted to the floor. Spermatangia are borne within simple pits in *Gracilaria* and multicavated pits in *Hydropuntia*, but only superficially in *Gracilariopsis* (review in Silva & al. 1996). Yet, Abbott & al. (1991) reduced *Hydropuntia* to a synonym of *Gracilaria* after finding both types of spermatangial morphology in a single gracilarioid species, and a similar proposal was independently made by Gargiulo & al. (1992), who could not find discrete character combinations in nine Mediterranean species that they referred to *Gracilaria*, including the new endemics *G. dendroides* Gargiulo & al.

(1985) and *G. longa* Gargiulo & al. (1987a). Steentoft & al. (1995) suggested a close relationship between *Gracilaria longa* and *Gracilaria gracilis* (Stackhouse) Steentoft. Chromosome numbers in *Gracilaria* and *Gracilariopsis* are summarized by Culoso & al. (1994), who also reported a basic number of 24 for *G. armata* (C. Agardh) J. Agardh.

CRYPTONEMIALES

Saunders & Kraft (1996) have recently emended the circumscription of this order to comprise two families with twenty-two genera together. Five genera have been molecularly analysed and these show a sister-taxon relationship to the *Rhodymeniales* (Saunders & Kraft 1996, fig. 3; cf. Choi & al. 2000, fig. 2, as *Halymeniales*). One of the diagnostic characters of this order remains Kylin's 'cryptonemialean' development of auxiliary cells 'on separate [accessory] cortical branches' (Saunders & Kraft 1996: 703).

HALYMENIACEAE

Species of *Cryptonemia* J. Agardh, *Halymenia* C. Agardh and *Aeodes* J. Agardh have been studied by Codomier (1972, 1974) who also applied culture techniques. Starting from (carpo)spores of *Halymenia latifolia* Kützinger, Codomier (1974) reported the development of acrochaetioid filaments with monosporangia that recycled the acrochaetioid phase. Van den Hoek & Cortel-Breeman (1970a) reported a similar type of life history in *Halymenia floresii* (Clemente) C. Agardh from Rovinj and Banyuls, but they also found that some acrochaetioid plants developed into normal gametophytes. On the other hand, isomorphic tetrasporophytes of British *Halymenia latifolia* were obtained in culture by Maggs & Guiry (1982a), who also suggested that at least '...some populations of *H. floresii* in the Mediterranean have ...meiosis ...in ...monosporangia or in the ...upright fronds.' These two species of *Halymenia* are known to have isomorphic generations in the wild, and the same applies for the endemic *H. asymetrica* Gargiulo & al. (1986) described from the western Mediterranean. The genus *Grateloupia* C. Agardh is now represented by at least five species in the western Mediterranean, two of which [*G. doryphora* (Montagne) Howe and *G. lanceola* (J. Agardh) J. Agardh] are considered to be adventives (De Masi & Gargiulo 1982a, Riouall & al. 1985; Pérez-Cirerra & al. 1989). Updating the records from Thau Lagoon on the French coast, Verlaque (2001) referred the record of *G. doryphora* to *G. cf. turuturu* Yamada and also reported the new adventives *G. filicina* var. *luxurians* Gepp & Gepp, *G. lanceolata* (Okamura) Kawaguchi, and *Prionitis patens* Okamura (all three previously known from Japan and Korea). Kawaguchi & al. (2001) compared Mediterranean plants of *G. filicina* (Lamouroux) C. Agardh to Pacific *G. asiatica*. Of the two species of *Cryptonemia* known in the Mediterranean (Gallardo & al. 1985), *C. lomatium* (Bertoloni) J. Agardh was included in the Cryptonemialean studies of Chiang (1970).

SEBDENIACEAE

The genus *Sebdenia* Berthold (1884) exhibits isomorphic gametophytes and tetrasporophytes and is represented by at least four species in the Mediterranean (Codomier 1972, 1973a). *Sebdenia monnardiana* (Montagne) Berthold is the largest Mediterranean red alga reaching 1 meter in diameter (Funk 1955).

RHODYMENIALES

Members of this group represent a homogenous assemblage having multiaxial organi-

zation, *Polysiphonia*-type of life history with cruciately (rarely tetrahedrally) divided tetrasporangia, procarys with 4- (rarely 3-) celled carpogonial branches and relatively short ooblasts (the auxiliary cells occurring on short filaments issued from the supporting cell). In addition, their thallus is often hollow and mucous. Forty-six genera are currently recognized, ten of which are known in the Mediterranean Sea. None is endemic but several include species with restricted distributions in the Adriatic and/or the western Mediterranean. A comparison of SSU rDNA sequences from thirty species (representing twenty-six genera) has indicated the presence of four major groups represented by the families *Faucheaceae*, *Rhodomeniaceae*, *Champiaceae*, and *Lomentariaceae* (Saunders & al. 1999). All these families are represented in the Mediterranean by a total of some thirty-six species (Funk 1955; Ercegovic 1956; Huvé 1971; Guiry 1978; De Masi & Gargiulo 1981, 1982c; Gallardo & al. 1985; Ben Maïz & al. 1987; Gargiulo & al. 1990). The largest genus in the Mediterranean is *Lomentaria* Lyngbye including nine endemics and a recent adventive to Thau Lagoon on the French coast (*L. hakodatensis* Yendo; Verlaque 2001). Some of the species were previously accommodated in the genus *Chondrosiphon* Kützinger (see Guiry 1978). *Chrysomenia wrightii* (Harvey) Yamada, previously known from Japan and Korea, is now also growing at Thau Lagoon (Ben Maïz & al. 1987; Verlaque 2001).

Floristics

Floristics are the first step in taxonomy and remain popular in the Mediterranean. Apart from ecological and phenological data, floristics here include the preparation of regional check-lists, the description of new records and new characteristics of taxa and even the cataloging of literature records and herbarium collections.

Giaccone's (1969) first revised Italian checklist includes 620 taxa of which 336 are red algae. This number has now been superseded from Sicily alone (see below), while in a recent communication during the Xth Optima Meeting in Palermo, Furnari & al. (2001) reported a total number of 869 taxa in Italy (including 510 red algae). Boudouresque & al. (1990) have published a useful account of the endangered Mediterranean macrophytes, where seventeen red algal species are illustrated and briefly described. Undoubtedly, this list needs to be expanded to cover many other endemics such as members of the genera *Gulsonia* Harvey, *Ptilocladopsis*, *Aeodes*, *Kallymenia*, *Sebdenia*, *Mesophyllum*, and *Tenarea*. The first checklist of the Mediterranean *Ceramiales* has been published by Gómez Garreta & al. (2001).

Mediterranean Spain

Seoane-Camba (1969) has catalogued the Menorcan collections of Rodríguez y Femenías, housed in the herbaria of Thuret-Bornet and Sauvageau (at PC). Among these collections there is material of at least eleven species of red algae to be described. The herbarium of Miranda (at MA) has been catalogued by Valenzuela & Pérez-Cirera (1982), while the collections of Clemente (at MA) and Cabrera (at MA) have been studied by Cremades Ugarte (1993) and Cremades (1995). Previously, Cremades & Pérez Cirera (1990a, 1990b) and Cremades (in Cremades & Pérez Cirera 1990c) lectotypified several taxa of Clemente and proposed several new combinations, some of which have not been accepted (Silva 1992). A preliminary checklist of Iberian benthic marine algae has been

published by Gallardo & al. (1985), taking into account records since 1889. They reported 620 Mediterranean macroalgae, 385 taxa of which are red algae. Additional local records of red algae have been published by Cremades (1985, 1989) and Soto & Conde (1989), while revised checklists from Catalonia and Andalusia have been published by Ballesteros (1990) and Conde & al. (1996). The marine flora of the island of Alboran has been investigated by both Spanish (see *Nemastomataceae*) and Italian workers (Rindi & Cinelli 1995). The latter authors included in their findings an uncertain record of *Polyneura bonnemaisonii* (C. Agardh) Maggs & Hommersand, pointing out the resemblance of their material with *Erythroglossum laciniatum* (Lightfoot) Maggs & Hommersand. Both species are not known with certainty in the Mediterranean Sea (cf. Athanasiadis 1985a; Gómez Garreta & al. 2001). The reproductive phenology of several species of *Peyssonnelia* has been examined by Boisset (1992a, 1992b).

Mediterranean France & Corsica

Since Feldmann's classical studies on the marine algae of the coast of Albères, the local flora has received numerous additions which have been summarized in a checklist published by Boudouresque & al. (1984). The total number of taxa reaches 540, 332 of which are red algae. At least three new species have been formally described, viz. *Acrochaetium molinierii* Coppejans & Boudouresque, *Pseudolithophyllum cabiochia* Boudouresque & Verlaque [*Lithophyllum cabiochia* (Boudouresque & Verlaque) Athanasiadis (1999b)] and *Polysiphonia banyulensis* Coppejans. Further additions to the local flora have been made by Verlaque (1989, 1994, 2001), Verlaque & Riouall (1989), and Verlaque & Latala (1996). These papers have also included several new records of exotic species in the Mediterranean Sea.

An updated checklist of the Corsican seaweeds has been published by Boudouresque & Perret-Boudouresque (1987), partly based on eight papers entitled «Végétation marine de la Corse (Méditerranée) I-VIII» (Verlaque 1990b). Since then, several new records have been added by Frick & al. (1996).

Ligurian sea

Since the first record of *Acrothamnion preissii* (Sonder) Wollaston from Livorno (Cinelli & Sartoni 1969), algologists have continued the search of new elements in the local flora. Rindi & al. (1996) reported several new records of ceramialean species such as, *Antithamnion amphigeneum* Millar (= *A. algeriense*), *Laurencia glandulifera* (Kützinger) Kützinger (originally described from Rovinj but also reported from the Indo-Pacific; see Silva & al. 1987: 66), and *L. minuta* Vandermeulen, Garbary & Guiry [originally described from Aquaba and now reported (introduced ?) in several localities of the western basin and the Ionian Sea]. The ecology and reproductive phenology of *Acrothamnion preissii* has been studied by Piazzzi & al. (1996) who reported sexually reproducing plants for the first time in the Mediterranean. Apart from these investigations, it should be reminded that the Ligurian coast is the type locality of many imperfectly known Mediterranean taxa described by Dufour, Meneghini, Ardissoni, and De Notaris (see Appendix II). The deep-water delesseriaceous *Apoglossum gregarium*, previously known from South Africa and both sides of the Isthmus of Panama, has been reported from the Tuscan Islands in the

southern Ligurian Sea (Sartoni & Boddi 1993), the Gulf of Taranto (Petrocelli & al. 1999) and other localities of the western basin (see Gómez Garreta & al. 2001).

Tyrrhenian sea

Basso's coralline studies from this region are particularly important and have been mentioned above. She also reported the exclusive presence of *Peyssonnelia rosa-marina* Boudouresque & Denizot at soft circalittoral bottoms, 33-111 meters depth (Basso 1990). The marine flora of Lazio (central Italy) has been studied in an unpublished thesis by D'Archino, and the part covering the *Ceramiales* was subsequently published by Abdelahad & D'Archino (1998). As mentioned previously, the taxonomic studies of De Masi & Gargiulo (1981, 1982b, 1982c) and Gargiulo & al. (1985, 1986, 1987) have covered several members of the genera *Gracilaria*, *Rhodomenia*, *Lomentaria*, *Solieria*, and *Halymenia* from this region and Sicily.

Adriatic sea

A revised checklist of Adriatic algae has been published by Giaccone (1978) who listed 591 taxa including 349 red algae. Records from the Italian coast of the Adriatic Sea have been catalogued by Furnari & al. (1999) in an account that presents information of 642 taxa (381 red algae) reported since the days of Nardo and Zanardini. In the latter work, taxa appear alphabetically followed by authorities, locations, references, original taxon citations, and biogeographic affinity. Taxonomic comments are given in some cases. Additional observations regarding the macroalgae of the Venice lagoon are published by Gargiulo & al. (2000). The flora of the Slovenian coast in the North Adriatic, and in particular the flora of Rovinj, has been surveyed by Munda between 1967 and 1983 and Vukovic (1976, 1984). Munda's work is extensive, covering principally ecological aspects. Munda (2000) also published a thorough comparative analysis of historical records since the time of Kuckuck (1894-99) and reported a floristic impoverishment (the number of red algal species dropping from 155 to 58). Similarly, Vucovic reported only 55 species of red algae in the area, but Span & al. (1996) have listed some 146 rhodophyte taxa after summarizing investigations between 1982 and 1986. Since then, certain new records of rare or alien species have been added by Sartoni & Rossi (1998). On the Croatian coast of the Middle Adriatic, Span & Antolic (1994) listed some 225 rhodophyte taxa.

Ionian sea & Sicily

The first records of *Agardhiella subulata* and *Solieria filiformis* from Mar Piccolo (Taranto) fueled the longstanding controversy of Tethyan relics of the pantropical family *Areschougiales* (see above). The phenology of the marine flora of Mar Piccolo has been examined by Cecere & al. (1991), who found a decrease in the number of brown algal taxa in the last 70 years. A floristic investigation of the Cheradi Islands resulted in a list of 295 macroalgae including 218 red algae. New records to the Ionian Sea are *Ceramium graecum* Lazaridou & Boudouresque (a putative alien species; see below), *Chondria polyrhiza* Collins & Hervey, *Laurencia glandulifera* (Kützinger) Kützinger and *Polystrata fosliei* (Cecere & al. 1996).

A revised checklist of benthic marine algae of Sicily and adjoining islands has been prepared by Giaccone & al. (1985), who summarized the results of floristic and taxonomic investigations since Ardisson and reported a total number of 770 taxa including 477 red

algae. Since then, the Sicilians have added several new species [e.g. *Antithamnion piliferum* Cormaci & Furnari (1987), *Cordylecladia guiryi* Gargiulo & al. (1990), *Hypnea furnariana* Cormaci & al. (1993)], new Mediterranean records [e.g. *Grateloupia doryphora* (Montagne) Howe (De Masi & Gargiulo 1982a), *Plocamium secundatum* (Kützinger) Kützinger (Cormaci & al. 1991), *Botryocladia madagascariensis* G. Feldmann, *Ceramium strobiliforme* Lawson & John, and *Chondria pygmaea* Garbary & Vandermeulen (Cormaci & al. 1992)], and other new local records (Cormaci & Furnari 1988; Cormaci & al. 1992). The reproductive phenology of ceramiceous algae on the Sicilian east coast has been monitored over a period of 12 years (Cormaci & al. 1984). The authors reported differences at species level related both to season and depth. Similar (species specific) results were obtained in a study of the spatial distribution and reproductive phenology of certain rhodomelacean algae from the Ligurian coast (Rindi & Cinelli 2000).

Aegean sea

A survey of the Aegean seaweeds has been published by Athanasiadis (1983, 1985a, 1985b, 1986, 1987) who reported 440 species including 265 red algae. Further contributions on the taxonomy, systematics and biogeography have been published by Athanasiadis (1988, 1989, 1995, 1997a, 1997b, 1999a, 1999b), Lazaridou & Boudouresque (1992), Orfanidis (1990), Tsekos & Orfanidis (1990), and Sartoni & de Biasi (1999). In one of these papers, *Mesophyllum macedonis* Athanasiadis (1999a) was recognized as a putative Tethyan relic joining the group of other rare Aegean endemics described by Giaccone (1968) and Huvé (1962). On the other hand, the discovery of the new species *Ceramium graecum* Lazaridou & Boudouresque (1992) in the South Aegean could represent an introduction (Verlaque 1994), since this species was subsequently reported from Mar Piccolo (Cecere & al. 1996) and recently discovered in a harbor in the North Aegean (Athanasiadis unpubl. observations). On the Turkish coast, Marcot & al. (1976) described several species of the genera *Peyssonnelia* and *Metapeyssonnelia*. Aysel (1983, 1984) described species of *Chondria* C. Agardh and *Polysiphonia* section *Oligosiphonia*, and Dural & al. (1997) surveyed the benthic flora of Smyrna. An updated checklist of the Turkish marine algae has been published by Aysel (1997).

Levant sea

The algal vegetation along the Syrian coast has been surveyed by Mayhoub (1976) who reported an impressive number of 293 species including 185 red algae. Previous studies of the flora of Palestina were made by Rayss (1963) and Edelstein (1964). On the Israeli coast, records between 1973 and 1995 from twenty-two stations have been catalogued by Lundberg (1996). Rachel Einav (personal communication) catalogued the Mediterranean collections at the Jerusalem Algal Herbarium and reported about 151 species of red algae (excl. synonyms). Records of marine algae from Alexandria since the Bonapart Expedition (1798-1801) have been catalogued by Aleem (1993), who also included his own observations over a period of 50 years. In this work, 244 taxa (141 red algae) are briefly described and illustrated.

Northern Africa

The first catalogue of marine algae from Libya including records made by Ascherson since 1878 has been published by Nizamuddin & al. (1979). The taxonomy of the Libyan

Dictyota has been studied in a significant contribution by Nizamuddin (1981), while Godeh & al. (1992) surveyed the flora of Cyrenaica and added several new records. The study of the marine algae of Tunisia made a part of Meñez's dissertation that was subsequently published as a catalogue presenting a historical account starting with Piccone's contributions in 1879 (Meñez & Mathieson 1981). An updated Tunisian checklist has been published by Ben Maïz & al. (1988). An annotated catalogue of Algerian seaweeds has been published by Perret-Boudouresque & Seridi (1989). The discovery of the new species *Antithamnion algeriense* was later shown to belong to the Southern Hemisphere *A. amphigeneum* (Athanasiadis 1996a). The Mediterranean coast of Morocco has been more recently surveyed by González García (1994) and Benhissoune & al. (2001).

