A catalogue with keys to the non-geniculate coralline algae (Corallinales, Rhodophyta) of South Africa

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Abstract:

Non-geniculate coralline red algae are common in all of the world's oceans, where they often occupy close to 100% of the primary rocky substratum. The South African rocky subtidal and intertidal habitats in particular, are rich in diversity and abundance of non-geniculate coralline red algae. Despite their ubiquity, they are a poorly known and poorly understood group of marine organisms. Few scattered records of non-geniculate coralline red algae were published prior to 1993, but these should be treated with caution since many taxa have undergone major taxonomic review since then. Also, generic names such as *Lithophyllum* and *Lithothamnion* were loosely used by many authors for a host of different non-geniculate coralline algae. A series of taxonomic studies, based mainly on the Western Cape Province of South Africa, published particularly between 1993 and 2000, has significantly extended our knowledge of these algae from southern Africa. References to these latter papers and the older records are now gathered here and a list of the well delimited families (3), subfamilies (4), genera (17) and species (43) are presented. A catalogue with keys to the various taxonomic categories is also provided. A marked reduction in the number of real taxa has been found largely because many earlier recorded taxa have been reduced to synonymy, or have not been verified, or examined in a modern context and so their placement is considered dubious, particularly because the Corallinales have undergone major taxonomic revisions in recent years.

Keywords: Catalogue, Corallinales, Key, Non-geniculate coralline algae, South Africa.

Introduction

The South African rocky intertidal and subtidal habitats are rich in diversity and often high in cover of non-geniculate coralline algae (Isaac, 1937; 1949; Stephenson, 1944; 1948; Barnard, 1954; Seagrief, 1967; Stephenson and Stephenson, 1972; Stegenga et al.,

1997). Despite their ubiquity, however, they are not easily recognised and have been a relatively poorly studied group of marine organisms. Few records of non-geniculate coralline red algae from South Africa were published before 1993 (e.g. Harvey, 1849; Heydrich, 1897a; b; 1901; 1902; Foslie, 1900; 1902; 1906; 1907a; b; 1909; Lemoine, 1971), much of these providing less than adequate descriptions that certainly have not been of modern use in delimiting many of the earlier recorded taxa.

Much of the more recent lack of knowledge of the non-geniculate coralline algae stems from a legacy of poor quality taxonomic work (Woelkerling and Lamy, 1998) and it was not surprising that these algae were considered to constitute a 'difficult' taxonomic group (see Taylor, 1942; 1960; Stephenson, 1944; Woelkerling, 1988; Woelkerling and Lamy, 1998). Such difficulties have, however, been created by taxonomists rather than by any intrinsic characteristics of the group itself (van Steenis, 1957; Woelkerling and Lamy, 1998). The fact that these algae are not collected by the vast majority of seaweed biologists, and thus are poorly represented in most collections, is due largely to the fact that they require specific collection (hammer and chisel) and special laboratory methods (dissolving away of the calcium carbonate). These factors aside, they really are not more difficult to work with than other seaweeds.

According to Chamberlain (1991), it was a widely accepted practice to describe taxa largely or even solely on differences in growth forms. Throughout his career Foslie, for example, described some 192 taxa in this manner, quite often using very specific vegetative features to delineate whole taxa, and often basing his descriptions on single specimens or collections (see Woelkerling, 1984). With many researchers following suit, this led to a substantial increase in the number of described taxa, many of which were poorly delimited (Woelkerling, 1984; Chamberlain, 1991; Chamberlain et al., 1991). This problem was confounded by the fact that characters used then to delineate genera, are simply no longer considered reliable (e.g. Woelkerling, 1985; Penrose and Woelkerling, 1988; Penrose and Chamberlain, 1993). In their (Foslie, Lemoine, Harvey and others) defence, however, it should be noted that these pioneering researchers had comparatively primitive equipment and lacked the vast array of taxonomic criteria available to present-day taxonomists. So, although new records and new species are constantly being described, it is clear that a reduction in the number of valid species is imminent because many have, and will, prove to be synonymous (see Chamberlain, 1991). This is already true for South African non-geniculate corallines (see Table 1).

Table 1. Early (pre-1993) records of non-geniculate coralline algae documented for South Africa that have not been included in the KEY for reasons indicated below.

Basionym	Present status	(other) South African synonyms[i]
***Dermatolithon stephensonii* Lemoine**	***Titanoderma stephensonii* (Lemoine) Woelkerling, Chamberlain et P. Silva** **Woelkerling et al (1985: 333) transferred *D. stephensonii* to *Titanoderma* because it was concluded that the genus *Dermatolithon* is a nomenclatural synonym of *Titanoderma*. This change, however, was affected without examination of the relevant type and should be considered questionable particularly as Lemoine was shown to have had a different concept of the delimitation of taxa from the Lithophylloideae. Woelkerling et al. (1985) go on to conclude that some of the taxa they transferred to *Titanoderma* may ultimately be conspecific. Furthermore, this taxon has not been verified or examined in a modern context.**	
***Goniolithon elatocarpum* Foslie (Adey and Lebednik, 1967: 31 as '*elatocarpon*'; Tittley et al., 1984: 7)**	***Mesophyllum engelhartii* (Foslie) Adey (see Chamberlain and Keats, 1995: 134).**	**None.**
***Melobesia corticiformis* Kützing (see Barton, 1893: 202; Seagrief, 1984: 41)**	***Melobesia membranacea* (Esper) Lamouroux**	***Lithothamnion corticiformis* (Kützing) Foslie (see Seagrief, 1984: 41 as '*Lithothamnium*')**
***Melobesia crassiuscula* Kützing (see Harvey, 1849: 111)**	**This taxon has not been verified or examined in a modern context. Its placement should therefore be considered with caution particularly as the Corallinales have undergone major taxonomic revisions in recent years.**	
***Melobesia mamillaris* Harvey (see Harvey, 1849: 109)**	***Neogoniolithon mamillare* (Harvey) Setchell and Mason (see Seagrief, 1984: 42)** **Printz (1929: pl. 47) (see Woelkerling, 1993: 144) designated a specimen from Bahia Brazil as lectotype, but that specimen appears to be missing both from TRH and TCD (Woelkerling, *pers. com*.). As far as we are aware, there is no published study of the type material, and thus the name is used only by tradition rather than being based on a modern study of the type. Several descriptions (e.g. Taylor, 1960: 397; Lawson and John, 1982: 241; Lawson and John,**	

	1987: 211; John et al., 2003: 129) of plants attributed to *N. mamillare* exist, but because there is no information on the type, it is impossible to confirm whether any of the plants described by these authors really pertains to Harvey's species. Based on available published information, it is therefore not possible at present to provide a meaningful distinction, for example, between *N. mamillare* and *N. brassica-florida* because there is no information on the type of *mamillare*, and thus the status of *N. mamillare* as a species is uncertain.	
***Melobesia polymorpha* Linnaeus ex Harvey (see Seagrief, 1984: 41)**	***Lithophyllum incrustans* Philippi**	**None.**
***Melobesia stelligera* Endlicher et Diesing (see Barton, 1893: 202; De Toni, 1905: 1777; Suneson, 1945: 252 [as *Mastophora stelligera* Endlicher et Diesing]; Setchell, 1943: 132; Seagrief, 1984: 41)**	***Metamastophora flabellata* (Sonder) Setchell**	***Peyssonnelia caulescens* Kützing (see Barton, 1893: 142); *Mastophora hypoleuca* Harvey (see Barton, 1893: 202; Suneson, 1945: 252; Adey and Lebednik, 1967: 14); *Mastophora lamourouxii* Decaisne ex Harvey (see Barton, 1893: 202; De Toni, 1905: 1774; Setchell,1943: 131-132 [as *Metamastophora lamourouxii* Decaisne ex Harvey]; Suneson, 1945: 252)**
***Lithophyllum capense* Rosanoff (see Barton, 1893: 202; Seagrief, 1984:39 as *Lithophyllum lichenoides* (Ellis et Solander) Philippi; Adey and Lebednik, 1967: 68 [as *Lithothamnion capense*])**	**This taxon apparently lies within the circumscription of *Synarthrophyton patena* (Hooker et Harvey) Townsend, but has not yet been transferred or reduced to synonymy (see Silva et al., 1996: 273).**	
***Lithophyllum lichenoides* Philippi (see Barton, 1893: 202)**	**Currently regarded as a heterotypic synonym of *Lithophyllum byssoides* (Lamarck) Foslie (see Woelkerling, 1998: 258-259), this taxon was recorded for Algoa Bay by Barton (1893: 202). The alga has, however, not been verified or found since then and so its placement should be considered dubious.**	
***Lithophyllum marlothii* (Heydrich) Heydrich f. *subplicatum* Foslie ('*sublicata*') (see Adey and Lebednik,**	**Heterotypic synonym of *Spongites impar* (Foslie) Chamberlain**	***Lithophyllum impar* Foslie**

1967: 19)		
***Lithophyllum natalense* Foslie**	**Heterotypic synonym of *Spongites yendoi* (Foslie) Chamberlain**	***Pseudolithophyllum natalense* (Foslie) Adey**
***Lithophyllum pustulatum* (Lamouroux) Foslie var. *australe* Foslie**	**This taxon apparently lies within the circumscription of *Titanoderma pustulatum* (Lamouroux) Nägeli, but has not yet been transferred or reduced to synonymy (see Silva et al., 1996: 275).**	
***Lithothamnion crassiusculum* (Foslie) L.R. Mason (as '*Lithothamnium*') (see Seagief, 1984: 39)**	**Homotypic synonym of *Mesophyllum crassiusculum* (Foslie) P.A. Lebednik. It is unclear as to where Seagrief (1984: 39) found a reference to this taxon as all sources he cites made no reference to a South African collection, unless of course Seagrief himself identified this specimen from South Africa. None-the-less, no reference is made to a location, and furthermore, it is doubtful that Seagrief (1984) could have accurately identified this taxon.**	
***Lithothamnion fosliei* Heydrich (see Seagrief, 1984: 39 as '*Lithothamnium*')**	**Heterotypic synonym of *Neogoniolithon brassica-florida* (Harvey) Setchell et Mason**	**None.**
***Lithothamnion lichenoides* (Ellis et Solander) Foslie f. *patena* (Hooker et Harvey) Foslie (see Seagrief, 1984: 47 as '*Lithothamnium*')**	**This taxon has not been verified or examined in a modern context. Its placement should therefore be considered with caution particularly as the Corallinales have undergone major taxonomic revisions in recent years. However, Seagrief (1984: 47) did regard this taxon a synonym of *Synarthrophyton patena* (Hooker et Harvey in Harvey) Townsend.**	
***Lithothamnion patena* (Hooker et Harvey) Heydrich f. *capense* (Rosanoff) Heydrich**	**This taxon apparently lies within the circumscription of *Synarthrophyton patena* (Hooker et Harvey) Townsend, but has not yet been transferred or reduced to synonymy (see Silva et al., 1996: 273).**	***Lithophyllum capense* Rosanoff**
***Lithothamnion polymorphum* (Linnaeus) Areschoug (see Barton, 1893: 202)**	**Heterotypic synonym of *Phymatolithon purpureum* (P. et H. Crouan) Woelkerling et L. Irvine**	***Phymatolithon polymorphum* (Linnaeus) Foslie (see Seagrief, 1984: 45)**
***Lithothamnion prolixum* Foslie (see**	**Heterotypic synonym of *Leptophytum ferox***	***Mesophyllum prolixum* (Foslie) Adey**