Epilogue and the future

If the scope of systematics is the discovery of monophyletic groups, the field of taxonomy extends beyond that. It is the understory that links many disciplines, seeking answers in all kinds of biological data taking into account published and unpublished information, and necessitating an almost 'intimate' relation to the group under consideration. Taxonomy is often criticized for being subjective and there exists its power: the human ability to analyse data independently and put forward new hypotheses to be tested. The Linnaean classification system along with the type method are the basic taxonomic tools and currently stand for our understanding of more than 1.7 million species (Benton 2000). The discovery of a higher molecular diversity in red algae than in other eucaryotes has emphasized the need to extent our investigations, particularly at ultrastructural level, but we also must update the traditional taxonomy through monographic studies of monophyletic groups in light of phylogenetic systematics.

The study of the Mediterranean seaweeds presents particular problems due to the inheritance of a large number of poorly known taxa and the heterogeneous character of the present-day flora. On the other hand, the unique geological events that are associated with the genesis and formation of the Mediterranean Sea allow us to estimate the age of hypothetical speciation events, and therefore the Mediterranean species, extant and extinct, are the key to our understanding of the evolutionary history of red algae.

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Appendix I. Landmarks in Mediterranean Phycology.

Apart from Theophrastus's (371-288 ? b.C.) descriptions of several species of PHYKOS from the Black Sea and the Mediterranean, and Plinius's (23-79) association of *Chara* with land plants (Huss & Kranz 1997), the first taxonomic contributions must be attributed to Imperato's 'Historia Naturale' (1599) where several species from Naples are described and illustrated under uninomials or binomials, such as *Sertolara* (*Halimeda*; see Naccari 1828: 45), *Porus cervinus* and *Millepora taenialis* (see Pallas 1766: 263; Ellis & Solander 1768: 134) and *Mosco petroso* (Harvey 1847, pl. 73). Pre-

Linnaean botanists, such as J. Bauhin (1541-1613), G. Bauhin (1560-1624), P. A. Micheli (1679-1737) and J. Parkinson, included Mediterranean algae in their contributions 'Historia plantarum universalis...' (1650-51; posth.), 'Pinax theatri botanici. Ed. II.' (1623), 'Nova Plantarum Genera...' and 'Theatrum Botanicum' (1640), respectively.

During the early Linnaean period many other imperfect descriptions of Mediterranean species are provided by Gmelin, Wulfen, Roth, Olivi, Desfontaines, Lamarck and others (see Naccari 1828). Until the end of the 19th century, most of the Mediterranean macroalgae have been described in the accounts of J. Agardh, Kützinger, Zanardini, Meneghini, and Ardisson. Moreover, Zanardini publishes the first illustrated flora, 'Iconographia phycologica adriatico-mediterranea' (1860-76). At the start of the 20th century, the Italian school continues with significant contributions, such as Preda's Cryptogamic flora and De Toni's 'Sylloge Algarum'. The account below concentrates on phycologists with contributions on the taxonomy of Mediterranean seaweeds published between the Linnaean period and the end of the 20th century. Many citations of older papers and books have not been confirmed from the original publications, but are compiled from bibliographic accounts such as of Cesati (1882), Saccardo (1895), and De Toni (1932). In some cases, corrections have been made by Paul Silva. Locations of authentic herbarium collections have been compiled from the accounts of Koster (1969) and Stafleu & Cowan (1976, 1979, 1981, 1983, 1985), unless otherwise stated.

The Italian school

Ginanni G. (1692-1753). In his 'Opere postume' (1755), he describes and illustrates 114 Adriatic species, such as *Opuntia* (*Halimeda*), *Tussilagine* (*Flabellia petiolata*) and *Epatica spirale minore* (*Osmundaria volubilis*) (Cesati 1882; Naccari 1828: 45, 47, 58).

Targioni-Tozzetti G. (1712-1783). In his 'Catalogus vegetabilium marinorum musei sui' (1826; posthum.), he treats several marine algae such as *Hormisus opuntioideus* (*Halimeda tuna*), *Euspiros volubilis* (*Osmundaria*), *Lophyros confertus* (*Halopitys incurva*) and *Pterigospermum pavonium* (*Padina*) (Cesati 1882). He was a pupil of Micheli and their collections are in the Micheli-Targioni Herbarium in Florence (Nepi 1999).

Donati A. Gargiulo & al. (2000) list a pre-Linnaean contribution 'Trattato de semplici, pietre et pesci marini, che nascono nel lito di Venezia...' (1631), which is used today to study changes in the flora composition.

Donati V. (1713-1763). Major contributions are 'Della storia naturale marina dell'Adriatico' (1750), in 1758 translated to French ('Essai sur l'histoire naturelle de la mer Adriatique'; Cesati 1882), as also his 'Auszug seiner Natur-Geschichte des adriatischen Meers...' (1753). In these publications, he describes several early generic names, viz. *Ceramianthemum* 1753 (*Gracilaria-Gracilariopsis*) and *Ceramianthemum* 1758 (*Ceramium*), *Polyostea* 1753 (*Polysiphonia*), *Pterigospermum* 1753 (*Padina*), *Acinaria* 1753 (a synonym of *Sargassum* originally used by Imperato), *Callophilophora* 1753 (a synonym of *Acetabularia* based on *Androsace* of Mattioli) and *Fitocoma* 1753 (based on Imperato's 'Gongolaria ou Abies marina de Theophraste') (Silva 1952).

Griselini F. (1717-1783). His pre-Linnaean name 'La baillouviana' was taken over both as a genus (by Adanson in 1763, as *Baillouviana*) and a species (by Gmelin in 1768, as *Fucus baillouvianus*). The latter is the basionym of the well-known *Dasya baillouviana*.

Scopoli G. A. (1723-1788). Several Adriatic species appear in his 'Flora Carniolica...' (1772), inclusive *Spongia vermicularis* (*Dasycladus*) (Cesati 1882).

Turra A. His 'Flora Italicae Prodromus' (1780) includes the first description of *Ulva petiolata* (*Flabellia*).

Olivi G. (1769-1795). In his 'Zoologia Adriatica' (1792), he includes several Linnaean species, i.e. *Corallina opuntia* (*Halimeda tuna*), *Corallina officinalis*, *C. rubens* and also his *Lamarckia vermilata* (*Codium*). According to Cesati (1882), he publishes (?) several other notes on *Ulva atropurpurea* (*Porphyra*; see Olivi 1791), *Ulva petiolata* and on the new genus *Lamarckia*. His types are in Venice (Mus. Civ. Stor. Nat.).

Bertoloni A. (1775-1869). In his 'Lettera...al Signor Lamouroux' (1818), he describes *Fucus lomation* (*Cryptonemia*), while in his 'Historia Fucorum maris Ligustici' (1819) he describes 39 species, most of which are later synonyms (e.g., *Fucus flabellum* = *Flabellia petiolata*). Other significant publications are 'Rariorum Italiae plantarum decas tertia. Accedit specimen zoophytorum Portus Lunae.' (1810) where some coralline species are described together with *Fucus sertolara* (*Halimeda tuna*) and *Fucus luteus* (*Laurencia* ?), 'Flora italica cryptogama I-II' (1858-67), and comparative accounts between *Chondria* and *Uvaria*, *Valonia* and *Syphunculus* and between *Codium tomentosum* and *C. bursa* (Cesati 1882). Descriptions of new species include those of *Chara ulvoides* and *Fucus verruculosa* (*Rissoella*). Several of his taxa are *nomina nuda* (e.g., *Ceramium fulvum* Bertol. in herb. = *Sphacelaria tribuloides* Meneghini).

Bivona-Bernardi A. (1776-1834) describes the new genus *Scinaia* based on *S. forcillata* (*S. furcellata*). Other contributions are made on the genus *Nostoc* (Cesati 1882).

Pollini C. (1782-1833). In his 'Flora Veronensis' (1822-24), he treats the genera *Linckia*, *Ulva*, *Conferva* and *Fucus*. Several species are recorded, some of which are new taxa such as *Ulva sertolara* (*Halimeda tuna*) (Cesati 1882).

Corinaldi J. (1782-1847) publishes contributions on *Sphaerococcus plicatus*, *Conferva* (*Polysiphonia*) *parasitica*, *Hutchinsia pinnata*, *Conferva ruchingerii*, *C. diffusa*, and on *Laminaria debilis* (Cesati 1882).

Naccari F. L. (1793-1860). He provides a thorough bibliographic account of previous publications on Adriatic algae in his 'Algologia Adriatica' (1828), where he also describes numerous genera and species of diatoms, blue-greens, planktonic green algae as well as macroalgae. He often introduces new names (e.g., *Opuntia reniformis*; a synonym of *Halimeda tuna*) but most of them are superfluous because he cites earlier synonyms. Two valid taxa in this work are *Palmella crassa* (*Palmophyllum*) and *Callithamnion naccarianum* Rudolphi in Naccari (*Antithamnion cruciatum*). Other new names, e.g. *Zonaria squamaria* var. *umbilicalis* and *Z. dichotoma* var. *nana* (Naccari 1828: 81), appear with references to his 'Flora Veneta' (1826-28).

Biasoletto B. (1793-1858). In 'Streifzug von Triest nach Istrien im Frühlinge' (1837), he describes *Dasya kützingeriana* and coauthors Tommasini, M. in the description of *Conferva minuta* (Silva pers. comm.; cf. Cesati 1882). In other publications he introduces *Hydrodictyon granulatum* (later referred to as *H. graniforme* Biasoletto; Silva pers. comm.), *Halimeda multicaulis*, *H. tuberosa* (a nom. nudum; Silva pers. comm.), *Zonaria aureolata* (a nom. nudum; Silva pers. comm.), and *Conferva echinus*. He also publishes on *Cystoseira discors* (*C. ercegovicii*) and on unicellular algae (Cesati 1882, De Toni 1932).

Delle Chiaie S. (1794-1860). In his 'Hydrophytologiae Regni Neapolitani Icones' (1829), he lists and illustrates 100 species within 28 genera and introduces the combination *Codium effusum* (Rafinesque) Delle Chiaie (Cesati 1882).

Moris G. G. (1796-1869). His 'Stirpium Sardoarum Elenchus III' is a catalogue of 68 algae, two of which are new species of *Ceramium* (Cesati 1882).

Titius P. (1801-1884). 'Algae Maris Adriatici exiccatae editae a R. F. Hohenacker' (1876, in collaboration with Kalkbrenner; see Cesati 1882).

Nardo G. D. (1802-1877). He erected *Hildenbrandia* (based on *H. prototypus* from Venice and later synonymised with *Verrucaria rubra* from Norway), *Stiffitia* (based on *S. prototypus*, now *Zanardiniatypus*), *Agardina* and *Petrobryum* (both superfluous names of *Nullipora*), *Sertolara* (based on *S. typus*, now *Halimeda*) and *Titanephrium* (*Corallina*). He also publishes on the medical uses of algae (Cesati 1882).

Zanardini G. A. M. (1804-1878). His main work focuses on the Adriatic flora that he describes in several significant publications, such as 'Synopsis algarum in mari Adriatico collectarum' (1841), 'Saggio di una classificazione delle Ficee' (1843), 'Notizie intorno alle cellulari marine...' (1847; where 13 new species of *Ectocarpus* are described alone), and 'Iconographia phycologica adriatico-mediterranea' (1860-76). He establishes many new genera such as *Chondrymenia*, *Halydictyon*,

Aglaozonia, *Choristocarpus*, *Nereia*, *Contarinia*, *Nardoa*, *Dichophycus* (*Fauchea*) and numerous new species such as *Callithamnion cladodermum* (*Balliella*), *C. hirtellum*, *C. rigescens*, *C. flagellare*, *C. elongatum*, *C. unilaterale*, *C. inordinatum*, *C. pallens*, *C. posidoniae*, *Griffithsia torulosa*, *Bryopsis furcellata*, *Valonia caespitula* (*V. utricularis* ?), *Sphacelaria plumula*, *Mesogloia fistulosa* (*Cladosiphon mediterraneus* ?), *Polysiphonia parvula*, *Halydictyon mirabile*, *Nitophyllum venulosum*, *Rytiphlaea pumila*, *Callithamnion nodulosum* (*Gulsonia* ?), *Ceramium inconspicuum*, *Callithamnion dubium* (*Antithamnion cruciatum*), *Callithamnion cruciatum* f. *fragillissimum* (*Antithamnion descipiens*), *Rhodymenia ligulata*, *Lomentaria linearis*, *Nardoa polymorpha* (*Peyssonnelia*), *Squamaria vulgaris*, *Bangia alsidii* (*Stylonema*), *Galaxaura adriatica* (*Tricleocarpa fragilis* ?), *Gracilaria corallicola*, and *Peyssonnelia multiloba* (*P. squamaria*). Amongst corallines, he describes *Corallina verrucosa* (*Amphiroa cryptarthrodia* ? = *Amphiroa rubra* ?), *Lithothamnion papillosum* (*Goniolithon*), *Jania plumula* (*J. corniculata*), *Corallina virgata* (*Corallina granifera* ?), and several species of *Lithophyllum* that remain little known or *nomina nuda*. He also studies the reproductive structures of *Galaxaura* and *Schizymenia*. Zanardini also publishes contributions on the algae of Borneo, Ceylon, Australia and Red Sea. His herbarium is in Venice (Mus. Civ. Stor. Nat.) and includes collections referred to some 2425 taxa (De Toni & Levi 1888) of which 57 species have been referred to *Polysiphonia* (Schiffner 1937).

De Notaris G. (1805-1877). His contributions comprise in total some 13 publications of which two cover desmids and other planktonic green algae. The other papers focus on the seaweeds of Liguria (see Cesati 1882; Preda 1908-9; Abdelahad & Bazzichelli 1999). Several new species are described, in particular *Erinacea rissoana* (*Rissoella verrucosa*), *Mesogloia bertolonii*, *Cystoseira squarrosa*, *Sphacelaria bertiana* (the fructification of *Cladostephus*; Prud'homme van Reine 1982), *Callithamnion nemalionis*, *Lomentaria exigua*, *Polysiphonia funebris*, *P. montagnei*, *P. subtilis*, *Bryopsis duplex*, *B. tenuissima* (*Derbesia*), *B. dichotoma*, *B. comoides*, *Ectocarpus nitens*, and *Enteromorpha confervicola*. Together with Cesati, they contribute in the foundation of the Erbario Crittogamico Italiano. His herbarium collections are at GE, RO, PAD and TO (see also Iberite 1999).

Cesati V. (1806-1883). Vincenzo Cesati's botanical work largely comprises mycological papers and his contributions to algology are in the foundation of the 'Erbario Crittogamico Italiano' (in collaboration with De Notaris) and his work on G. L. Rabenhorst's exsiccatae. His personal herbarium is also one of the largest and most complete that exist in Italy (RO). He also publishes on blue-greens and on *Hydrodictyon utriculatum* (Cesati 1882, Saccardo 1895, Millozza 1999, Iberite 1999).

Meneghini G. G. A. (1811-1889). His prolific interests cover botany, physical geography, and geology. He publishes papers on several marine genera, including desmids, diatoms, *Characeae*, algae of hot springs, but also on the palaeontology of plant and marine animal fossils, angiosperms, and on the classification of primitive animals (Canavari 1889). An important algological contribution is 'Algae Italiane e Dalmatiche' (1842-43), where numerous taxa (previously also published in *Giornale Botanico Italiano*) are described such as *Liagora distenta* var. *major*, *L. viscidula*, *Bryopsis thuioides*, *B. seminuda*, *B. petteri*, *B. intricata*, *B. apiocarpa*, *B. penicillum*, *Griffithsia pogonoidea*, *Callithamnion sessile*, *C. graniferum*, *C. trifarium*, *C. truncatum*, *C. mesarthrocarpum*, *C. plumula* var. *macropterum*, *Chondrus vidovichii* (*Acrodiscus*), and *Ceramium*. In 'Del genere *Ceramium* e di alcune sue specie' (1844), he described 19 species under the subgenera *Hormoceras*, *Congroceras*, *Echinoceras*, *Acanthoceras* and *Centroceras*. Another important but little-known contribution is 'Algologia Dalmatica' (1841) where he describes 172 species, 53 of which are new or rare (Cesati 1882). In other contributions and letters to Dr. Corinaldi, several other species are described such as *Iridaea foliosa* (*Neurocaulon*), *Rivularia medusae*, *Bangia zanardinii*, *Callithamnion savianum*, *Hutchinsia radicans*, *H. corinaldii*, *Sphacelaria tribuloides*, *S. spartioides*, *Wormskioldia squamariae* (*Rhizophyllis*), *Lithophyllum cristatum* (*L. lichenoides*), *Grateloupia filicina* var. *multifida*, *G. cuneata*, *Rhodymenia nicaeensis* and *Polysiphonia lepadicola* var. *paradoxa*. He also publishes on the chordariaceous algae ('Osservazioni su alcuni generi della famiglia delle Chordariee'; 1844), *Sargassum* and on *Cladophora*. Kützing provided descriptions for many of his *nomina nuda*, such as

Delesseria sandriana (*Erythrogloussum*) (Silva in Athanasiadis 1985a: 461). Meneghini's collections are at FI, with many duplicates in the herbarium of Kützinger (L).

Trevisan V. B. A. (1818-1897). In 'Saggio di una monografia delle alghe coccothalle' (1848), he describes the new genus *Porphyrostromium* (which has recently replaced *Erythrotrichopeltis* Kornmann 1984; see Wynne 1986) and the species *Bangia pulchella*. Elsewhere he examines the reproduction of the ceramiceous and coralline algae (*Amphiroa heterarthra*) and also considers the supradivision of algae within the 'Bissaceae', 'Fucaceae', 'Ulvaceae', and 'Licheni' (Cesati 1882).

Massalongo A. B. (1824-1860). Lichenologist and palaeobotanist at Verona. Cesati (1882) lists 4 papers, one of which is on fossil corallines. In a fifth contribution, he describes the fossil coralline genus *Melobesites* (see Woelkerling 1988: 44).

Caruel T. (1830-1898). French-born Italian botanist, active at Milan, Pisa and Florence, with publications on *Characeae*, *Cladophora* and *Limnodietyon* (Cesati 1882).

Dufour L. (1830-1901). In his 'Quadro delle Melobesie del mare di Genova' (1861) he provides information of nine species of encrusting coralline algae, two of which (*Melobesia notarisi* and *M. frondosa*) are new to science. In his 'Elencho delle Alghe di Liguria' (1864) he lists 229 species within 83 genera of which *Cruoriopsis crucialis* (*Plagiospora*?) and *Ectocarpus meneghini* are new to science. Some of his collections are in herb. Thuret (PC) and as a part of the 'Erbario Crittogamico Italiano. No. Genova', while duplicates exist in Foslie's herbarium (TRH).

Ardisson F. (1837-1910). His work on seaweeds starts with the 'Enumerazione delle Alghe di Sicilia' (1864), where he describes 15 new species, some of which remain little known (e.g. *Sphacelaria intricata*). In 'Studi sulle Alghe Italiane' (1869), he presents an account on many gigartinean-cryptonemialean genera such as *Nemastoma*, *Grateloupia*, *Schizymenia*, *Halymenia*, *Schimmelmannia*, *Chrysymenia*, *Cryptonemia*, *Acrodiscus*, *Gigartina*, *Rissoella*, *Kallymenia*, *Constantinea*, *Gymnogongrus*, *Phyllophora*, and *Rhizophyllis*. In 'Rivista dei Ceramii della flora italiana' (1871), he accepts 26 species of the cumbersome genus *Ceramium* but in his 'Phycologia Mediterranea' the number is reduced to 14. In 'Le Floridee italiane' (1874-1878), he describes numerous infraspecific taxa and 5 new species viz. *Nitophyllum albidum*, *Rhodophyllis strafforelli*, *Lomentaria ligustica*, *Chrysymenia linearis*, and *Chrysymenia flagelliformis*. His account on the *Rhodomelaceae* results in 72 species of which 45 belong to *Polysiphonia* ('Studi sulle Alghe Italiane della famiglia Rodomelaceae'; 1878). Other taxonomic contributions are made on *Carpoblepharis* (*Halymenia*) *mediterranea*, *Halymenia* (*Schizymenia*) *fastigiata*, and *Spermothamnion torulosum*. Together with Strafforello, they publish the 'Enumerazione delle Alghe di Liguria' (1877) where 602 taxa are recorded of which 11 are new species. In 'Phycologia Mediterranea' (1883-1886), three new species are described [*Chrysymenia strafforelli*, *Rhodymenia corallicola* (*Rhodymenia ardissoni*), and *Polysiphonia cladophora*], but numerous new sections and subgenera while several species are reduced to infraspecific (usually varietal) level. Two new genera are established, viz. *Endosiphonia* (*Choreonema*) and *Agardhia* (a new name for *Agardhina* Nardo and a superfluous name of *Nullipora*). Ardisson even considers biogeographic aspects in the distribution of cosmopolitan seaweeds ('Le alghe cosmopolite'; 1894) and also publishes papers on diatoms. His herbarium is at MI with duplicate collections at IH.

Pedicino N.A. (1839-1883). Diatomologist, teacher at Naples, and professor at Rome succeeding De Notaris. Numerous studies on diatoms, algae of hot springs, and marine macroalgae such as *Valonia uvaria*, *Callithamnion*, *Halymenia monnardiana*, and *Ginannia furcellata* (Cesati 1882). His types are at BOLO and ROM.

Arcangeli G. (1840-1921). Italian botanist at Pisa with publications on blue-greens, the anatomy of siphonous genera (*Codium*, *Bryopsis*, *Caullerpa*), and descriptions of new varieties of *Batrachospermum* (Cesati 1882). Other algological contributions include papers on *Laminaria* and *Compsopogon corinaldii* (Preda 1908-1909).

Piccone A. (1844-1901). His early 'Nota sul genere *Lemanea*' (1867) is followed by studies on the 'Florula Algologica della Sardegna' (1878), where he also describes a new species (*Gigartina*

notarisii). In his 'Catalogo delle alghe raccolte durante la crociera de Cutter Violante e specialmente in alcune piccole isole Mediterranee' (1879) he describes 71 taxa, two new to science (*Palmophyllum gestroi* and *Halimeda tuna* var. *albertisii*), and includes the first algal records from Tunisia. Tunisian algae are also treated in his 'Risultati algologici della crociera del Violante comandata dal capitano-amatore Enrico D'Albertis' (1884).

Mazza A. (1844-1929). He monographs several red algal genera in the 'Saggio di algologia oceanica' (1905-1926), and also publishes papers on *Schimmelmanna*, *Nitophyllum*, and *Laminaria* (Preda 1908). His collections are included in the herbarium of A. Forti (PAD; G. M. Gargiulo personal communication) and other material is at PI, BR and L.

Saccardo P.-A. (1845-1920). Mycologist at Padua with contributions on the *Characeae* (Cesati 1882) and a bibliographic account on the Italian botany (Saccardo 1895). His herbarium is at PAD.

Borzi A. (1852-1921). Apart from his 'Studi Algologici' (1883-1886) where he extensively studies the reproduction of green, blue-green, and planktonic genera (e.g. *Kentrosphaera* and *Botrydiopsis*; Cammerloher 1915; Silva 1980: 123), Borzi describes *Nitophyllum charybdaeum* in 'Nuove Floridee mediterranee' (1886) and also the «gemmae» of *Hildenbrandia rivularis* in 'Sugli spermazi della *Hildenbrandia rivularis*, Ag.' (1880) (incorrectly identified by him as male organs; see Sherwood & Sheath 2000b). A biography of Antonino Borzi has been published by Mannino & Naselli-Flores (1999).

De Toni G. B. (1864-1924). His monumental 'Sylloge Algarum omnium hucusque cognitarum' (1889-1924) includes taxonomic information of diatoms, green, brown and red algae, in 6 volumes with nearly 5,500 pages. He also edits 'La Nuova Notarisia' between 1890 and 1924. His other scientific papers exceed 400 in number and include studies on phytoplankton (coauthored by Achille Forti), fungi, angiosperms and their diseases, nomenclature, trading of natural resources incl. algae, aquaculture, and physiology. Some papers are coauthored by David Levi while 16 remain unpublished. His work on Mediterranean algae focuses on the flora of Venice ('Flora algologica della Venezia'; 1885-98; parts 1-3, coauthored by D. Levi) and includes contributions on the algae of Liguria, Tripoli, Cyrinaica, and Attica. He also develops an interest in the scientific work of Leonardo da Vinci and writes papers about his discoveries (Forti 1925). De Toni's extensive herbarium and library are housed at NAP (Santangelo 1999). His son G. De Toni validates the name *Predaea* and starts the publication of 'Bibliographia algologica universalis' (1931-32; 3 parts, Ab-Bz).

Preda A. (1870-1941). Botanist at Pisa and Siena. His red algal flora of Italy (Preda 1908-9) is a major contribution and remains unsurpassed.

Forti A. (1878-1937). A pupil of Saccardo at Padua with publications on diatoms and macroalgae in collaboration with De Toni (e.g. 'Algae di Australia, Tasmania e Nuova Zelanda'; 1923). Forti's herbarium and library are housed in the Botanical Garden of Padua (Marcucci & Moro 1999).

Pierpaoli I. (1891-1967). The herbarium of Irma Pierpaoli is kept at the Stazione di Biologia Marina of Porto Cesareo and has been recently revised. It includes collections from Mare Piccolo and Mare Grande (Cecere & Saracino 1999).

Valiante R. Raffaele Valiante was one of the first algologists to use the marine station at Naples in 1878 (Buia & Groeben 1999). He describes 'Le Cystoseirae del golfo di Napoli' (1883) and also the new genus and species *Streblonemopsis irritans* (growing on *Cystoseira opuntoides*).

The French school

Lamarck de, J. B. P. A. (1744-1829). Extremely prolific naturalist with interests in most fields of biology. He describes a large number of species of the animal and plant kingdoms, amongst them several Mediterranean seaweeds. His types of coralline algae have been recently catalogued and re-examined by Woelkerling (in Woelkerling & Lamy 1998).

Desfontaines R. L. (1750-1833). Professor at the Jardin des plantes in Paris. In his 'Flora atlantica' (1789-1799), he describes some new Atlantic-Mediterranean taxa such as *Fucus implexus* (*Dictyota*

dichotoma var. *implexa*), *Fucus crinitus* (a later homonym of *Fucus crinitus* Gmelin 1768), and *Fucus gelatinosus* (a later homonym of *Fucus gelatinosus* Hudson 1762). His types are at PC and FI.

Bonnemaison T. (1773-1829). Contemporary and close friend of Lamouroux, with main studies on Atlantic marine algae in his two main contributions 'D'une classification des Hydrophites loculées, ou Plantes marines articulées qui croissent en France' (1822) and 'Sur les Hydrophites loculées (ou articulées) de la famille des épidermées et des Céramiées' (1828). Some observations on Mediterranean material are included in the latter work with citations to collections provided by Grateloup, Ducluzeau, Risso and others.

Delile A. R. (1778-1850). He took part in Bonaparte's Egyptian campaign, being responsible for the algal collections (Granel & al. 1967; Silva 1980: 123). He provides the first description of *Fucus taxiformis* (*Asparagopsis*) from material collected in Alexandria. In 1819 he replaces A.-P. De Candolle in the Botanical Garden of Montpellier where part of his collections are presently housed (the type of *F. taxiformis* was located in the herbarium of Lamouroux; Dixon 1964).

Bory de Saint-Vincent J. B. G. M. (1778-1846). His early papers examine freshwater algae of the genera *Conferva*, *Byssus*, *Phytoconis*, *Thorea*, *Batrachospermum*, *Lemanea*, *Audouinella*, the planktonic *Anthophysa* (*Chrysophyceae*), and the blue-green *Anabaena*. Later contributions are made on the flora of Peloponnese, in connection to the 'Expédition scientifique de Morée' (1832-33; published by Fauché M., Brongniart A., Chaubard & Bory de Saint-Vincent J. P. J. M) and where several red algae are described such as *Nullipora trochanter* (*Goniolithon*), *Tenarea undulosa* (*T. turtulosa*), *Gelidium neglectum* (*Grateloupia* ?), and also species of *Liagora* and *Laurencia* (*Chondrophycus* ?). His types are at PC.

Lamouroux J. V. F. (1779-1825). He actualizes the subdivision of macroalgae according to their pigmentation, which system has largely persisted until today. He describes several species and genera based on material from the Mediterranean such as *Acetabularia*, *Anadyomene*, and *Dictyopteris*. *Acetabularia* is apparently synonymous with two other Mediterranean genera, viz. *Callophilophora* Donati 1753 (based on *Androsace* of Mattioli) and *Olivia* Bertoloni 1810 [based on *O. androsace* (Pallas) Bert.]. His algological interest expands to coralline algae. He is also credited with the first paper on seaweed biogeography, 'Memoire sur la Geographie des plantes marines' (1826). His types are at CN.

Montagne J. P. F. C. (1784-1866). His algological contributions are equally important as his other botanical research and expand far beyond the Mediterranean to remote regions such as Patagonia, Chile, Peru, Newfoundland, Cuba, New Zealand, and Tahiti. His phycological part in 'Flore d'Algérie' (1846) is an outstanding achievement preceded by 'Cryptogames Algériennes' (1838), an account on some littoral collections made by M. Roussel (1795-1874; 'naguère pharmacien en chef de l'armée d'Afrique') and who is also credited with the description of the rare red alga *Halymenia* (*Aeodes*) *marginata* Roussel in Montagne. The latter work contains descriptions of some 7 new species and one variety, viz. *Dasya ornithorhyncha* (*Eupogodon planus*), *Chondria fastigiata*, *Halymenia marginata*, *H. algeriensis*, *H. monnardiana*, *Padina omphalodes* (*Zanardinia*), *Cystoseira granulata* var. *turneri*, and *Sargassum megalophyllum*. Several other taxa are described in 'Flore d'Algérie' such as, *Sporochmus agardhii*, *Dictyota spiralis* (*Dilophus*), *Sphacelaria compacta*, *Codium filiforme*, *Faucheia* (in collaboration with Bory), *Plocaria* (*Gracilaria*) *conferta*, *P. divergens*, *P. heteroclada*, *Dasya sanguinea*, *Laurencia fastigiata*, *Chrysomenia radicans*, *Grateloupia fimbriata*, *Gelidium pectinatum* (with *Fucus serra* Gmelin as synonym), *Halymenia cystophora*, *Olivia* (a synonym of *Caulacanthus* and a homonym of Bertoloni's name for *Acetabularia*), *Corallina deshayesii*, *Amphiroa polyzona*, *Melobesia grandiuscula* (*Lithophyllum*), *Spyridia berkeleyana*, *Griffithsia duriae*, *Porphyra boryana* (*Porphyrostromium*), *Phyllactidium arundinaceum*, and *Conferva lepidula*. In the phycological part of Barker-Webb & Berthelot's 'Histoire naturelle des îles Canaries', he describes several Atlantic-Mediterranean species such as *Halymenia cyclocolpa* (*Platoma*). Genera that he establishes on the basis of extra-Mediterranean material include *Hydropuntia* (now referred to *Gracilaria*) and *Heterosiphonia*. His types are at PC.

Ducluzeau, J. A. P. His thesis 'Essai sur l'histoire naturelle des Conferves des environs de Montpellier' appears in 1806 without plates leaving uncertain the status of several new described taxa. It is not known if he kept a herbarium. Two of his species, *Ceramium crispum* (*Pterothamnion*) and *C. granulatum* (*Callithamnion*) have been neotypified (see Athanasiadis 1985b; Maggs & Hommersand 1993: 126).

Solier A. J. J. (1792-1851). An entomologist and algologist with studies in Paris and later lieutenant in Napoleons's army at Marseille and Montpellier. He describes the genus *Derbesia* in 'Memoire sur deux algues zoosporées devant former un genre distinct, le genre *Derbesia*' (1847) and several other taxa in collaboration with Derbès. His types are at C, FI, KIEL, LZ, and other material at LD.

Duby J. E. (1798-1885). In his 'Botanicon Gallicum' (1830), he includes collections of many Mediterranean species from Marseille, Corsica and Nice and validates *Halymenia nicaeensis* (*Schottera*) and *Cystoseira crinita*. He also publishes 3 illustrated papers on the *Ceramiales* (Cesati 1882).

De Candolle A. P. (1806-1893). Apart from his studies on the angiosperms, he describes several Mediterranean macroalgae, such as *Fucus nervosus* (*Phyllophora*), *Ulva interrupta* (*Scinaia*), and *Fucus miniatus* (*Wurdeimannia*). His types are at G and PC.

Decaisne J. (1807-1882). In his 'Mémoire sur les Corallines' (1842), he studies the calcified (mostly green) algae and describes *Espera mediterranea* (a stage in the growth of *Penicillus*) from Villefranche. In his 'Plantes de l'Arabie heureuse' (1841) he describes the genera *Microdictyon* and *Peyssonnelia*, the latter later typified with the Mediterranean *P. squamaria*. His types are at PC, P and G.

Thuret G. A. (1817-1875). He is mostly known for his 'Études Phycologiques' (1878; in collaboration with Bornet), where they also introduce the term 'procarp' for the first time in the *Ceramiales*, and his contribution in Le Jolis 'Liste des algues marines de Cherbourg' (1863). He describes several new genera, such as *Ptilothamnion*, *Bornetia*, *Thamnidium* (*Rhodochorton*), *Rhodochaete*, and the new species *Rhodochaete parvula*, *Porphyra leucosticta*, *Crouania schousboei* (*Thuretelia*), *Chantransia corymbifera*, *Polysiphonia schousboei*, *Castagnea contorta* (*Cladosiphon*), and *Streblonema fasciculatum*. His types are at PC.

Derbès A. A. (1818-1894). Together with Solier, they publish on algal physiology and describe the new genera *Streblonema*, *Monosporus*, and *Giraudia* in Castagne's 'Catalogue des plantes qui croissent naturellement aux environs de Marseille' (1845). He also describes the genus *Ricardia* and studies the male structures in 'Sur les organes reproducteurs des Algues' (1850). His collections are at BP, G and PC.

Debeaux J. O. (1826-1910). In a paper on littoral algae from Corse, he reports *Cladopora membranacea* (*Siphonocladus*) for the first time in the Mediterranean. His types are at P.

Bornet J. B. E. (1828-1911). Together with Thuret they publish the magnificent 'Notes Algologiques' (1876, 1880) where the post-fertilization of several red algae is for the first time illustrated in detail. His account on Schousboe's algae from the Mediterranean and Atlantic coast of Morocco is also a major contribution. Other publications are on the *Nostocaceae*, the acrochaetioid complex and on the algae of Madagascar. Bornet describes several new genera such as *Acinetospora*, *Lejolisia*, *Gomontia* (in collaboration with Flahault), and *Zosterocarpus*, and the new species *Gelidium melanoideum* (*Pterocladia*), *Polysiphonia hillebrandii* (*Falkenbergia*), *Callithamnion tingitanum* (*Callithamniella*), *Spermothamnion flabellatum*, *Lejolisia mediterranea*, *Melobesia thuretii* (*Choreonema*), *Faucheia microspora*, and *Laminaria rodriguezii*. His types are at PC.