Adey and Lebednik, 1967: 80) **(Foslie) Chamberlain et Keats**

***Lithothamnion synanablastum* Heydrich f. *speciosum* Foslie ('*speciosa*')** **Heterotypic synonym of *Mesophyllum engelhartii* (Foslie) Adey** ***Lithothamnion speciosum* (Foslie) Foslie (see Adey and Lebednik, 1967: 69); *Lithothamnion discrepans* Foslie**

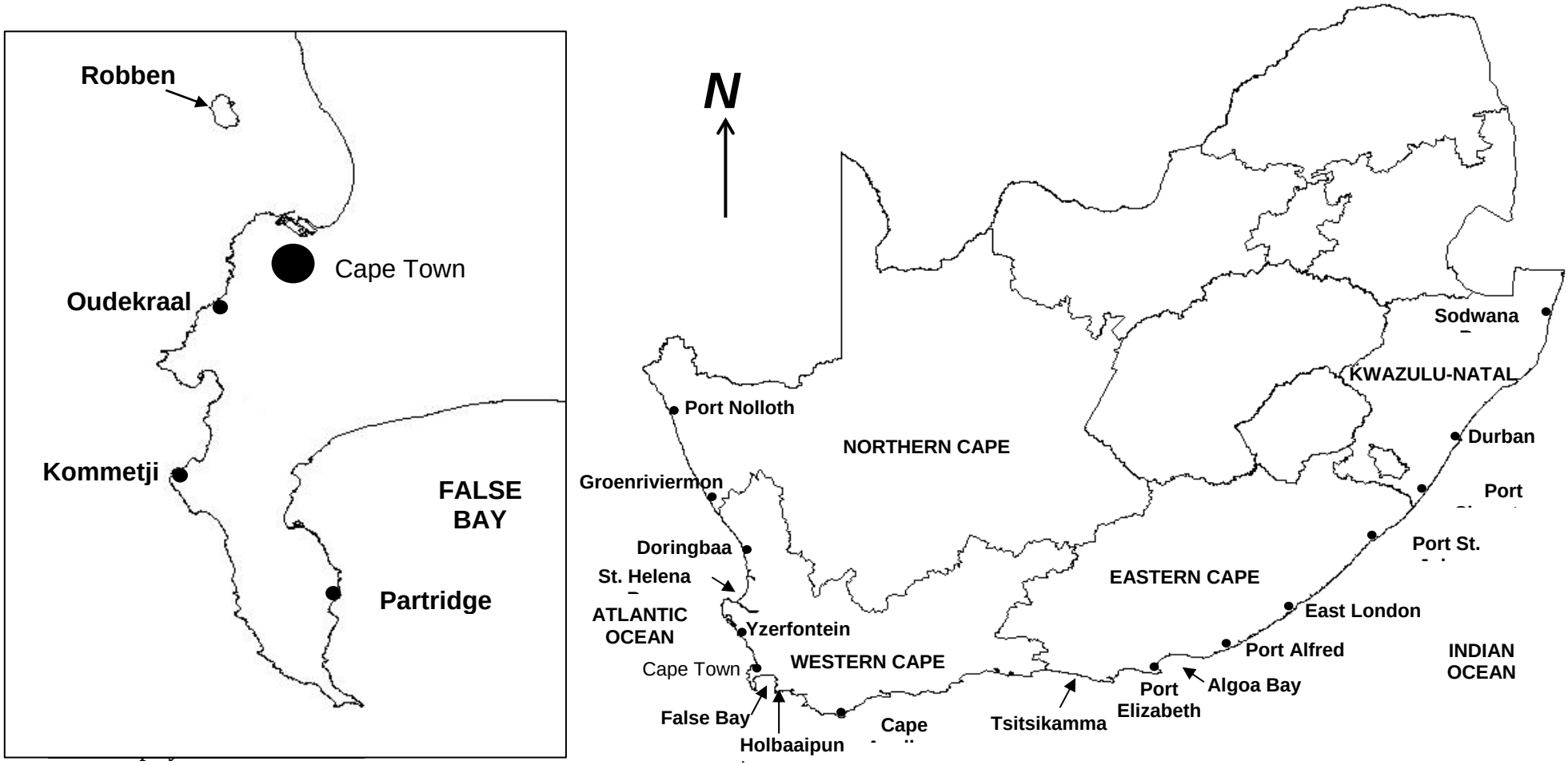
Besides the early records, still other scattered species lists and compendia that included non-geniculate coralline red algae from South Africa were also made (e.g. Seagrief, 1967; 1984; 1988; Simons, 1976; Bolton and Stegenga, 1987; Farrell et al., 1993), but again, these are contentious since many taxa have undergone major taxonomic review in recent years (see e.g. Penrose and Woelkerling, 1988; 1992; Womersley, 1996; Harvey et al., 2003; 2004). Furthermore, genus names such as *Lithophyllum* and *Lithothamnion* (The genus name *Lithothamnion* as understood by Foslie at around 1895, encompassed virtually all non-geniculate coralline algae except for the very thin *Melobesia*-like taxa – see Woelkerling, 1984) were loosely used by many authors (e.g. Stephenson, 1939; 1944; 1948; Seagrief, 1967; 1984; 1988; Stephenson and Stephenson, 1972; Simons, 1976; Branch, 1971; 1975a; b; 1976; Branch and Newell, 1978; Farrell et al., 1993) for a variety of non-geniculate coralline algae, largely because as a group, these red algae were poorly known and their taxonomy poorly understood.