Debray F. (1854-1900). Professor à l'École Supérieure d'Alger from where he publishes the 'Catalogue des algues du Maroc, d'Algérie et de Tunisie' (1897). He also studies the structure and development of *Chylocladia*, *Champia*, and *Lomentaria*.

Sauvageau M. C. (1861-1936). He becomes professor at Bordeaux and principally takes over algal research in France after the death of Bornet. He is mostly active at the Atlantic station

d'Arcachon and the Mediterranean station Laboratoire d'Arago (Banyuls-sur-mer) where he studies the brown algae *Myrionema*, *Ectocarpus*, *Cystoseira*, *Fucus* (near Cadiz), *Phyllaria*, *Nemoderma*, *Cutleria-Aglaozonia* spp., *Stypocaulon*, *Halopteris*, and even diatoms. He is one of the first algologists to apply laboratory cultures in the taxonomy. He also has an interest in Mycology, aquatic phanerogams (his thesis) and in the utilization of algae for their chemical components. He describes several brown algal taxa such as *Fucus dichotomus*, *Cystoseira platyclada*, *C. spinosa*, *Sphacelaria sympodiocarpa*, *Colpomenia peregrina*, *Ascocyclus hispanicus* (*Phycocelis*), several species of *Streblonema*, *Strepsithalia*, *Myrionema* and also the genera *Climacosorus*, *Polytretus*, *Hecatonema*, and *Chilionema*. His types are at PC with duplicates in many other herbaria (L, C, K, AHFH, BM).

Hamel G. G. H. (1883-1944). He works at the oceanographic station of the Muséum d'Histoire Naturelle and at the Laboratoire de Cryptogamie, both in Paris. His thesis 'Recherches sur les genres *Achrochaetium* Naeg. et *Rhodochorton* Naeg.' appears in 1927 and the results are incorporated in the series 'Floridées de France' (1924-1936; the final part *Gelidiales* in collaboration with J. Feldmann). In 1924 and 1925 he also publishes on *Cladophora* (the final part in 1929). The 'Chlorophycées des côtes françaises' appear in three parts (1930-1931) and the 'Phéophycées de France' in four parts (1931-1939). Many of these contributions are published in 'Revue Algologique', which Hamel founded together with P. Allorge. Other contributions of his are on the algae of Tunisia (see Menez & Mathieson 1981), on the *Bangiaceae* of Antilles and a bibliographic account on African algae (Hamel 1928). His exsiccatae collection 'Algues de France' (Fasc. I-III; 1927-1931) is at PC (Feldmann 1954). The publication 'Corallinacées de France et d'Afrique du Nord' (1953) appears posthumously, after being improved by J. Feldmann and illustrated by M. Lemoine. Hamel collects at various Mediterranean sites such as Tunisie, Tripoli and Skyros Island (following his friend Moazzo) and publishes minor papers on other Mediterranean algae (*Caulerpa* and *Cladostephus dubium*), but his main investigations are on Atlantic algae from sites on the coast of France (Saint-Malo, Saint-Servan, Ranche, Iles Chausey, Ile de Sein), Spain (Basque, Cape Saint-Vincent to Algésiras and Malaga), Portugal (Virgo), Morocco (Tanger), and also from the French Antilles (Gouadeloupe and Martinique). He describes several red and brown algal taxa, such as species of *Acrochaetium*, *Gelidium fasciculatum*, *Bonnemaisonia clavata*, *Pleurocladia ralfsioides*, *Cystoseira shiffneri*, *C. sauvageana*, and the genera *Gelidiella* (in collaboration with J. Feldmann), *Feldmannia*, *Kuckuckia*, *Stilopsis*, and *Leblondiella*.

Lemoine M. F. E. (1887-1984). Madame Paul Lemoine works most of her time at PC, studying collections from many regions of the world and publishing some 100 papers (Ardre & Cabioch 1985). She illustrates and updates Gontran Hamel's monumental account on Atlantic and Mediterranean corallines. She virtually continues alone in the field of coralline research, after the death of M. Foslie and F. Heydrich after 1911 (Chamberlain 1978, 1985). Mediterranean material is provided to her by Dr. Jean Charcot, commander of two French Antarctic expeditions (Silva 1980: 125). Lemoine describes several extinct and extant new genera, viz. *Mesophyllum*, the notorious *Pseudolithophyllum* (aimed to cause enormous confusion; the name being still used for three NW Pacific mastophoroid taxa of uncertain generic affinities), and the fossils *Hemiphyllum*, *Paraphyllum*, and *Kymalithon* (the last one in collaboration with Emberger). The number of extra-Mediterranean species she describes is larger, particularly the fossil ones. Her type are at PC (see Lamy & Woelkerling in Woelkerling & Lamy 1988: 140).

Dangeard P. (1895-1970). He works at the Faculty of Sciences of Bordeaux, where his types are presently housed. He studies many groups of marine algae, planktonic and benthic, from the Atlantic, especially Dacar, Morocco, and Atlantic France. Mediterranean contributions comprise studies on phytoplankton and *Bangiaceae* genera (*Erythrotrichia*, *Erythrocladia*) collected at Banyuls-sur-mer.

Chadefaud M. (1900-1984). He publishes cytological investigations on green and brown algae, and also studies the reproduction of *Rhodochaete parvula* and the morphology of the Ceramiales algae (Magne 1987).

Feldmann J. (1905-1978). His prolific work greatly affects the study of algae in Europe in the

past century. His early publications cover surveys of the Algerian flora ('Les algues de Cherchell'; 1931). He continues with studies on the Mediterranean laminarians ('Les Laminariacées de la Méditerranée et leur répartition géographique'; 1934) and later publishes descriptions of 14 new species from the western Mediterranean (mostly from the Banyuls area) ('Algues marines méditerranéennes novae'; 1935). His thesis 'Recherches sur la végétation marine de la Méditerranée' (1937) covers phytosociological aspects. In the following years he describes the flora of 'La côte des Albères' (1937-1942). The year 1954 marks his studies on the flora of Roscoff. He realises the greater richness of the tropics and publishes several new taxa from Madagascar (*Boergesenia*), Mauritania (*Ecklonia muratii*), Mauritius (*Titanophora*), French Antilles (*Griffithsia caribaea*), and Senegal (*Botryocladia senegalensis*). On his side, Geneviève Mazoyer publishes alone, or with him, significant papers on the taxonomy of the Ceramiales algae. Her contribution 'Recherches sur les Cérames de la Méditerranée occidentale' (1941) remains a standard reference in the taxonomy of this group. In 1955 she provides evidence for a heteromorphic life-history in *Acrosiphon*. They clarify the heteromorphic life histories of *Bonnemaïsonia asparagoides* (*Hymenoclonium serpens*) and *Asparagopsis armata* (*Falkenbergia rufolanosa*) and put forward the hypothesis that *B. hamifera* and *Trailliella intricata* are stages in the life cycle of a single species. Conclusive evidence for the latter was provided by Harder in 1948. New Mediterranean genera that Jean Feldmann recognizes are *Haraldia* (based on Derbès et Soliers's *Aglaophyllum lenormandii*), *Gelidiella* (a new name to replace *Echinocaulon* Kützinger; in collaboration with Hamel), and *Bryopsidella* (validated by H. Rietema). The number of new Mediterranean species he describes is greater, viz. *Endoderma majus*, *Pringsheimiella conchyliphila*, *Chaetomorpha adriani*, *Ascocylus conicicola*, *Composonema liagorae*, *Mesospora mediterranea*, *Leathesia mucosa*, *Acrochaetium duboscqii*, *Rhizophyllis codii*, *Ethelia van-bosseae*, *Halymenia rodrigueziana*, *[K]allymenia tenuifolia*, *Botryocladia boergesenii*, *Seirospora sphaerospora*, *Peyssonnelia coriacea*, *Chrysomenia coelarthroides*, *Predaea ollivieri*, *Kallymenia lacerata*, *K. mollis*, *K. rigida*, *Myriactula gracilariae*, *Cystoseira algeriensis*, *Griffithsia genovefae*, *Chondria mairei*, and *Caulacanthus rayssiae*. In 1949 he establishes the order *Scytosiphonales* and in 1953 the *Acrochaetiales*. The new genus *Rhodothamniella* is introduced in 1954, and later validated by Tyge Christensen. In 1951, using Mediterranean and Atlantic material, he confirms the heteromorphic life history of *Derbesia tenuissima* (previously shown to be the sporophyte of *Halicystis parvula* by P. Kornmann). In 1951, together with G. Feldmann, they start their studies on parasitic algae that culminate in the 'Recherches sur quelques floridées parasites' (1958). They introduce the term adelphoparasitism (for parasites having a sister-taxon relationship to their host). Other papers on algal reproduction cover members of the *Calosiphoniaceae* and various siphonous algae (*Halimeda*, *Bryopsis*, *Codium*, *Pseudobryopsis*, *Derbesia*). He also publishes on planktonic algae, *Characeae*, blue-greens, marine fungi and on the cytology, physiology and ultrastructure of algae. His herbarium is at PC.

Caram B. (1916-1990). She studies in culture several brown algae from the Atlantic and the Mediterranean, in particular species of *Chordaria*, *Cylindrocarpus*, *Sauvageaugloia*, *Striaria*, and *Cutleria* (Magne & Simon 1991).

Schotter G. (1922-1963). He publishes significant morphological contributions on Mediterranean and Atlantic species of the *Phyllophoraceae*, in particular on species of *Phyllophora*, *Ahmfeltia*, *Petroglossum nicaense* (Schottera), *Stenogramme*, *Rissoella*, *Harveyella*, *Gymnogongrus*, *Cottoniella*, and *Ceratocolax* (Feldmann 1964).

The Germanic school

Wulfen F. X. von (1728-1805). In his 'Cryptogamia aquatica' (1803) he describes 102 Adriatic taxa (14 species of *Ulva*, 35 species of *Conferva* and 53 species of *Fucus*), amongst them *Fucus hypnoides* (*Hypnea*), *Fucus botryoides* (*Botryocladia*), *Fucus filamentosus* (*Spyridia*), *Conferva simplex* (*Digenea*), *Fucus fruticulosus* (*Boergeseniella*), *Conferva flexuosa* (*Enteromorpha*), and *Ulva stellata* (*Anadyomene*). Some of his types are in W and WU.

Pallas P. S. (1741-1811). He publishes a few descriptions of coralline algae one of which is *Millepora agariciforme*, based on material from Algeria and considered to be related to *Lithophyllum dentatum* (see Athanasiadis 1999a: 243). No types of his algal material have been located.

Esper E. J. C. (1742-1810). His most important phycological contribution is 'Icones Fucorum' (1797-1808) where 39 new species are described. Twelve species are based on Adriatic material sent to him by Wulfen. However, Wulfen had already described some of these species (in Jacquin's 'Collectanea ad Botanicum, Chemiam, et Historiam Naturalem Spectantia. Vols 1-4'; 1786-1790) (Silva 1953). Esper's collections are at ER.

Roth A. G. (1757-1834). Several Mediterranean algae are described and illustrated in his 'Catalecta botanica' (1797-1806), such as *Fucus fasciola* (*Dilophus*), *Conferva utricularis* (*Valonia*), *Conferva cirrosa* (*Sphacelaria*), and *Conferva prolifera* (*Cladophora*). His herbarium is considered to be lost.

Martens, G. (1788-1872). Apart from his extensive studies on Indo-Pacific algae, he describes *Amphiroa pustulata* from Naples (Cesati 1882). His algal types are at LE.

Suhr de J. N. (1792-1847). In his 'Beiträge zur Algenkunde' (1840), Suhr describes a few Mediterranean species such as *Porphyra martensiana* from Catania (from material communicated to him by Martens in Stuttgart) and *Conferva prolifera* var. *aegagropila* from Villefrance. His types are at KIEL and other material at MEL, LD, and L.

Ehrenberg C. G. (1795-1876). He publishes on fossil and living algae, mostly on diatoms, but also a 'Beiträge zur physiologischen Kenntniss der Corallenthiere in Allgemeinen, und besonders des Rothen Meres' (1834) where he treats various coralline taxa such as *Pocillopora agariciformis*. His collections are in Berlin, Geol. Mus. Humboldt University.

Kützinger F. T. (1807-1893). His algological contributions are equally important as those of his contemporary J. Agardh. Kützinger studies most groups of macroalgae and diatoms, describing several hundreds of taxa from various places in the world and in particular from the Mediterranean. He is mostly known for his 'Phycologia generalis' (1843), 'Species algarum' (1849), and his magnificent 'Tabulae phycologicae' (19 vols; 1845-1871). In these and several other papers he describes numerous new Mediterranean genera such as *Spongites*, *Pneophyllum*, *Neurocaulon*, *Rhizophyllis*, *Caulacanthus*, *Chondrosiphon* (*Lomentaria*), *Ascothamnion* (*Valonia*), and numerous new species such as *Halymenia latifolia*, *Chondrosiphon mediterraneus* (*Lomentaria firma*), *Chondrosiphon meneghianus* (*L. uncinata*), and *Chondrosiphon compressus* (*L. compressa*) to name a few. In a paper on *Ceramium* and related taxa, he describes 5 new genera and 28 Mediterranean species many of which have unknown taxonomic status. Some of his types are at L, MEL (herb. Sonder), BM (diatoms), and AWH (diatoms). The types of his species referred to *Ectocarpus* are now lost, but some had previously been re-examined by P. Kuckuck (Prud'homme van Reine & den Hartog 1973).

Philippi R. A. (1808-1904). Prussian botanist who studies in Berlin and later becomes teacher at the technical school of Kassel. He stays in Italy between 1830 and 1832. Cesati (1882) cites a paper 'Sulle Coralline di Sicilia osservate durante gli anni 1830-32' (1837), that has been untracable (Silva pers. comm.) and may be a manuscript of the well-known 'Beweis das die Nulliporen Pflanzen sind' (published also in 1837). In the latter work, he establishes the widely known genus *Lithophyllum* on the basis of four new species from Sicily, viz. *L. expansum* (*Mesophyllum lichenoides*), *L. incrustans*, *L. lichenoides*, and *L. deccusata* (based on Ellis & Solander's *Millepora deccusata* from the Atlantic coast of Portugal). His genus *Lithothamnium* (non *Lithothamnion* Heydrich nom. cons.) was misapplied to include taxa not in accordance with any of his collections, viz. *L. crassum* (*Lithophyllum racemus*), *L. gracile* (*Amphiroa johansenii*), *L. rubra* (*Amphiroa*), *L. byssoides* (*Goniolithon*), and *L. ramulosum* (*Spongites*). His types have been re-examined by Woelkerling (1983a, 1983b).

Nägeli C. W. von (1817-1891). Swiss-born botanist, contemporary to Kützinger and active at Friburg, Zürich and München. His publications 'Neure Algensysteme' (1847) and 'Beiträge zur Morphologie und Systematik der Ceramiceae' (1862) include descriptions of several new genera such as *Acrochaetium*, *Rhodochorton*, *Herposiphonia*, *Titanoderma*, *Pleonosporium*, and

Antithamnion. He also introduces several subgeneric taxa and publishes separately a contribution on *Polysiphonia* and *Herposiphonia* (Cesati 1882).

Pringsheim N. (1823-1894). Botanist at Berlin, Jena and Leipzig with main contributions on filamentous brown and green algae (*Sorocarpus*, *Acrochaete*). He also publishes on species of the genus *Sphacelaria* from Italy, especially on *S. tribuloides* (Cesati 1882). His types are unknown.

Reinsch P. F. (1836-1914). In his 'Contributions ad Algologiam et Fungologiam', several new Mediterranean taxa are described from the Adriatic. Some remain little known (e.g. the tetrasporangia-bearing *Nemastoma inconspicuum*). His types are at W.

Solms-Laubach H. H. (1842-1915). He studies at Berlin and later becomes professor in Strasbourg and Göttingen. In his 'Die Corallinen-algae des Golfes von Neapel...' (1881), he describes several corallines, such as *Melobesia corallinae*, *Melobesia deformans* (*Choreonema thuretii*) and *Lithophyllum insidiosum* (now a form of *Neogoniolithon notarisii*). He publishes the first monograph on *Dasycladales*. One of his Pacific species, *Acetabularia moebii*, is later described from the Adriatic as *A. wettsteinii* (see Funk 1955: 19). His types are at GOET (?).

Reinke J. (1849-1931). His idea to establish a marine station at Naples was materialized by the Prussian zoologist Anton Dohrn (1840-1909) (Buia & Groeben 1999). Reinke confirms the heteromorphic life history of *Cutleria* (previously partly demonstrated by the Crouans and Derbès & Solier) using material from Naples. He also studies the *Dictyotales* from the same region. Descriptions of new Mediterranean taxa include *Endocladia viridis* (growing on *Derbesia lamourouxii*). His types are at KIEL.

Hauck F. (1849-1889). His early contributions on the Adriatic algae appear in a series of papers published in *Oesterreichische Botanische Zeitschrift* (1875-1879) and later in *Hedwigia* (1887-1888), while between 1882 and 1885 he publishes the algal part in Dr. L. Rabenhorst's *Kryptogamen-Flora 'Die Meeresalgen Deutschlands und Oesterreichs'*. Hauck describes several Adriatic macroalgae, such as *Myrionema liechtensternii*, *Polysiphonia sericea*, *Lithothamnion crispatum*, *Myriotrichia repens* and also blue-greens. His *Lithothamnion mamillosum* Hauck (a later homonym of *L. mamillosum* Gumbel) was given the new name *L. hauckii* (see Woelkerling 1993: 115).