Between 1993 and 2000, however, a series of detailed descriptive studies of South African non-geniculate coralline red algae was published in a variety of journals (e.g. Chamberlain, 1993; 1994; 1996; 2000; Chamberlain and Keats, 1994; 1995; Chamberlain et al., 1995; Keats and Chamberlain, 1993; 1994a; b; 1995; 1997; Keats and Maneveldt, 1997a; b; Keats et al., 2000). The purpose here is to gather together all the information from these references and other earlier records from South Africa, and to provide lists of the valid orders, families, subfamilies, genera and species. Keys to the various taxonomic categories are also provided.
Taxonomic list of South African species with references to publications

Distributions are given in a west to east coast pattern (see Figure 1 for a map of the locations mentioned in the text). The first citation(s) listed (i.e. not enclosed in brackets) is that which has provided a relatively detailed account of the taxonomy and/or ecology. This is followed by papers (in brackets: author, year, pagination) that only list the presence of the species, providing no, or little useful information with regard to its systematics. See also Table 1 for a list of species regarded as dubious and thus not cited below as well as the reasons for their exclusion.

Corallinales Silva et Johansen
Corallinaceae Lamouroux emend Harvey et al. (2003)

Figure 1. Map of South Africa showing the coastal provinces and locations mentioned in the text. Insert – A magnified view of the Cape Peninsula, Western Cape Province.



Lithophyllum acrocamptum Heydrich

Distribution: Seaview (Port Elizabeth) to Umdloti (Durban).
Chamberlain (1996, as *Lithophyllum incrassatum*) – (see also Foslie, 1900: 28 [as *L. incrustans* f. *lobata*]; Foslie, 1900: 29 [as *L. incrustans* f. *incrassata*]; Hariot, 1902: 472; Foslie, 1909:18; Printz, 1929: pl. 57; Adey and Lebednik, 1967: 21 [as *L. incrassatum*]; Woelkerling, 1993: 16-17; Silva et al., 1996: 246-247; Woelkerling, 1998: 299).

Lithophyllum incrustans Philippi
Distribution: Coffee Bay (south of Port St. Johns).
Chamberlain (1996).

Lithophyllum neoatalayense Masaki
Distribution: Groenriviermond (Northern Cape) to Cape Agulhas (Western Cape) (also found just south of Torra Bay, Namibia).
Chamberlain (1996); Pueschel and Keats (1997) – (see also Chamberlain, 1994: 149; 1997a: 147; Chamberlain and Keats, 1994: 113).

Titanoderma corallinae (P. Crouan et H. Crouan) Woelkerling, Chamberlain et Silva
Distribution: Kommetjie (Western Cape) to KwaZulu-Natal.
– (Chamberlain and Norris, 1994a: 14; Chamberlain, 1996: 219).

Titanoderma polycephalum (Foslie) Woelkerling, Chamberlain et Silva
Distribution: False Bay to Cape Agulhas (Western Cape).
Chamberlain (1996) – (see also Chamberlain and Keats, 1994: 122).

Titanoderma pustulatum (Lamouroux) Nägeli
Distribution: Occasional throughout the west coast and increasing in abundance toward KwaZulu-Natal where it is particularly abundant.
– (see Barton, 1893: 202 [as *Melobesia pustulata*]; Adey and Lebednik, 1967: 38 [as *Melobesia pustulatum*]; Seagrief, 1984: 39 [as *Lithophyllum pustulatum* and *L. pustulatum* f. *corallinae*]; Farrell et al., 1993: 152; Chamberlain and Norris, 1994b: 292; Chamberlain, 1996: 219).