Schmitz F. (1850-1895). His prolific work covers unicellular algae (e.g. *Halosphaera* based on studies at Naples), the green algae of Athens bay, the cytology of *Siphonocladales* (*Valonia*, *Caulerpa*, *Codium*), the reproduction of *Halimeda* and *Squamariaceae* algae, and also the taxonomy and systematics of several red algae (such as *Seirospora*, *Phyllophora*, *Platoma*, *Lophothalia*, and *Rodriguezella*). He describes at least one new Mediterranean species, *Rodriguezella strafforelli*. Schmitz's suprageneric classification of red algae makes the basis for all later consideration. His contribution in Engler & Prantl's 'Die natürlichen Pflanzenfamilien' (1896-1897; some chapters in collaboration with Hauptfleisch or Falkenberg) is outstanding and makes the background for Harald Kylin's 'Die Gattung der *Rhodophyceae*'. His types are at L.

Heydrich F. (1851-1911). He describes some Mediterranean corallines such as *Lithophyllum chalonii* (*Neogoniolithon notarisii*), *Lithophyllum cristatum* f. *ramosissima* (from Algeria) and the genus *Polystrota* (based on *Peyssonnelia compacta* from the Adriatic). His herbarium is considered to be lost (Lamy & Woelkerling in Woelkerling & Lamy 1998: 120).

Berthold G. (1854-1937). One of the first scientists to work at the Marine Biological Station of Naples between 1879 and 1881 with contributions on the taxonomy of *Nemastomataceae*, *Cryptonemiaceae*, *Siphonaceae*, and *Bangiaceae*, the reproduction of *Dasycladus*, *Ectocarpus*, and *Scytosiphon*, and on the local distribution of algae with descriptions of new genera (e.g. *Pseudobryopsis*) and species, such as *Erythrotrichia discigera*, *E. obscura* (both now in *Porphyrostromium*), *Antithamnion elegans* (*Antithamnionella*), *Calosiphonia neapolitana* (*Schmitzia*), *Gymnophylaea pusilla* (*Predaea*), *Ptilocladopsis horrida* (of uncertain status), *Crouania annulata* (*Gulsonia*), *Leathesia cervicornis*, *Myriotrichia protasperococcus*, *Derbesia neglecta*, *Microdictyon spongiola*, and *Bryopsis halymeniae* (shown to represent a stage in the life history of

Bryopsidella). His types are at GOET and KIEL, other material at BRNU, L and at the Zoological Station of Naples (Buia & Groeben 1999).

Ambronn A. (1856-1927). Mediterranean contributions include a study on the morphology of *Herposiphonia tenella* and *H. secunda* from material collected at Naples (Cesati 1882).

Falkenberg P. He was also one of the first scientists to work at the Marine Biological Station of Naples in 1877/78. His monograph 'Die Rhodomelaceen des Golfes von Neapel' (1901) remains a standard reference in the taxonomy of this group. He also describes the new brown algal genus *Discosporangium* [later recognized as a distinct family and order by Schmidt O. C. (1900-1951)] and the new species *Aglaozonia chilosa* (*Cutleria*) confirming its heteromorphic life history (previously observed by Reinke, Derbès & Solier and the Crouans). His types are unknown.

Schiffner V. F. (1862-1944). Bohemian-born Austrian botanist with several contributions on the Adriatic algae, viz. 'Studien über Algen des adriatischen Meeres' (1916), 'Neue und bemerkenswerte Meeresalgen' (1931), and 'Revision von Polysiphonien des algarum Zanardini' (1937). Together with Schussnig, they write the chapter on algae in Rechinger's 'Flora Aegaea' (1943). Together with Biebl, they describe the various types of 'gland cell' of antithamnoid algae. Other algal contributions include a paper on Tunisian algae. His types are at FH, B, HBG and BM; other exsiccatae collections at BM, FH, NY and SI.

Kuckuck E. H. P. (1866-1918) collects extensively in Rovinj and Cherso (between 1894 and 1899; see Munda 2000) and also describes several Mediterranean species such as *Mesogloia reticulata*. The remains of his types are at Helgoland, Biol. Anstalt, while some of his unpublished notes have been recently re-examined by Munda (2000).

Cammerlocher H. (1885-1940). Austrian botanist at Vienna. His publication 'Die Grünalgen der Adria' (1914) is a significant work on both planktonic and multicellular taxa of *Chlorophyta* and *Xanthophyta* (*Vaucheria*) from the Adriatic. His types are at WU and W.

Funk G. (1886-1958). The algological work of Georg Funk includes two important contributions on the seaweeds of Naples, while he was active at the Marine Biological Station between 1909 and 1956 (Buia & Groeben 1999). He describes several new species and varieties such as *Derbesia corallicola*, *D. sirenarum*, *D. attenuata*, *D. minima*, *Scinaia santa-luciana* (= *S. complanata*), *Antithamnion heterocladum*, *Dasya corallicola* (= *Polysiphonia biformis*), *Lomentaria chylocradiella*, *L. verticillata*, *Gastroclonium pygmaeum*, *Cryptonemia longiarticulata*, *Melobesia confervoides*, *Nitophyllum micropunctatum*, *N. rotundum*, *N. gaiolae*, *Ceramium bertholdii*, *Polysiphonia stichidiosa*, *Vickersia canariensis* var. *mediterranea*, *Callithamnion aegagropilae* (= *Callithamniella tingitana*), and also the new genera and species *Pseudocrouania ischiana* and *Dohrniella neapolitana*. He also examines the regeneration and epiphytic-endophytic relationships between algae. His types are at the Marine Biological Station of Naples (Buia & Groeben 1999).

Schussnig B. (1892-1976). Austrian-born botanist with prolific activities at Trieste, Vienna, Maltepe in Constantinople and Jena. His studies include ultrastructure observations on green algal plastids, life histories and cytology of green and red algae (*Cladophora*, *Valonia*, *Codium*, *Wrangelia*) and algal phylogeny. He describes the Mediterranean *Leptonema neapolitanum* (*Leptonematella*), *Acetabularia wettsteinii* (*A. moebii*) and 7 planktonic *Chrysophyta*. His herbarium and types are unknown.

The Scandinavian school

Linné, C. (1707-1778) describes several Mediterranean macroalgae, such as *Fucus volubilis* (*Osmundaria*), *Fucus acinarius* (*Sargassum*), *Fucus pavonicus* (*Padina*), and *Millepora coriacea* (a superfluous name for *Lithophyllum agariciforme*). Some of his coralline collections remain in UPS while most other material is at LINN. Amongst his students: **Solander D.** (1733-1782) has a successful career in Oxford and at the British Museum and together with **Ellis J.** (? 1710-1776) describe several coralline taxa (see below). The Swedish-Finnish **Forsskål P.** (1736-1763) describes *Fucus viscidus* (*Liagora*), from the eastern Mediterranean and *Fucus uvifer* (*Laurencia*?) from

Constantinople. The Swedish-born **Schousboe** P.K.A (1766-1832), who later becomes Danish consul-general in Morocco, collects extensively on the Atlantic and Mediterranean coast of northern Africa. His collections are later studied by Bornet and the material is distributed in various herbaria (such as C, BM, L, LD and PC).

Agardh C. A. (1785-1859). The major bulk of early taxonomic descriptions on algae is published by the bishop Carl Adolph Agardh and his son Jacob Georg Agardh, both active in Lund. They did a limited number of travels outside Scandinavia and they never left Europe but received extensive material from contemporary colleagues such as Schousboe, Bonnemaison, Montagne, Desfontaines, Gaudichaud, Desvaux, Harvey, Hooker, Kützinger, de Bonnay and others. Red algal genera that are described by C. Agardh on the basis of Mediterranean material include *Digenea*, *Alsidium*, *Rytiphlaea*, and *Wrangelia*. During his visit to Tergeste (Trieste) in 1827, he collects material that makes the basis for some 26 descriptions of new Adriatic macroalgae such as *Callithamnion seminudum*, *C. cruciatum* (*Antithamnion*), *Hutchinsia subulifera* (*Polysiphonia*), *H. arachnoidea* (*Polysiphonia*), *H. sanguinea* (*Polysiphonia*), *H. ruchingerii* (*Polysiphonia*), *H. biasoletiana* (*Polysiphonia*), *H. rigens* (*Dipterosiphonia*), *Rytiphlaea pumila*, *Alsidium corallinum*, *Ectocarpus simpliciusculus*, *E. minutus*, *Sphaerococcus curvicornis*, *S. pumila*, *Chondria nana*, *C. furcata*, *C. striolata*, *Das[y]a spinella* (*Eupogodon*), *D. plana* (*Eupogodon*), *Sphaerococcus armatus*, *S. secundus*, *S. divaricatus*, *Halymenia pinnulata*, *Sporochnus verticillatus*, *S. adriaticus*, *Zonaria lineolata* and many unicellular and blue green algae. The descriptions of these and many other Mediterranean taxa such as *Sargassum hornschurchii*, *Griffithsia tenuis* (*Anotrichium*) and *Rhodomela spinosa* are improved in his 'Species Algarum' (1820-28). For example, his account on *Callithamnion cruciatum* reads: «*Callithamnion cruciatum*. Ag. in Bot. Zeit. 1827. p. 637. I have collected it on *Sphaerococcus* in the Adriatic at Trieste and Venice and also have it from the coasts of France and Spain. Tuft interwoven, an inch high. Filaments branched, with branches little ramified, long, at the tip brush-like somewhat club-shaped, in all directions clad with very short ramelli, 1/2 line long, but all alike in size, densely set and approximately imbricate, usually so tight together at the tip of the branches that the almost form a little head there...The fruit I must admit, not discovered with certainty, it is no doubt enclosed in small heads of branches...but then it is analogous with the favellae [cystocraps] of *Callithamnion plumula*...The situation of the ramelli, being difficult to see, is also uncertain. I have seen them in a plane sheet turned towards the stem (that is to say like the spikelets of *Triticum*, not as those of *Lolium* towards the axis).» (Translated by the late Tyge Christensen).

Areschoug J. E. (1811-1887). He describes a few new Mediterranean taxa, such as *Elachista rivulariae* Suhr ex Areschoug from material collected at Ancona and the corallines *Melobesia stictaeformis* (*Lithophyllum*) and *Corallina mediterranea* (*C. elongata*). He also publishes a paper on a few algal collections from Alexandria made by Dr. Hedenborg. His types are at S with duplicates in other Scandinavia herbaria including LD.

Agardh J. G. (1813-1901). Jacob Agardh continues his father's work describing and classifying algae from the entire world. He receives further collections from contemporary colleagues working in the Mediterranean, such as Solier, Biasoletto, Risso, Nardo, Giraudi, and Zanardini. He also visits a few sites in France and Italy, such as Nice, Marseilles and Livorno. He usually cites that on the herbarium collections or in his publications (i.e. «Ipse!» or «...ad Massiliam legi»). In 'Historiam Algarum Symbolae' (1841) he describes several presently well-known Mediterranean species such as *Desmarestia filiformis* (*Nereia*), *Bryopsis secunda*, *Bornetia secundiflora*, *Halymenia multifida* (*Platoma cyclocolpum*?), *Rhodymenia requienii* (*Kallymenia*) from material collected at Tangier, Trieste, Marseilles and other sites in the western basin. Other taxa such as *Rhodymenia polyides* and *Griffithsia opuntia* remain imperfectly known. His 'Algae maris mediterranei et adriatici' (1842) is an important Mediterranean contribution, where several new genera such as *Gloiocladia*, *Zonotrichia*, *Diplotrichia* (all blue-greens), *Liebmannia*, *Crouania*, *Gloiocladia*, *Nemastoma*, *Kallymenia*, *Cryptonemia*, *Chrysomenia*, *Solieria* and many new species and infraspecific taxa are described, such as *Bryopsis myura* (*Pseudobryopsis*), *Mesogloia mediterranea* (*Cladosiphon*), *Bryopsis corymbosa*,

Chylocladia phalligera (*Lomentaria linearis* ?), *Polysiphonia nodulosa*, *Griffithsia phyllamphora*, *G. opuntioidea* and *Bryopsis balbisiana* var. *lamourouxii* (*Pedobesia*). His final classification of many algal groups appears in 'Analecta Algologica' (1892-1896). The parallel work during the 19th century resulted in the publication of many synonyms, creating sometimes nomenclatural problems because of uncertainties regarding the date of publication of papers. Such a case is the several theses of J. Agardh 'In systema algarum hodierna adversaria', in one of which he described several new taxa of *Ceramium*. These theses were defended by his students early in 1844, while in the same year Meneghini described several species of *Ceramium* from the Mediterranean using in some cases the same epithets. Another case is *Asparagopsis* Montagne and *Lictoria* J. Agardh that were both published in 1841 (but with 10 months interval), and both being based on Delile's *Fucus taxiformis* from Alexandria. As his paper was going to press, Agardh found out that Montagne's name was already published and was able to add a footnote explaining the situation. The types of C. and J. Agardh are housed at LD, with duplicates distributed in some other herbaria (GB, C and BM).

Foslie M. H. (1855-1909). Amongst his numerous contributions on the coralline algae (see Woelkerling 1993), Foslie included descriptions of 19 taxa based on Mediterranean material, viz. *Lithophyllum andrussowii* (Sea of Marmara), *Lithophyllum incrustans* f. *angulata* (Banyuls-sur-mer), *Lithothamnion fruticulosum* f. *clavulata* (Val di Bora in the Adriatic), *Lithothamnion fruticulosum* f. *crassiuscula* (Brioni Island in the Adriatic), *Goniolithon tortuosum* f. *decumbens* (Algiers), *Lithophyllum decussatum* f. *decumbens* (Corsica), *Lithophyllum expansum* f. *exigua* (Baie de Side Ferruch, Algeria), *Lithothamnion expansum* f. *foliacea* (Balears), *Lithophyllum inops* (Sea of Marmara), *Lithothamnion macroblastum* (Naples), *Litholepis mediterranea* (Banyuls-sur-mer), *Lithothamnion philippii* (Naples), *Lithothamnion propontidis* (Sea of Marmara), *Lithophyllum cristatum* f. *ramosissima* (Algeria), *Lithophyllum expansum* f. *repens* (Naples), *Lithothamnion fruticulosum* f. *soluta* (Rovinj), *Lithothamnion philippi* f. *subdura* (Brioni Island), *Lithophyllum trabuccoi* (fossil from Italy ?) and *Lithothamnion valens* (Adriatic ?). He also describes the new Adriatic genus *Goniolithon* (based on *G. papillosum*) and the gigartinean species *Peyssonnelia compacta* (*Polystrota*). Foslie's herbarium is at TRH with duplicates in several other herbaria including GB and PC.

Peterson H. E. (1877-1946). He publishes papers on the genera *Ceramium* and *Enteromorpha* and also the report on 'Algae (Excluding calcareous Algae)' (1918) of the Danish oceanographical expeditions 1908-10 to the Mediterranean and adjacent seas. His types are at C.

Kylin H. (1879-1949). He includes numerous Mediterranean species in the following publications on red algae: 'Studien über die Delesseriaceen' (1924), 'Über *Wrangelia penicillata* und ihre systematische Stellung' (1928), 'Über die Entwicklungsgeschichte der Florideen' (1930), 'Die Florideenordnung *Rhodymeniales*' (1931), 'Die Florideenordnung *Gigartinales*' (1932), and in his posthumously published 'Die Gattung der Rhodophyceen' (1956). His types are at LD with duplicates in many Scandinavian herbaria including GB.

Bliding C. (1891-?). He describes certain species of *Ulvaceae* from Naples and Rovinj and also includes material of *Chrysomenia ventricosa* and *C. uvaria* (*Botryocladia botryoides*) (collected by Sjöstedt in Naples) in his 'Stü dien ü ber die Florideenordnung *Rhodymeniales*' (1928).

Sjöstedt L. G. (1894-1975). In his 'Floridean Studies' (1926), he studies several Mediterranean (-Atlantic) species and establishes the genus *Acrosymphyton* (unaware of the earlier name *Helminthopsis* J. Agardh 1899, later considered to be a homonym of *Helminthopsis* Heer 1877). He collects at Mallorca and Naples material of *Dudresnaya coccinea* (*D. verticillata*), *Sebdenia monardiana*, *Sphaerococcus coronopifolius*, *Gigartina teedi* (*Chondracanthus*), *Gracilaria confervoides* (? *Gracilariopsis*) and *Gracilaria compressa* (*G. bursa-pastoris*). He also erects the new order *Sphaerococcales* (to include even *Plocamium* now placed in the order *Plocamiales*) and supports Kylin's *Nemastoma*[ta]les.

Sunesson S. (1904-1997). In his classical coralline studies (see Athanasiadis & Wallentinus 1998), he includes material of *Lithophyllum expansum* (*L. stictaeforme*), *Amphiroa rigida*, and *Choreonema thuretii* from Banyuls-sur-mer. His herbarium is at GB.

Levring T. (1913-1982). He publishes the contribution 'Meeresalgen aus dem Adriatischen Meer, Sizilien und dem Golf von Neapel' (1942), where he describes a new species, *Chantransia mediterranea* (*Acrochaetium*). His herbarium is at GB.

Christensen T. (1918-1996) publishes one paper on the brown alga *Ascocyclus mediterraneus*. His types are at C.

The Anglo-American school

Ellis J. (1711-1776). In 'The Natural History of many curious and uncommon Zoophytes....' (1786; in collaboration with Solander), they describe a few Mediterranean calcified algae such as *Corallina tuna* (*Halimeda*), *Corallina loricata* (status unknown), *Corallina granifera*, *Millepora calcarea* (a later homonym of *M. calcarea* Pallas), *Millepora cervicornis* (with *M. aspera* L. as a synonym and Marsilli's 'Hist. de la Mer, tab. 32. fig- 152' as reference) and *M. tubulosa* (status unknown). His types are considered to be lost.