2. Mastophoroideae Setchell

Hydrolithon farinosum (Lamouroux) Penrose et Chamberlain
Distribution: Lala Neck (north of Sodwana Bay, KwaZulu-Natal).
– (see Seagrief, 1984: 26 [as *Fosliella farinosa*]; Penrose and Chamberlain, 1993: 296).

Hydrolithon onkodes (Heydrich) Penrose et Woelkerling
Distribution: Sodwana Bay (KwaZulu-Natal).
Keats and Chamberlain (1994a).

Hydrolithon pellire Chamberlain et R. Norris
Distribution: Port Alfred (Eastern Cape) to Durban (KwaZulu-Natal).
Chamberlain and Norris (1994b) – (see also Chamberlain and Norris, 1994a: 10; Keats and Chamberlain, 1994a: 20).

Hydrolithon samoënse (Foslie) Keats et Chamberlain
Distribution: Yzerfontein (Western Cape) to Sodwana Bay (KwaZulu-Natal).
Keats and Chamberlain (1994a) – (see also Chamberlain, 1994: 149; Chamberlain and Keats, 1994: 113; Keats and Chamberlain, 1995: 52, 55; Keats and Maneveldt, 1997b: 450, 456; Keats et al., 2000: 386).

Hydrolithon superficiale Keats et Chamberlain
Distribution: Sodwana Bay (KwaZulu-Natal).
Keats and Chamberlain (1994a).

Metamastophora flabellata (Sonder) Setchell
Distribution: Palm Beach (south of Port Shepstone, KwaZulu-Natal) eastward, extending into Mozambique.
– (See Setchell, 1943: 130; Woelkerling, 1980: 239; Seagrief, 1984: 41; 1988: 52; Farrell et al., 1993: 152; Silva et al., 1996: 260; De Clerck et al., 2005: 178). Silva et al., (1996: 260-261) provide a list of all synonyms and additional localities for this species. Seagrief (1984: 41) also provides a list of names that have been applied to South African taxa synonymous with *Metamastophora flabellata*.

Neogoniolithon brassica-florida (Harvey) Setchell et Mason
Distribution: Algoa Bay (Eastern Cape).
– (see Harvey, 1849: 110; Barton, 1893: 202 [as *Lithothamnion brassica-florida*]; Setchell and Mason, 1843: 91; Seagrief, 1984: 42).

Pneophyllum amplexifrons (Harvey) Chamberlain et R. Norris
Distribution: Palm Beach (south of Port Shepstone, KwaZulu-Natal) northward into Mozambique.

Chamberlain and Norris (1994a) – (see also Barton, 1893: 202 [as *Melobesia amplexifrons*]; Chapman and Parkinson, 1974; Tittley et al., 1984; Chamberlain and Norris, 1994b: 292).

Pneophyllum coronatum (Rosanoff) Penrose in Chamberlain
Distribution: Oudekraal (western Cape Peninsula, Western Cape).
Chamberlain (1994).

Pneophyllum fragile Kützing
Distribution: Widespread along the west coast.
– (see Chamberlain, 1994: 146; Chamberlain and Norris, 1994a: 10).

Pneophyllum keatsii Chamberlain
Distribution: Oudekraal (western Cape Peninsula, Western Cape) to Cape Agulhas (Western Cape).
Chamberlain (1994).

Spongites discoideus (Foslie) Penrose et Woelkerling
Distribution: Port Nolloth (Northern Cape) to Cape Agulhas (Western Cape).
Chamberlain (1994) – (see also Chamberlain, 1996: 210, 212, 214).

Spongites impar (Foslie) Chamberlain
Distribution: Cape St. Martin (just south of St. Helena Bay, Western Cape) to Oudekraal (western Cape Peninsula, Western Cape).
Chamberlain (1994) – (see also Adey and Lebednik, 1967: 18 [as *Lithophyllum impar*]; Branch et al., 1994: 340; Chamberlain and Keats, 1994: 118; Stegenga et al., 1997: 19).

Spongites yendoi (Foslie) Chamberlain
Distribution: Throughout South Africa (Namibia to the Mozambican border). Most abundant along the southern west and south coasts, becoming less common toward the east.
Chamberlain (1993); Keats et al. (1993); Keats, Wilton and Maneveldt (1994); Keats, Matthews and Maneveldt (1994) – (see also Branch et al., 1994: 340; Chamberlain, 1994: 142, 149, 153, 155, 156; Chamberlain and Keats, 1994: 113, 118, 122; Chamberlain, 1996: 216; Stegenga et al., 1997: 19; Keats et al., 2000: 387; Maneveldt et al., 2006: 620, 622, 625).

Hapalidiaceae J.E.Gray emend Harvey et al. (2003)

1. Choreonematoideae Woelkerling

Choreonema thuretii (Bornet) Schmitz
Distribution: Widespread but sporadic, mostly abundant in False Bay (Western Cape) becoming sparse toward the east coast.
– (see Pocock, 1956: 12, pl. 1a-b; Bolton and Stengenga, 1987: 173; Seagrief, 1984: 16; 1988: 52).

2. Melobesioideae Bizzozero

Clathromorphum tubiforme Chamberlain, R. Norris, Keats et Maneveldt
Distribution: Partridge Point (western False Bay, Western Cape) to Tiger Rocks (south of Durban, KwaZulu-Natal).
Chamberlain et al. (1995).
"*Leptophytum*[1]" *acervatum* (Foslie) Chamberlain et Keats
Distribution: False Bay (Western Cape) to western KwaZulu-Natal.
Chamberlain and Keats (1994) – (see also Foslie, 1907b: 4-5; Adey and Lebednik, 1967: 49 [as *Lithothamnion acervatum*]; Branch et al., 1994: 340; Chamberlain, 1994: 149; Chamberlain, 1996: 212; Keats and Maneveldt, 1997b: 451, 456).

"*Leptophytum*" *ferox* (Foslie) Chamberlain et Keats
Distribution: Throughout South Africa into Mozambique (see also Chamberlain, 1997b), but most common from Groenriviermond (Northern Cape) to Cape Agulhas (Western Cape).
Chamberlain and Keats (1994); Keats, Matthews and Maneveldt (1994); Keats, Wilton and Maneveldt (1994) – (see also Foslie, 1907b: 7; Printz, 1929: 40; Adey and Lebednik, 1967: 64 [as *Lithothamnion ferox*]; Branch et al., 1994: 340; Chamberlain, 1996: 216; Maneveldt et al., 2006: 620, 622).

"*Leptophytum*" *foveatum* Chamberlain et Keats
Distribution: From Namibia to Cape Agulhas (Western Cape).

[1] The genus name *Leptophytum* Adey (1966) is considered nomenclaturally illegitimate (see Düwel & Wegeberg 1996, Woelkerling et al. 2002) and synonymous with *Phymatolithon* Foslie (1898). While some (e.g. Adey et al. 2001, Athanasiadis & Adey 2003) have argued for its conservation, these authors have been shown to be nomenclaturally incorrect (see Compère 2004). In this catalogue, we have used the genus name "*Leptophytum*" in quotation marks because South African taxa ascribed to this genus have not been formally transferred or reduced to synonymy.

Chamberlain and Keats (1994); Keats and Maneveldt (1994) – (see also Branch et al., 1994: 340; Chamberlain, 1994: 153; Keats, Matthews and Maneveldt, 1994: 110, 112; Keats and Maneveldt, 1997b: 451; Maneveldt et al., 2006: 620).

Lithothamnion muelleri Lenormand ex Rosanoff
Distribution: Robben Island (off the Cape Peninsula, Western Cape) to just east of False Bay (Western Cape).
Record unpublished.

Lithothamnion superpositum Foslie
Distribution: From Namibia to Bird Island (Algoa Bay, Eastern Cape); less common toward the east.
Keats et al. (2000) – (see also Adey and Lebednik, 1967: 82; Keats and Maneveldt, 1997: 451)

Melobesia membranacea (Esper) Lamouroux
Distribution: Throughout South Africa.
– (see Barton, 1893: 202; Harvey, 1849: 111; Seagrief, 1984: 41; Bolton and Stegenga, 1987: 175; Farrell et al., 1993: 152; Chamberlain and Norris, 1994b: 292).

Mesophyllum capense (Rosanoff) Chamberlain
Distribution: Robben Island (off the Cape Peninsula, Western Cape) to KwaZulu-Natal.
Chamberlain (2000).

Mesophyllum engelhartii (Foslie) Adey
Distribution: From Namibia to East London (Eastern Cape).
Chamberlain and Keats (1995); Keats, Matthews and Maneveldt (1994 [as *M. discrepans*]) – (see also Adey and Lebednik, 1967: 67 [as *Lithothamnion synanablastum*]; Adey and Lebednik, 1967: 83 [as *Lithothamnion discrepans*]; Branch et al., 1994: 340; Chamberlain, 1994: 149; Chamberlain and Keats, 1994: 118, 122; Keats and Maneveldt, 1994: 248; Keats and Chamberlain, 1995: 55 [as *M. discrepans*]; Keats and Maneveldt, 1997a: 205, 208).

Mesophyllum erubescens (Foslie) Lemoine
Distribution: Robben Island (off the Cape Peninsula, Western Cape) to Sodwana Bay (KwaZulu-Natal).
Keats and Chamberlain (1994b); Keats and Maneveldt (1997a [as *M. incisum* – *M. incisum* was recently subsumed in *M. erubescens* (Foslie) Lemoine by Harvey et al., (2004)]). – (see also Keats and Chamberlain, 1994a: 9; Keats and Maneveldt, 1997a: 205, 208).

Mesophyllum funafutiense (Foslie) Verheij
Distribution: Sodwana Bay (KwaZulu-Natal).
Keats and Chamberlain (1994b) – (see also Keats and Maneveldt, 1997a: 205, 208).

Phymatolithon repandum (Foslie) Wilks et Woelkerling
Distribution: Port Nolloth (Northern Cape) to Holbaaipunt (east of False Bay, Western Cape).
Record previously unpublished, but specimens exist at UWC (D.W. Keats, 21.v.1993, UWC: 93/52; D.W. Keats, 21.vi. 1993, UWC: 93/63; UWC: 93/68; D.W. Keats, 17.vii.1993, UWC: 93/171; D.W. Keats, 19.viii.1993, UWC: 93/200; UWC: 93/201; D.W. Keats & G. Maneveldt, 19.i.1994, UWC: 94/16; D.W. Keats, 27.i.1994, UWC: 94/18; D.W. Keats, 26.v.1994, UWC: 94/128).