Greville R. K. (1794-1866). In his 'Some account of a collection of cryptogamic plants from the Ionian Islands' (1826), he describes *Zonaria rubra* (*Peyssonnelia*). His types are at E.

Harvey W. H. (1811-1866). Apart from his enormous contribution to the seaweed floras of the British Isles, North America, Australia and New Zealand, he describes at least one genus, *Spyridia*, based on *S. filamentosa* from the Adriatic and the species *Cryptonemia forbesii* (*Neurocaulon foliosum*) from Paros in the Aegean. His types are at TCD with duplicates at LD and S.

Dixon P.S. (1929-1993). One of the most productive British algologists of the past century with many contributions on the typification of taxa from the British Isles and the Mediterranean Sea. Dixon is anxious to compare original material with topotypes that he sometimes collects himself in parts of the Mediterranean (such as Banyuls and Split). During his active period in Europe, he studies the herbaria of Agardh, Montagne, the Crouans, Bonnemaison, Kützinger and Hauck. His taxonomic research focuses on the red algae and in particular on members of the *Nemaliales* (*Asparagopsis*, *Bonnemaisonia*), *Gelidiales*, *Gigartinales* (*Plocamium*) and *Ceramiales* (*Ptilothamnion*, *Seirospora*, *Ceramium*, *Compsothamnion*, *Sphondylothamnion*, *Dasya*). He also studies the life histories of red algae and proposes the *Liagora tetrasporifera*-type. His 'Biology of the *Rhodophyta*' (1973) remains a standard reference. Numerous other contributions are commemorated by Murray & Scott (1995).

Drew K. M. (1901-1957) visited the Mediterranean in 1951 and collected material at Genoa, Naples and Alexandria. In her papers 'Studies in the Bangioideae I' (1952) and 'Studies in the *Bangiophycidae* IV.' (1957), she compares Mediterranean material of *Bangia* with Welch specimens and reports the presence of genotypic differences in the development of *Conchoecelis*. Her nomenclatural investigations in the *Bangiophyceae* result in the resurrection of the genus *Stylonema* based on a Mediterranean type and including a second Mediterranean species.

Papenfuss G. F. (1903-1981). His prolific studies have peripherally included Mediterranean algae, in most cases with regard to nomenclature (e.g. in the *Acrochaetium-Rhodochorton* complex). Material of *Sphaerococcus* that he collects at Banyuls is included in the gigartinean studies of Searles (1968) who also investigates Mediterranean material of *Caulacanthus*.

Knight M. investigates cytologically the life history of *Ectocarpus siliculosus* from Naples.

The Spanish school

Cabrera A. (1762-1827). Priest at Cádiz and collector. His herbarium at MA has been reviewed by Cremades (1995).

Clemente y Rubio S. de R. (1777-1827). His prolific botanical work ranges from studies on cryptogams and phanerogams to considerations of the algal zonation (Silva 1992). Most of his collections come from Andalusia, especially Gádiz, and many are forwarded to C. Agardh and D. Turner. In 'Ensayo sobre las variedades de la vid común que vegetan en Andalucía, con un índice etimológico y tres listas de plants en que se caracterizan varias especies nuevas' (1807), he describes some 29 new

species. The taxonomic status of many of them has been clarified by Cremades (1993) and Silva (1992); viz. *Conferva delicata* (*Platysiphonia*), *Ulva divaricata* (*Sauvageaugloia*), *Ulva simplicissima* (*Scytosiphon*), *Fucus ambiguus* (*Dictyopteris*), *Fucus stackhousei* (*Helminthocladia* ?), *Fucus plicatus* var. *coccineus* (*Hypnea*), *Ulva muscoides* (*Enteromorpha*), and *Conferva gaditana* (*Ceramium*). His types are at MA.

Rodríguez y Femenías J. J. (1839-1905). Publications on marine algae comprise those of the flora of the Balearic Islands, where he includes descriptions of several new species, viz. *Nitophyllum carneum* (*Myriogramme*), *N. marmoratum*, *N. tristromaticum*, *Neurocaulon grandifolium*, and *Sphaerococcus rhizophylloides*. Some 10 other species remain *nomina nuda* (Seoane-Camba 1969). His main collections are at PC (Seoane-Camba 1969) with other material at L, LD, MS (Gargiulo *et al.* 1999).

Miranda, F. (1905-1964) completes his thesis 'Sobre las algas y Cianofíceas del Cantrá brico, especialmente de Gijón' (1931) and continues with studies in Madrid and Paris. He describes a new species of *Strepsithalia* and also studies certain algal collections from the English Channel 'Remarques sur quelques algues marines des côtes de la Manche' (1932). He emigrates to Mexico in 1939. His herbarium from the Galician and Cantabrian coast has been catalogued by Valenzuela & Pérez-Cirera (1982) and is housed at MA (Cremades & Barbara 1996).

The Yugoslavian and Kroatian schools

Vouk, V. (1886-1962). Eight marine papers are listed in Acta Adriatica's 22th vol. of the 50th anniversary of the Institute of Oceanography and Fisheries at Split, but Vouk's other scientific contributions (mostly on plant and animal physiology) exceed 200 in the biography published by the Yugoslavian Academia in 1986. His contributions on algae cover the physiology and ecology of phytoplankton, blue-greens, while in 'Stüdien über adriatische Codiaceen' (1936) he describes several forms and one new species (*Codium cattaniae*).

Ercegovic, A. (1895-1969). Thirty-seven papers on marine algae are listed in the 50th anniversary volume of the marine station at Split, while some other 80 papers on the physiology and ecology of phytoplankton and blue-greens appear in his biography (Alfirevic 1970). The following publications are on the taxonomy of Adriatic seaweeds: 'Contributo alla conoscenza di alcune alghe nuove o rare della costa orientale dell' Adriatico' (1943), 'Sur quelques algues Phaeophycées peu connues ou nouvelles récoltées dans le bassin de l'Adriatique moyen' (1948), 'Sur quelques algues rouges, rares ou nouvelles, de l'Adriatique' (1949), 'Sur la *Yadranelia*, nouveau genre d'algues de l'Adriatique et sur son développement' (1949), 'Contribution a la connaissance des Ectocarps (*Ectocarpus*) de l'Adriatique moyenne' (1955), 'Contribution a la connaissance des Phaeophycées de l'Adriatique moyenne' (1955), 'Famille des Champiacees (*Champiaceae*) dans l' Adriatique moyenne' (1956), 'La Flore sous-marine de l'ilot de Jabuka' (1957) and 'Contribution a la connaissance de certains genres d'algues rouges en Adriatique' (1963). In these publications he describes five new genera [i.e., *Adriogloia*, *Dalmatogloia*, *Padinopsis* (*Syringoderma* ?), *Pterocladopsis* (status unknown) and *Yadranelia* (*Predaea*)], 36 new species [i.e., *Acrochaetium extensum*, *A. incrassatum*, *Ascocyclus epilithicus*, *Chylocladia pelagosae*, *Desmarestia adriatica*, *Dudresnaya nodulosa* (*Gulsonia nodulosa*), *Ectocarpus adriaticus*, *E. battersiides*, *E. dalmaticus*, *E. geniculatus*, *E. hauckii*, *E. microscopicus*, *E. paradoxoides*, *E. pectenis*, *Endoderma endolithicum*, *E. hirsutum*, *Elachista jabukae*, *Halymenia hvari*, *H. mucosa*, *H. pluriloba*, *H. rhodymenoides*, *H. trabeculata*, *Lomentaria clavaeformis*, *L. jabukae*, *L. subdichotoma*, *L. tenera* (*L. ercegovicii* nom. invalid), *Myriactis microscopica*, *Nemastoma constrictum*, *Nitophyllum flabellatum*, *Peyssonnelia magna*, *Phaeosporium clavatum*, *Phyllophora fimbriata*, *Pseudochlorodesmis tenuis*, *Pseudodictyon inflatum*, *P. reticulatum*, and *Rodriguezella pennata*], several new forms and five new varieties (i.e., *Crouania attenuata* var. *maior*, *Nemastoma constrictum* var. *longitrichogynum*, *Rhodymenia corallicola* var. *robustior*, *R. corallicola* var. *torta* and *Spermatochmus paradoxus* var. *adriaticus*). His herbarium remains unlocated.

The Israeli and Egyptian schools

Rayss T. (1890-1965) publishes contributions on the genus *Caulerpa* and other green algae from the coast of Palestina but also on the occurrence of certain rare members of *Areschougaceae*. Her papers on Red Sea algae appear in Papenfuss's 'A history, catalogue, and bibliography of Red Sea benthic algae' (1968).

Nasr A. H. (1908-?). Professor at the University of Alexandria. Between 1938 and 1968, he publishes numerous taxonomic contributions on the marine algae of Red Sea and Alexandria, as also papers on the physiology and ecology of certain Mediterranean seaweeds. His Alexandrian records are catalogued by Aleem (see below) while the Red Sea records appear in Papenfuss's (1968) catalogue.

Aleem A. A. (1918-1996). In his 'Marine Algae of Alexandria' (1993), over 100 listed publications cover the study of algae in various aspects. In his early years he studies diatoms, blue-greens and marine fungi, taking advantage of his visits to laboratories in Europe and Scandinavia. He later focuses on the marine algae and seagrasses of the eastern Mediterranean and the Red Sea. Two of his papers, 'The recent migration of certain Indo-Pacific algae from the Red Sea into the Mediterranean' (1948) and 'Some new records of marine algae from the Mediterranean Sea' (1950) are classical and frequently cited.

The modern Greek school starts with the botanist Th. **Orphanides** who collects algae around 1857-62. The first paper on the local flora, 'Beiträge zur Kenntnis der Algenvegetation von Griechenland: I. Die Meeressalgen der Insel Sciathos' (1887), is published by S. **Miliarakis**. Between 1928 and 1953, J. **Politis** contributes with several papers (most in form of check-lists) on the marine algae of the North and South Aegean, Crete, Cyprus and the Sea of Bosphorus. Katsikopoulos publishes a checklist on the 'Algues marines d'Alexandroupolis' (1939). **Anagnostidis, K.** (1924-1994) extensively studies the blue-greens, especially from hot springs and includes a catalogue of North Aegean seaweeds in his thesis 'Untersuchungen über die Salz- und Süßwasser-Thiobiocöten (Sulphuretum) Griechenlands' (1968).

The Russian school

Gmelin J. G. (1709-1755). In his 'Historia fucorum' (1768), he describes some presently well-known Mediterranean species, such as *Fucus capillaceus* (*Pterocladia*), *Fucus squamarius* (*Peyssonnelia*) and *Fucus baillouvianus* (*Dasya*). Several other Mediterranean taxa of his remain unclarified (e.g. *Fucus serra*, type locality: Proti Island, Ionian Sea; and *Fucus salicifolius*, type locality: Rodosto). His types are at LE.

Appendix II. The classification of Rhodophyta as proposed by Kylin (1956), Kraft & Wynne (1981) and Kraft (1981), and the latest data. Nomenclatural corrections are applied retroactively. The Kylinian classification appears in bold or in parenthesis. Question marks indicate uncertain position within respective group. Underlined genera are reported from the Mediterranean Sea. The arrangement of taxa is alphabetically except of classes, orders, and tribes (in the Ceramiales) that is systematically.

TAXA ¹	GENERA(SPECIES)		
	Kylin	K & W	Present
CYANIDIOPHYCEAE			
CYANIDIACEAE			3
<i>Cyanidioschyzon</i> , <i>Cyanidium</i> , <i>Galdieria</i>			
BANGIOPHYCEAE (Bangioideae)	24(94)	31(110)	34
PORPHYRIDIALES (& Goniotracheales)			21
PORPHYRIDIAEAE (& Goniotracheae)	11(20)	12	15
<i>Bangiopsis</i> (Goniotracheae), <i>Chroodactylon</i> (Goniotracheae),			
<i>Chrootheca</i> , <i>Colacodictyon</i> , <i>Dicomiella</i> , <i>Flintiella</i> , <i>Glaucosphaera</i> ,			
<i>Goniotracheopsis</i> (Goniotracheae), <i>Petrovianella</i> , <i>Porphyridium</i> ,			
<i>Rhodella</i> , <i>Rhodorus</i> , <i>Rhodospira</i> , <i>Stylonema</i> (Goniotracheae),			
<i>Vanhoeffenia</i>			

PHRAGMONEMATACEAE (Goniotrichales)	4(5)	7	6
<i>Cyanoderma</i> , <i>Empselium</i> , <i>Kneuckeria</i> , <i>Kyliniella</i> , <i>Neevea</i> (Goniotrichaceae), <i>Phragmonema</i>			
ERYTHROPELTIDALES			
ERYTHROTRICHACEAE (Erythropeltidaceae, Bangiales)	4(26)	6	7
<i>Erythrocladia</i> , <i>Erythrotrichia</i> , <i>Membranella</i> , <i>Porphypopsis</i> , <i>Porphyrostromium</i> , <i>Sahlingia</i> , <i>Smithora</i> (Bangiaceae)			
COMPSOPOGONALES			
COMPSOPOGONACEAE	1(8)	2	2
<i>Compsopogon</i> , <i>Compsopogonopsis</i>			
BANGIALES			
BANGIACEAE	3(34)	3	2
<i>Bangia</i> , <i>Porphyra</i>		2	
BOLDIACEAE		1	1
<i>Boldia</i>			
RHODOCHAETACEAE	1(1)	1(1)	1(1)
<i>Rhodochaete</i>			
FLORIDEOPHYCEAE (Florideae)	547(3515)	637(3990)	791
<i>Aiolocolax</i> , <i>Chalicostroma</i> (?), <i>Dorella</i> (?), <i>Endosira</i> (?), <i>Estebania</i> (?), <i>Gracilariocolax</i> (?), <i>Herpophyllum</i> (?), <i>Liagorothamnion</i> , <i>Perinema</i> (?), <i>Rhododiplobia</i> , <i>Tiarophora</i> (?)			
HILDENBRANDIALES			
HILDENBRANDIACEAE (Cryptonemiales)	1(10)	2(11)	2
<i>Apophloea</i> (?), <i>Hildenbrandia</i>			
CORALLINALES ²	36(410)	50(500)	44
CORALLINACEAE (Cryptonemiales)			40
CORALLINOIDEAE (Corallina-group)			12
<i>Alatocladia</i> , <i>Arthrocardia</i> , <i>Bossiella</i> , <i>Calliarthron</i> , <i>Cheilosporum</i> , <i>Chiharaea</i> , <i>Corallina</i> , <i>Halipitlon</i> , <i>Jania</i> , <i>Marginisporum</i> , <i>Serraticardia</i> , <i>Yamadaea</i>			
LITHOPHYLLOIDEAE (Lithophyllum-group)			7
<i>Amphiroa</i> (Corallina-g), <i>Ezo</i> , <i>Goniolithon</i> , <i>Lithophyllum</i> , <i>Lithothrix</i> (Corallina-g), <i>Tenarea</i> , <i>Titanoderma</i>			
MASTOPHOROIDEAE (Lithophyllum-group)			9
<i>Fosliella</i> , <i>Hydrolithon</i> , <i>Lesueuria</i> , <i>Lithoporella</i> , <i>Mastophora</i> , <i>Metamastophora</i> , <i>Neogoniolithon</i> , <i>Pneophyllum</i> (?), <i>Spongites</i>			
MELOBESIOIDEAE (Lithothamnion-group)			11
<i>Choreonema</i> (Lithophyllum-g), <i>Clathromorphum</i> , <i>Exilicrusta</i> , <i>Kvaleya</i> , <i>Leptophyllum</i> , <i>Lithothamnion</i> , <i>Mastophoropsis</i> , <i>Melobesia</i> (Lithophyllum-g), <i>Mesophyllum</i> , <i>Phymatolithon</i> , <i>Synarthrophyton</i>			
METAGONIOLITHOIDEAE (Corallina-group)			1
<i>Metagoniolithon</i>			
AUSTROLITHACEAE			2
<i>Austrolithon</i> , <i>Boreolithon</i>			
SPOROLITHACEAE (Sporolithon-group)			2
<i>Heydrichia</i> , <i>Sporolithon</i>			
RHODOGORGONALES			
RHODOGORGONACEAE			2
<i>Renouxia</i> , <i>Rhodogorgon</i>			
BALLIALES			
BALLIACEAE			1
<i>Ballia</i> (Crouania-g)			
BATRACHOSPERMALES			9
<i>Balliopsis</i>			
BATRACHOSPERMACEAE (Nemaliales)	5(59)		4
<i>Batrachospermum</i> , <i>Nothocladus</i> , <i>Sirodotia</i> , <i>Tuomeya</i>			
LEMANEACEAE (Nemaliales)	1(15)		4
<i>Lemanea</i> , <i>Paralemanea</i> , <i>Pseudochantransia</i> , <i>Psilosiphon</i>			
THOREALES			
THOREACEAE (Nemaliales)	2(8)		2
<i>Nemalionopsis</i> , <i>Thorea</i>			
BALBIANALES			
BALBIANIACEAE			2
<i>Balbiantia</i> , <i>Rhododraparnaldia</i>			
ACROCHAETIALES			
ACROCHAETIACEAE (Nemaliales)	8(166)	1	7
<i>Acrochaetium</i> , <i>Audouinella</i> , <i>Colaconema</i> , <i>Kylinia</i> , <i>Liagorophila</i> , <i>Rhodochorton</i> , <i>Rhodochortonopsis</i> (?)			
NEMALIALES (incl. Batrachospermales, Thoreales, Acrochaetiales & Bommemaisoniales)	39(462)	48(600) ³	27
LIAGORACEAE	8(88)	13(101) ⁴	15
<i>Cumagloia</i> , <i>Cylindraxius</i> , <i>Dermonema</i> , <i>Dotyophycus</i> , <i>Ganonema</i> , <i>Gloiotrichus</i> , <i>Helminthocladia</i> , <i>Helminthora</i> , <i>Liagora</i> , <i>Liagoropsis</i> , <i>Nemalion</i> , <i>Patenocarpus</i> , <i>Trichogloea</i> , <i>Trichogloeopsis</i> , <i>Yamadaella</i>			
GALAXAURACEAE	7(102)	8(80)	9
<i>Actinotrichia</i> , <i>Galaxaura</i> , <i>Gloiophloea</i> , <i>Nothogenia</i>			

<i>Pseudogloiothlella</i> , <i>Pseudoscinaia</i> , <i>Scinaia</i> , <i>Tricleocarpa</i> , <i>Whidbeyella</i>			
NACCARIACEAE	3(4)	2	3
<i>Atractophora</i> , <i>Naccaria</i> , <i>Reticulocaulis</i>			
PALMARIALES			14
PALMARACEAE		4(15)	4
<i>Devaleracea</i> , <i>Halosaccion</i> (Rhodymeniaceae), <i>Neohalosaccitocolax</i> , <i>Palmaria</i>			
RHODOPHYSEMATAEAE			8
<i>Coriophyllum</i> (Peyssonneliaceae), <i>Halosaccitocolax</i> , <i>Meiodiscus</i> , <i>Pulvinaria</i> , <i>Pseudorhododiscus</i> , <i>Reingardia</i> , <i>Rhodophysemma</i> , <i>Rhodophysemopsis</i>			
RHODOTHAMNIELLACEAE			2
<i>Camontagnea</i> , <i>Rhodothamniella</i>			
AHNFELTIALES			
AHNFELTIACEAE (Phylloporaceae, Gigtrinales)			1
<i>Ahnfeltia</i>			
CERAMIALES (incl. Balliales)	252(1328)	325(1500)	382
CERAMIACEAE	69(396)	105(500)	129
<i>Callidictyon</i> , <i>Episporium</i> (?), <i>Inkyulea</i> , <i>Mortensenia</i> (?), <i>Perischetia</i> (?), <i>Pterocladopsis</i> , <i>Ptilocladopsis</i> (?), <i>Scagelionema</i> , <i>Siegrafia</i> , <i>Spencerella</i> (?)			
CALLITHAMNIOIDEAE			
WARRENIEAE			1
<i>Warrenia</i> (Crouania-g)			
DELESSERIOPSEAE			2
<i>Balliella</i> , <i>Delesseriopsis</i> (?)			
HALOSIEAE			1
<i>Halosia</i>			
PLUMARIELLEAE			1
<i>Plumariella</i> (Ptilota-g)			
PTILOTEAE (Ptilota-group)	10(20)		10
<i>Dasyptilon</i> , <i>Diapse</i> , <i>Euptilota</i> , <i>Falklandiella</i> , <i>Georgiella</i> , <i>Neoptilota</i> , <i>Plumaria</i> , <i>Plumariopsis</i> , <i>Ptilota</i> , <i>Tokidaea</i>			
GYMNOTHAMNIEAE			1
<i>Gymnothamnion</i> (Ptilota-g)			
CALLITHAMNIEAE (Callithamnion-group)	5(67)		7
<i>Aglaothamnion</i> , <i>Aristothamnion</i> , <i>Callithamnion</i> , <i>Carpothamnion</i> , <i>Hirsutiathalia</i> , ? <i>Pseudospora</i> , <i>Seirospora</i>			
MONOSPORAEE			7
<i>Anisochizus</i> , <i>Desikacharyella</i> , <i>Deucalion</i> , <i>Guiryella</i> , <i>Mazoyerella</i> , <i>Monosporus</i> (Griffithsia-g), <i>Tanakaella</i>			
ANTARCTICOTHAMNIEAE			1
<i>Antarcticothamnion</i>			
LASIOTHALIEAE			1
<i>Lasiothalia</i> (?)			
COMPSOTHAMNIEAE (Compsothamnion-group)	7(19)		6
<i>Compsothamnion</i> , <i>Compsothamnionella</i> , <i>Dasythamnionella</i> , <i>Gymnophycus</i> , <i>Haloplegma</i> , <i>Rhododictyon</i>			
SPONGOCOLONIEAE (Callithamnion-group)			3
<i>Lophothamnion</i> , <i>Pleonosporium</i> , <i>Spongoclonium</i>			
RHODOCALLEAE (Dasyphila-group)			2
<i>Rhodocallis</i> , <i>Psilothalia</i>			
RADIATHAMNIEAE			3
<i>Laurenciophila</i> , <i>Ochmapexis</i> , <i>Radiathamnion</i>			
SPERMOTHAMNIEAE (Spermothamnion-group)	6(26)		9
<i>Gordoniella</i> , <i>Interthamnion</i> , <i>Lejolisia</i> , <i>Lomathamnion</i> , <i>Ptilothamnion</i> , <i>Ptilothamnionopsis</i> , <i>Rhipidothamnion</i> , <i>Spermothamnion</i> , <i>Tiffaniella</i>			
CERAMIOIDEAE			
PTEROTHAMNIEAE			1(26)
<i>Pterothamnion</i> (Crouania-g)			
SCAGELIEAE			1(2)
<i>Scagelia</i>			
SCAGELOTHAMNIEAE			1(1)
<i>Scagelothamnion</i>			
DOHRNIELLEAE (Dohrniiella-group)	3(4)		6(31)
<i>Acrothamnionopsis</i> , <i>Antithamnionella</i> (Crouania-g), <i>Callithamnionella</i> , <i>Dohrniiella</i> , <i>Irtugovia</i> , <i>Trithamnion</i>			
ANTITHAMNIEAE (Crouania-group)			5(41)
<i>Acrothamnion</i> , <i>Antithamnion</i> , <i>Hollenbergia</i> , <i>Macrothamnion</i> , <i>Perikladosporon</i>			
PERITHAMNIEAE			2(3)
<i>Perithamnion</i> , <i>Scageliopsis</i>			
CERAMIEAE (Ceramium-group)	10(87)		16
<i>Amoenothamnion</i> , <i>Ardreanema</i> , <i>Boryna</i> , <i>Campylaeophora</i> , <i>Carpoblepharis</i> (Delesseriaceae), <i>Centroceras</i> , <i>Ceramium</i> , <i>Corallophila</i> , <i>Gungroceras</i> , <i>Herpochondria</i> , <i>Leptokionion</i> , <i>Microcladia</i> , <i>Reinholdiella</i> , <i>Symphodothamnion</i> , <i>Syringocolax</i> , <i>Centrocerocolax</i>			
HETEROTHAMNIEAE			3(8)
<i>Elisiella</i> , <i>Heterothamnion</i> (Crouania-g), <i>Tetrathamnion</i>			
CROUANIEAE (Crouania-group)	12(75)		7
<i>Crouania</i> , <i>Crouanophycus</i> , <i>Euptilocladia</i> , <i>Gattyia</i> , <i>Gulsonia</i> , <i>Pseudocrouania</i> , <i>Ptilocladia</i>			
DASYPHILEAE (Dasyphila-group)	3(7)		2
<i>Dasyphila</i> , <i>Muellerena</i> (?)			
SPYRIDIEAE (Spyridia-group)	1(15)		2
<i>Spyridia</i> , <i>Spyridiocolax</i>			

WRANGELIEAE (Wrangelia-group)	1(25)	2
<i>Grallatoria</i> (Cronania-g), <i>Wrangelia</i>		
GRIFFITHSIEAE (Griffithsia-group)	3(42)	6
<i>Anotrichum</i> , <i>Baldockia</i> , <i>Griffithsia</i> , <i>Halurus</i> , <i>Calliclavula</i> , <i>Ossiella</i>		
BORNETIEAE		1
<i>Bornetia</i> (Spermothamnion-g)		
SPHONDYLOTHAMNIEAE (Spermothamnion-group)		9
<i>Diplothamnion</i> , <i>Dreviana</i> , <i>Involucrana</i> , <i>Mediothamnion</i> , <i>Nwynea</i> , <i>Shepleya</i> , <i>Sphondylothamnion</i> , <i>Wollastoniella</i> , <i>Vickersia</i>		
DELESSERIAEAE	67(260)	86(300) 96
<i>Arachnophyllum</i> (?), <i>Sorellocolax</i> , <i>Nienburgiella</i>		
DELESSERIOIDEAE		1
APOGLOSSEAE		1
<i>Apoglossum</i> (Delesseria-g)		
BOTRYOCARPEAE		1
<i>Botryocarpa</i> (Hypoglossum-g)		
CALOGLOSSEAE (Caloglossa-group)	1(6)	2
<i>Caloglossa</i> , <i>Taenioma</i> (Sarcomenia-g)		
CLAUDEAE (Claudea-group)	4(8)	2
<i>Claudea</i> , <i>Vanvoorstia</i>		
CONGREGATOCARPEAE		3
<i>Congregatocarpus</i> , <i>Neohypophyllum</i> (Yendonia-g), <i>Tokidadendron</i>		
CUMATHAMNIEAE		1
<i>Cumathamnion</i>		
DELESSERIEAE (Delesseria-group & Membranoptera-group)	3(20)	14
<i>Apoglossocolax</i> , <i>Austrofolium</i> , <i>Delesseria</i> , <i>Holmesia</i> (Membranoptera-g), <i>Membranoptera</i> (Membranoptera-g), <i>Microrhinus</i> (Membranoptera-g), <i>Neoholmesia</i> , <i>Odontolaingia</i> , <i>Pantoneura</i> (Membranoptera-g), <i>Paraglossum</i> , <i>Phycodrina</i> , <i>Pseudolaingia</i> , <i>Heteroglossum</i> , <i>Pseudogrinnellia</i>		
DICROGLOSSEAE		1
<i>Dicroglossum</i>		
GRINNELLIEAE (Grinnellia-g)		1
<i>Grinnellia</i>		
HEMINEUREAE (Hemineura-group)	1(3)	4
<i>Hemineura</i> , <i>Laingia</i> (Hypoglossum-g), <i>Marionella</i> , <i>Patulophycus</i>		
HYPOGLOSSEAE (Hypoglossum-g)	7(29)	12
<i>Bartoniella</i> , <i>Branchioglossum</i> , <i>Chauviniella</i> , <i>Frikkiella</i> , <i>Hypoglossum</i> , <i>Duckerella</i> , <i>Phitycolax</i> , <i>Phitymophora</i> , <i>Pseudobranchioglossum</i> , <i>Tsengiella</i> , <i>Yoshidaphycus</i> , <i>Zellera</i> (Claudea-g)		
SARCOMENAEAE (Sarcomenia-group)	5(13)	6
<i>Cottoniella</i> , <i>Dotyella</i> , <i>Malacoenema</i> , <i>Platysiphonia</i> , <i>Sarcomenia</i> , <i>Sarcotrichia</i>		
SYMPODOPHYLLEAE		1
<i>Sympodophyllum</i>		
ZINOVAEAE		2
<i>Kurogia</i> , <i>Zinovaea</i>		
NITOPHYLOIDEAE		
CRYPTOPLEYREAE (Cryptopleura-group)	6(43)	5
<i>Acrosorium</i> , <i>Botryoglossum</i> , <i>Cryptopleura</i> , <i>Gonimophyllum</i> , <i>Hymenena</i>		
MARTENSIEAE (Martensia-g)	2(11)	2
<i>Martensia</i> , <i>Opephyllum</i>		
NITOPHYLLEAE (Nitophyllum- & Valeriemaya-group)	1(5)	6
<i>Calonitophyllum</i> (Valeriemaya-g), <i>Nitophyllum</i> , <i>Polyneurella</i> (Phycodrys-g), <i>Polyneuropsis</i> (Valeriemaya-g), <i>Radicilingua</i> (Phycodrys-g), <i>Valeriemaya</i> (Valeriemaya-g)		
PAPENFUSSIA (Papenfussia-group)	1(2)	1
<i>Papenfussia</i>		
PSEUDOPHYCODRYEAE (Pseudophycodrys-group)		2
<i>Pseudophycodrys</i> , <i>Pseudonitophylla</i>		
PHYCODYOIDEAE		
MYRIOGRAMMEAE (Myriogramme-g)	7(45)	5
<i>Gonimocolax</i> , <i>Haraldiophyllum</i> , <i>Hidecophyllum</i> , <i>Myriogramme</i> , <i>Platyclinia</i>		
PHYCODYEAE (Phycodrys-g)	15(42)	16
<i>Anisocladella</i> , <i>Asterocolax</i> , <i>Calloseris</i> , <i>Cladodonta</i> , <i>Crassilingua</i> , <i>Erythroglossum</i> , <i>Halicnide</i> , <i>Haraldia</i> , <i>Heterodoxia</i> , <i>Mikamiella</i> , <i>Nienburgia</i> , <i>Phycodrys</i> , <i>Polyneura</i> , <i>Sorella</i> , <i>Womersleya</i> , <i>Yendonia</i> (Yendonia-g)		
SCHIZOSERIDEAE (Myriogramme-g)		5
<i>Abroteia</i> , <i>Drachiella</i> , <i>Neuroglossum</i> , <i>Polycoryne</i> , <i>Schizoseris</i>		
DASYACEAE	14(105)	12(100) 18
<i>Amphisbetema</i> , <i>Colacodasya</i> , <i>Dasya</i> , <i>Dasyella</i> , <i>Dasyisiphonia</i> , <i>Dictyurus</i> , <i>Dipterocladia</i> , <i>Endogenia</i> (?), <i>Eupogodon</i> , <i>Halydictyon</i> (?), <i>Haplodasya</i> , <i>Heterosiphonia</i> , <i>Nematophora</i> (?), <i>Pogonophorella</i> , <i>Rhodopitulum</i> , <i>Sinosiphonia</i> , <i>Tapeinodasya</i> , <i>Thuretia</i>		
RHODOMELACEAE	102(567)	124(650) 139
<i>Abbottella</i> , <i>Dawsoniella</i> , <i>Digeneopsis</i> , <i>Dipterocolax</i> , <i>Ditria</i> , <i>Erythrostachys</i> , <i>Exophyllum</i> (?), <i>Hawaii</i> , <i>Heterostroma</i> , <i>Laurencicolax</i> , <i>Lynkiella</i> , <i>Melanothamnus</i> (?), <i>Moridiocolax</i> , <i>Pycnothamnion</i> , <i>Trichidium</i> , <i>Wilsonaea</i> (?)		
AMANSIEAE (Amansia-group)	11(45)	14
<i>Adamsiella</i> , <i>Amansia</i> , <i>Enantiocladia</i> , <i>Epiglossum</i> , <i>Geraldia</i> , <i>Halopinys</i>		