Synarthrophyton eckloniae (Foslie) Keats et Chamberlain
Distribution: Ouderkraal (western Cape Peninsula, Western Cape) to Cape Agulhas (Western Cape).
Keats and Chamberlain (1997) – (see also Adey and Lebednik, 1967: 51 [as *Lithothamnion eckloniae*]; Chamberlain, 1994: 145, 146, 147, 148 [as *Lithothamnion eckloniae*]; Keats and Maneveldt, 1997b: 448, 465, 466).

Synarthrophyton magellanicum (Foslie) Keats et Chamberlain
Distribution: Robben Island (off the Cape Peninsula, Western Cape) to Holbaaipunt (east of False Bay, Western Cape).
Keats and Chamberlain (1997) – (Keats and Maneveldt, 1997b: 448, 465, 466).

Synarthrophyton munimentum Keats et Maneveldt
Distribution: Namibia to Holbaaipunt (east of False Bay, Western Cape).
Keats and Maneveldt (1997b).

Synarthrophyton patena (Hooker et Harvey) Townsend
Distribution: Robben Island (off the Cape Peninsula) to Sodwana Bay (KwaZulu-Natal).
– (see Barton, 1893: 202 [as *Lithophyllum patena*]; Adey and Lebednik, 1967: 68 [as *Lithothamnion capense*]; Seagrief, 1967: 144; 1984: 41 [as *Melobesia patena*]; Seagrief, 1980: 25; 1984: 47; 1988: 52; Lambert and Steinke, 1986: 211, Farrell et al., 1993: 152 [as *Polyporolithon patena*]; Keats and Maneveldt, 1997b: 465, 466).

Synarthrophyton papillatum Maneveldt, Keats et Chamberlain
Distribution: Groenriviermond (Northern Cape) to Holbaaipunt (east of False Bay, Western Cape).
Maneveldt et al. (2007).
Synarthrophyton robbenense Keats et Maneveldt

Distribution: Robben Island (off the Cape Peninsula, Western Cape) to Partridge Point (western False Bay, Western Cape).
Keats and Maneveldt (1997b).

Sporolithaceae Verheij

Heydrichia groeneri Keats et Chamberlain
Distribution: Namibia to Holbaaipunt (east of False Bay, Western Cape).
Keats and Chamberlain (1995) – (see also Keats and Maneveldt, 1997b: 456).

Heydrichia woelkerlingii Townsend, Chamberlain et Keats
Distribution: Doringbaai (Western Cape) to Stormsriviermond (Tsitsikamma, Eastern Cape).
Townsend et al. (1994) – (see also Keats, Matthews and Maneveldt, 1994: 109-110; Branch et al., 1994: 340; Chamberlain and Keats, 1995: 136; Keats and Chamberlain, 1995: 55, 57; Keats and Maneveldt, 1997b: 451, 456; Keats et al., 2000: 387).

Sporolithon episporum (Howe) Dawson
Distribution: Holbaaipunt (east of False Bay, Western Cape) and Sodwana Bay (KwaZulu-Natal).
Keats and Chamberlain (1993) – (see also Keats and Chamberlain, 1995: 56; Keats and Maneveldt, 1997b: 451; Keats et al., 2000: 387).

Sporolithon ptychoides Heydrich
Distribution: Sodwana Bay (KwaZulu-Natal).
Keats and Chamberlain (1993) – (see also Keats and Chamberlain, 1995: 56).

KEYS to the non-geniculate coralline algae of South Africa
Thallus terminology follows Chamberlain (1990) and growth-forms terminology follows Woelkerling et al. (1993).

Key to the families of Corallinales
1. Tetra/bisporangia cruciately divided, borne in diffuse sori ..... Sporolithaceae
Tetra/bisporangia zonately divided, borne in roofed conceptacles.....2
2. Tetra/bisporangia producing apical plugs AND borne in multiporate conceptacles ..... Hapalidiaceae

Tetra/bisporangia not producing apical plugs AND borne in uniporate conceptacles ..... Corallinaceae

Key to the subfamilies of Hapalidiaceae
1. Secondary pit connections AND cells fusions absent; tetra/bisporangial conceptacle pore plate acellular at maturity, composed only of a calcium carbonate matrix ..... Choreonematoideae
Cell fusions present, secondary pit connections absent or very rare; tetra/bisporangial conceptacle pore plate composed of cells at maturity ..... Melobesioideae

A further subfamily, the Austrolithoideae Harvey et Woelkerling (Harvey and Woelkerling, 1995: 363) has representative taxa from Australia (*Austrolithon* Harvey et Woelkerling – Harvey and Woelkerling, 1995: 363), and the British Isles and France (*Boreolithon* Harvey et Woelkerling – Harvey and Woelkerling, 1995: 374) (see also Harvey et al., 2003).