<i>Kuetzingia</i> , <i>Lenormandia</i> , <i>Lenormandiopsis</i> , <i>Melanamansia</i> , <i>Neurymenia</i> , <i>Osmundaria</i> , <i>Protokuetzingia</i> , <i>Rytiphlaea</i>			
BOSTRYCHIEAE (<i>Bostrychia</i> -group)	1(25)		2
<i>Bostrychia</i> , <i>Stictosiphonia</i> (?)			
BRONGNIARTELLAEAE			8
<i>Brongniartella</i> (<i>Lophothalia</i> -g), <i>Heterodasya</i> , <i>Micropeuce</i> (<i>Lophothalia</i> -g), <i>Murrayellopsis</i> , <i>Rhodolophia</i> (<i>Lophothalia</i> -g), <i>Schizochlaenion</i> , <i>Thaumatella</i> (<i>Lophothalia</i> -g), <i>Velerua</i> (<i>Lophothalia</i> -g)			
CHONDRIEAE (<i>Chondria</i> -group)	8(42)		10
<i>Acanthophora</i> , <i>Acrocystis</i> , <i>Chondria</i> , <i>Cladhymenia</i> , <i>Cladurus</i> , <i>Coeloclonium</i> , <i>Dolichoscelis</i> , <i>Jantiniella</i> , <i>Rhododactylis</i> , <i>Waldoia</i>			
HERPOSIPHONIEAE (& <i>Placophora</i> -group)	8(36)		9
<i>Amphisiphonia</i> (<i>Placophora</i> -g), <i>Dipterosiphonia</i> , <i>Herposiphonia</i> , <i>Herpopteros</i> , <i>Jeannerettia</i> , <i>Metamorphe</i> , <i>Oligocladella</i> (<i>Lophosiphonia</i> -g), <i>Periphykon</i> (<i>Placophora</i> -g), <i>Placophora</i> (<i>Placophora</i> -g)			
HETEROCLADIEAE			2
<i>Heterocladia</i> (?), <i>Trigenea</i> (?)			
LAURENCIEAE (<i>Laurencia</i> -group)	4(91)		6
<i>Chondrophycus</i> , <i>Erythrocytis</i> , <i>Janczewskia</i> , <i>Laurencia</i> , <i>Osmundea</i> , <i>Rodriguezella</i>			
Levringiella-group	7(10)		7
<i>Benzaitenia</i> , <i>Chamaethamnion</i> , <i>Colacops</i> , <i>Jantiniella</i> , <i>Levringiella</i> , <i>Stromatocarpus</i> , <i>Tylocolax</i>			
LOPHOSIPHONIEAE (<i>Lophosiphonia</i> -group)	6(14)		5
<i>Ctenosiphonia</i> , <i>Falkenbergiella</i> , <i>Lophosiphonia</i> , <i>Ophidocladus</i> , <i>Stichothamnion</i>			
LOPHOTHALIEAE (<i>Lophothalia</i> -group)	14(29)		13
<i>Antarctocolax</i> , <i>Doxodasya</i> , <i>Endosiphonia</i> , <i>Gonatogenia</i> , <i>Holotrichia</i> , <i>Lophocladia</i> , <i>Lophothalia</i> , <i>Murrayella</i> , <i>Onychocolax</i> , <i>Pachychaeta</i> (<i>Polysiphonia</i> -g), <i>Spirocladia</i> , <i>Spirophycus</i> , <i>Wrightiella</i>			
Picconella-group	3(4)		3
<i>Ardissoula</i> , <i>Picconella</i> , <i>Sporoglossum</i>			
PLEUROSTICHIDIEAE (<i>Pleurostichidium</i> -group)	1(1)		1
<i>Pleurostichidium</i>			
POLYSIPHONIEAE (<i>Polysiphonia</i> -group)	18(190)		20
<i>Alsidium</i> , <i>Aphanocladia</i> (<i>Pterosiphonia</i> -g), <i>Bryocladia</i> , <i>Bryothamnion</i> , <i>Carradoriella</i> , <i>Chiracanthia</i> , <i>Digenea</i> , <i>Diptocladia</i> , <i>Echinotamnion</i> , <i>Enelittosiphonia</i> , <i>Fernadosiphonia</i> (<i>Streblotocladia</i> -g), <i>Leptosiphonia</i> , <i>Lophurella</i> , <i>Neosiphonia</i> , <i>Orcasia</i> , <i>Phaeocolax</i> , <i>Pityophykos</i> , <i>Polysiphonia</i> , <i>Tolypocladia</i> , <i>Womersleyella</i>			
POLYZONIEAE (<i>Polyzonia</i> -group)	6(15)		6
<i>Cliftonaea</i> , <i>Dasyclonium</i> , <i>Echinosporangium</i> , <i>Euzonia</i> , <i>Leveillea</i> , <i>Polyzonia</i>			
PTEROSIPHONIEAE (<i>Pterosiphonia</i> -group)	5(32)		8
<i>Dictyomenia</i> , <i>Kintarosiphonia</i> , <i>Pterochondria</i> , <i>Pterosiphonia</i> , <i>Pterosiphoniella</i> (?), <i>Rhodomelopsis</i> , <i>Symphocladia</i> , <i>Tayloriella</i> (<i>Polysiphonia</i> -g)			
RHODOLACHNEAE			1
<i>Rhodolachne</i>			
RHODOMELEAE (<i>Rhodomela</i> -group)	2(15)		4
<i>Beringiella</i> , <i>Neorhodomela</i> , <i>Odonthalia</i> , <i>Rhodomela</i>			
SONDERELLEAE			2
<i>Lembergia</i> , <i>Sonderella</i> (<i>Sarcomenia</i> -g)			
<i>Streblotocladia</i> -group	3(8)		2
<i>Microcolax</i> , <i>Streblotocladia</i>			
BONNEMAISONIALES			
BONNEMAISONIACEAE (<i>Nemaliales</i>)	5(20)	6(22)	6
<i>Asparagopsis</i> , <i>Bonnemaisonia</i> , <i>Delisea</i> , <i>Leptophyllis</i> , <i>Pleuroblepharidella</i> , <i>Ptilonia</i>			
GELIDIALES	11(70)	10(136)	14
GELIDIACEAE	11(70)	9(115)	13
<i>Acanthopeltis</i> , <i>Acropeltis</i> , <i>Beckerella</i> , <i>Capreolia</i> , <i>Gelidium</i> , <i>Onitkusa</i> , <i>Porphyroglossum</i> , <i>Pterocladia</i> , <i>Pterocladiastrum</i> , <i>Pterocladella</i> , <i>Ptilophora</i> , <i>Suhria</i> , <i>Yatabella</i>			
GELIDIELLACEAE (<i>Gelidiaceae</i>)		1(21)	1
<i>Gelidiella</i>			
GIGARTINALES (incl. <i>Ahnfeltiales</i> , <i>Gracilariales</i> , <i>Plocamiales</i> & <i>Cryptonemiales</i> p.p. 83(645)100(700))		184	
<i>Sterrocladia</i> (<i>Nemaliales</i>)			
ACROSYMPHYTACEAE			1
<i>Acrosymphyton</i> (<i>Dumontiaceae</i> , <i>Cryptonemiales</i>)			
ACROTYLACEAE	4(4)	4(6)	7
<i>Acrotytus</i> , <i>Amphiplexia</i> , <i>Antrocentrum</i> , <i>Clavicolonium</i> , <i>Hennedya</i> , <i>Ranavalona</i> , <i>Reinboldia</i>			
ARESHOUGIACEAE (<i>Solieriaceae</i>)	14(65)	15(50)	25
<i>Agardhiella</i> , <i>Anatheca</i> , <i>Areschougia</i> (<i>Rhabdoniaceae</i>), <i>Betaphycus</i> , <i>Callophycus</i> , <i>Erythroclonium</i> (<i>Rhabdoniaceae</i>), <i>Encheuma</i> , <i>Euryomma</i> , <i>Flahaultia</i> , <i>Gardneriella</i> , <i>Kappaphycus</i> , <i>Lukinia</i> , <i>Melanema</i> , <i>Meristiella</i> , <i>Meristotheca</i> , <i>Notophycus</i> , <i>Opuntiella</i> , <i>Placentophora</i> , <i>Rhabdonia</i> (<i>Rhabdoniaceae</i>), <i>Reticulobotrys</i> , <i>Sarcoditheca</i> , <i>Sarconema</i> , <i>Solieria</i> , <i>Tikvahiella</i> , <i>Turnerella</i>			
BLINKSIACEAE		1(1)	1
<i>Blinksia</i>			

CALOSIPHONACEAE	2(3)	2(4)	2
<i>Calosiphonia</i> , <i>Schmitzia</i>			
CAULACANTHACEAE		11(30)	7
<i>Catenella</i> (Rhabdoniaceae), <i>Catenellocolax</i> (Rhabdoniaceae), <i>Caulacanthus</i> (Sphaerococcaceae), <i>Feldmannophycus</i> , <i>Heringia</i> (Sphaerococcaceae), <i>Montemaria</i> , <i>Taylorophycus</i>			
CHONDRIELLACEAE	1(1)	1(1)	1
<i>Chondriella</i>			
CHOREOCOLACEAE (Cryptonemiales)	2(3)	4(9)	5
<i>Bostrychocolax</i> , <i>Choreocolax</i> , <i>Dawsonicolax</i> , <i>Harveyella</i> , <i>Leachiella</i>			
CORYNOMORPHACEAE	1(2)		1
<i>Corynomorpha</i> (Halymeniaceae, Cryptonemiales)			
CROSSOCARPACEAE			7
<i>Beringia</i> , <i>Cirrularcarpus</i> , <i>Crossocarpus</i> , <i>Hommersandia</i> , <i>Ionia</i> , <i>Kallymeniopsis</i> , <i>Velatocarpus</i>			
CRUORIACEAE	4(20)	1	1
<i>Cruoria</i>			
CUBICULOSPORAEEAE		1(1)	1
<i>Cubiculosporum</i>			
CYSTOCLONACEAE (& Stictosporaceae)	8(35)	10(35)	10
<i>Acanthococcus</i> , <i>Austroclonium</i> , <i>Calliblepharis</i> , <i>Craspedocarpus</i> , <i>Cystoclonium</i> , <i>Erythronema</i> , <i>Fimbriifolium</i> , <i>Gloiophyllis</i> , <i>Rhodophyllis</i> , <i>Stictosporum</i> (Stictosporaceae)			
DICRANEMATACEAE	1(2)	4(5)	5
<i>Dicranema</i> , <i>Peltasta</i> (?), <i>Reptataxis</i> , <i>Tenaciphyllum</i> , <i>Tylotus</i> (Gracilariaceae)			
DUMONTIACEAE (Cryptonemiales)	14(32)	16(46)	18
<i>Constantinea</i> , <i>Cryptosiphonia</i> , <i>Dasyphloea</i> , <i>Dilsea</i> , <i>Dudresnaya</i> , <i>Dumontia</i> , <i>Furlowia</i> , <i>Gibsmithia</i> , <i>Hyalosiphonia</i> , <i>Kraffia</i> , <i>Leptocladia</i> , <i>Masudaphycus</i> , <i>Neodilsea</i> , <i>Orculiferum</i> , <i>Pikea</i> , <i>Rhodopeltis</i> , <i>Thurellopsis</i> , <i>Weeksia</i>			
ENDOCLADIACEAE (Cryptonemiales)	2(10)	2	2
<i>Endocladia</i> , <i>Gloiopeltis</i>			
FURCELLARIACEAE	3(5)	3	3
<i>Furcellaria</i> , <i>Halarachnion</i> , <i>Neurocaulon</i>			
GAINIACEAE			1
<i>Gainia</i>			
GIGARTINACEAE	5(128)	5(130)	7
<i>Chondracanthus</i> , <i>Chondrus</i> , <i>Gigartina</i> , <i>Iridaea</i> , <i>Mazaella</i> , <i>Rhodoglossum</i> , <i>Sarcothalia</i>			
GLOIOSIPHONACEAE (Cryptonemiales)	3(8)	6(15)	7
<i>Cruoriopsis</i> , <i>Gloiophycus</i> , <i>Gloiosiphonia</i> , <i>Peleophycus</i> , <i>Plagiospora</i> , <i>Schimmelmanna</i> , <i>Thurella</i>			
HAEMESCHARIACEAE			1
<i>Haemescharia</i>			
HYPNEACEAE	3(28)	2	2
<i>Hypnea</i> , <i>Hypneocolax</i>			
KALLYMENACEAE (Cryptonemiales)	12(99)	18(110)	15
<i>Austrophyllis</i> , <i>Callocolax</i> , <i>Callophyllis</i> , <i>Ectophora</i> , <i>Erythrophyllum</i> , <i>Euthora</i> , <i>Glaphyrymenia</i> , <i>Hormophora</i> , <i>Kallymenia</i> , <i>Meredithia</i> , <i>Nereoginkgo</i> , <i>Polycoclia</i> , <i>Pugetia</i> , <i>Rhizopogonia</i> , <i>Thamnophyllis</i>			
MYCHODEOPHYLLACEAE		1(1)	1
<i>Mychodeophyllum</i>			
MYCHODIACEAE	2(17)	1(11)	2
<i>Ectoclinium</i> , <i>Mychodea</i>			
NEMASTOMATACEAE	4(29)	6(50)	4
<i>Adelophyton</i> , <i>Itonoa</i> , <i>Nemastoma</i> , <i>Tsengia</i>			
NIZYMENIACEAE		2	2
<i>Nizymenia</i> (Sarcodiaceae), <i>Stenocladia</i> (Sphaerococcaceae)			
PETROCELIDACEAE			1
<i>Mastocarpus</i>			
PEYSSONNELIACEAE (Cryptonemiales)	9(52)	12(70)	10
? <i>Chevaliericrusta</i> , <i>Cruoriella</i> , <i>Ethelia</i> (?), <i>Metapeyssonnella</i> , <i>Peyssonnelia</i> , <i>Polysipata</i> , <i>Pulvinia</i> , <i>Ramicrusta</i> , ? <i>Riquetophycus</i> , <i>Sonderopelta</i>			
PHACELOCARPACEAE		1	1
<i>Phacelocarpus</i> (Sphaerococcaceae)			
PHYLLOPHORACEAE	5(64)	11(70)	11
<i>Ahnfeltiopsis</i> , <i>Besa</i> (Gigartiniaceae), <i>Ceratocolax</i> , <i>Coccolyx</i> , <i>Erythrodermis</i> , <i>Gymnogongrus</i> , <i>Ozophora</i> , <i>Petroglossum</i> , <i>Phyllophora</i> , <i>Schottera</i> , <i>Stenogramme</i>			
POLYIDACEAE (Cryptonemiales)	2(4)	2	2
<i>Polyides</i> , <i>Stenopeltis</i>			
PSEUDOANEMONIACEAE		2	2
<i>Humbrella</i> , <i>Pseudoanemonia</i>			
RHIZOPHYLLIDACEAE (Cryptonemiales)	3(15)	4	5
<i>Porteria</i> , <i>Contaritia</i> , <i>Nesophila</i> , <i>Ochtodes</i> , <i>Rhizophyllis</i>			
RISSEOELLACEAE	1(1)	1	1
<i>Rissoella</i>			
SARCODIACEAE	5(11)	3	3
<i>Chondrymenia</i> , <i>Sarcodia</i> , <i>Trematocarpus</i>			
SCHIZYMENIACEAE (Nemastomataceae)			4
<i>Platoma</i> , <i>Predaea</i> (Solieriaceae), <i>Scizymenia</i> , <i>Titnophora</i>			

SCHMITZIELLOIDEAE			1
<i>Schmitziella</i> (Lithophylloideae, Corallinales)			
SPHAEROCOCCACEAE (Gigartinales)	5(18)	1	1
<i>Sphaerococcus</i>			
TICHOCARPACEAE (Cryptonemiales)	1(1)	1	1
<i>Tichocarpus</i>			
WURDEMANNIACEAE		1	1
<i>Wurdemannia</i> (?)			
PLOCAMIALES			
PLOCAMIACEAE (Gigartinales)	2(51)	2(40)	2
<i>Plocamiocolax</i> , <i>Plocamium</i>			
GRACILARIALES			10
GRACILARIACEAE (Gigartinales)	8(140)	6(130)	7
<i>Congracilaria</i> , <i>Curdia</i> , <i>Gracilaria</i> , <i>Gracilariophila</i> , <i>Gracilariopsis</i> , <i>Hydropuntia</i> , <i>Melanthalia</i>			
PTEROCLADIOPHILACEAE		1(1)	3
<i>Gelidiocolax</i> (Gelidiaceae), <i>Holmsella</i> (?), <i>Pterocladophila</i>			
CRYPTONEMIALES (incl. Corallinales, Hildenbrandiales & Gigartinales p.p.)	107(792)	130(950)	24
HALYMENIACEAE	19(148)	17(160)	23
<i>Acrodiscus</i> , <i>Aeodes</i> , <i>Blastophye</i> , <i>Carpopeltis</i> , <i>Codiophyllum</i> , <i>Cryptonemia</i> , <i>Dactylymenia</i> , <i>Dermocorynus</i> , <i>Epiphloea</i> , <i>Gelinaria</i> , <i>Grateloupia</i> , <i>Grateloupiocolax</i> , <i>Halymenia</i> , <i>Isabbottia</i> , <i>Kintokiocolax</i> , <i>Neoabbottia</i> , <i>Norrissia</i> , <i>Pachymenia</i> , <i>Phyllomenia</i> , <i>Polypops</i> , <i>Prionitis</i> , <i>Thamnoclonium</i> , <i>Zymurgia</i>			
SEBDENIACEAE (Gigartinales)	1(2)	1	1
<i>Sebdenia</i>			
RHODYMENIALES	35(194)	38(265)	47
<i>Minium</i> , <i>Hymenocladopsis</i>			
RHODYMENIACEAE	29(151)	31(190)	20
<i>Asteromenia</i> , <i>Cephalocystis</i> , <i>Chamaebotrys</i>			
<i>Botryocladia</i> -group	3(17)		2
<i>Botryocladia</i> , <i>Gloiosaccion</i>			
<i>Chrysomenia</i> -group	6(19)		4
<i>Agardhinula</i> , <i>Chrysomenia</i> , <i>Coelothrix</i> , <i>Erythrymenia</i>			
<i>Erythrocolon</i> -group	3(7)		3
<i>Coelarthrum</i> , <i>Erythrocolon</i> , <i>Fryella</i>			
<i>Rhodymenia</i> -group	8(72)		7
<i>Cordylecladia</i> , <i>Epymenia</i> , <i>Leptosomia</i> , <i>Maripelta</i> , <i>Microphyllum</i> , <i>Rhodymenia</i> , <i>Rhodymeniocolax</i>			
<i>Hymenocladia</i> -group	1(10)		1
<i>Hymenocladia</i>			
FAUCHEACEAE (Faucheae-group, Rhodymeniaceae)	8(26)		12
<i>Cenacrum</i> , <i>Faucheae</i> , <i>Faucheocolax</i> , <i>Faucheopsis</i> , <i>Gloiocladia</i> , <i>Gloioocolax</i> , <i>Gloioderma</i> , <i>Gloiodermatopsis</i> , <i>Halichrysis</i> (Chrysymenia-g.), <i>Leptofaucheae</i> , <i>Sciadophycus</i> , <i>Weberianhossea</i>			
CHAMPIACEAE (Champia-group)	4(26)	4(35)	6
<i>Champia</i> , <i>Champiocolax</i> , <i>Chylocladia</i> , <i>Coeloseira</i> , <i>Dictyothamnion</i> , <i>Gastroclonium</i>			
LOMENTARIACEAE (Lomentaria-group)	2(17)	3	7
<i>Binghamia</i> , <i>Binghamiopsis</i> , <i>Ceratodictyon</i> (Gracilariaceae), <i>Gelidiopsis</i> (Gracilariaceae), <i>Lomentaria</i> , <i>Semnocarpa</i> , <i>Stirnia</i>			
TOTAL	571(3609)	675(4100)	828

1 Authorships and references are provided at <http://www-algaebase.com> (M. Guiry's Algae-Base), <http://rathbun.si.edu/botany/ing/ingForm.cfm> (ING on line version), and <http://ucjeps.herb.berkeley.edu/INA.html> (P. Silva & R. Moe's INA on line version).

2 Fossil genera are not included.

3 Including the Dermonemataceae and Nemaliaceae.

4 Including the Acrochaetiaceae and the Gelidiales.

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