Key to the subfamilies of Corallinaceae
1. Secondary pit connections present, cell fusions absent or very rare ..... Lithophylloideae
Cell fusions present, secondary pit connections absent or very rare ..... Mastophoroideae

Key to the genera of Sporolithaceae, Corallinaceae and Hapalidiaceae
1. Tetra/bisporangia cruciately divided AND borne in loosely aggregated sori 2
Tetra/bisporangia zonately divided AND borne in conceptacles 3
2. Tetra/bisporangia with single stalk cells ..... *Sporolithon*
Tetra/bisporangia with up to 5 stalk cells ..... *Heydrichia*
3. Tetra/bisporangial conceptacles uniporate 4
Tetra/bisporangial conceptacles multiporate 10
4. Cells of contiguous thallus filaments joined by secondary pit connections 5
Cells of contiguous thallus filaments joined by cell fusions 6
5. Basal filaments composed of squarish cells, primary or regenerating thallus lacking a bistratose margin ..... *Lithophyllum* Basal filaments composed of palisade cells, primary or regenerating thallus margin bistratose ..... *Titanoderma*
6. Thallus arborescent (tree-like) and flabelliform (fan-shaped) in growth form, and anchored to the substratum by a distinct holdfast and stipe ..... *Metamastophora*
Thallus not arborescent and flabelliform, but encrusting 7

7. Tetra/bisporangial conceptacle pores lined by small papillae initially lying more or less parallel to roof surface, sometimes later becoming long and filamentous 8

Tetra/bisporangial conceptacle pores surrounded at their base by a ring of enlarged, vertically orientated cells ..... *Hydrolithon*

8. Tetra/bisporangial conceptacle roof formed from filaments interspersed among AND filaments peripheral to the sporangia ..... *Pneophyllum*

Tetra/bisporangial conceptacle roof formed ONLY from filaments peripheral to the sporangia 9

9. Male conceptacles containing simple spermatangial systems that are restricted to the conceptacle floor, gonimoblast filaments of carposporangial conceptacles arising only from the margins of the fusion cell ..... *Spongites*

Male conceptacles containing simple spermatangial systems that are found on the floor, walls and roof of the conceptacle, gonimoblast filaments of carposporangial conceptacles arising dorsally from fusion cells ..... *Neogoniolithon*

10. Vegetative thallus entirely endophytic in geniculate corallines, with external colourless conceptacles ..... *Choreonema*

Vegetative thallus epiphytic, epilithic and/or epizoic, but not endophytic 11

11. Thallus dimerous, conceptacles often distinctly dark-centered ..... *Melobesia*

Thallus monomerous, conceptacles not characteristically dark-centred 12

12. Epithallial cells with flared outer walls ..... *Lithothamnion*

Epithallial cells with domed to flattened outer walls 13

13. Spermatangial systems simple all round conceptacle chamber, or with more elaborated ones ONLY in centre of conceptacle floor 14

Spermatangial systems dendroid 16

14. Spermatangial systems in centre of conceptacle floor elaborated ..... *"Leptophytum"*

Spermatangial systems simple throughout 15

15. Epithallial cells up to 7 layers thick, subepithallial initials conspicuous by staining more densely than surrounding cells ..... *Clathromorphum*

Epithallial cells only a single layer, subepithallial initials not conspicuously differing from surrounding cells ..... *Mesophyllum*

16. Tetra/bisporangial conceptacles initiated adventitiously within the thallus from ordinary thallus cells ..... *Phymatolithon*

Tetra/bisporangial conceptacles initiated in subepithallial layer ..... *Synarthrophyton*

Key to Sporolithaceae

1. Tetra/bisporangia with a single stalk cell 2
   Tetra/bisporangia with up to 5 stalk cells 3
2. Old tetrasporangial complexes buried in rows in the thallus ..... *Sporolithon ptychoides*
   Old tetrasporangial complexes shed, not becoming buried in the thallus ..... *Sporolithon episporum*
3. Thallus massive with matt, chalky surface; tetra/bisporangial chamber 62-111 µm high ..... *Heydrichia woelkerlingii*
   Thallus thin, surface matt, often with distinctive swirls of flaking cells; tetra/bisporangial chamber 31-62 µm high ..... *Heydrichia groeneri*

Key to Lithophylloideae

1. Basal filaments composed of squarish cells, primary or regenerating thallus lacking a bistratose margin 2
   Basal filaments composed of palisade cells, primary or regenerating thallus margin bistratose 4
2. Conceptacle pore lined with long, vertically orientated filaments ..... *Lithophyllum neoatalayense*
   Conceptacle pore unelaborated or lined with papillae orientated parallel to roof surface . 3
3. Conceptacle roof 6-17 cells thick, pore canal long, with parallel sides ..... *Lithophyllum incrustans*
   Conceptacle roof 3-5 cells thick, pore canal short, tapering markedly towards the pore ..... *Lithophyllum acrocamptum*
4. Thalli epilithic, lumpy, becoming massive and protuberant ... *Titanoderma polycephalum*
   Mainly epiphytic, sometimes epilithic or epizoic, comprising thin, flat thalli 5
5. Tetra/bisporangial conceptacles more or less flush with thallus surface or slightly raised, conceptacle floor immersed up to 7 cells deep in thallus ..... *Titanoderma corallinae*
   Tetra/bisporangial conceptacles raised, conceptacles with floor immersed no more than 3 cells deep in thallus ..... *Titanoderma pustulatum*

Key to Mastophoroideae

1. Thallus arborescent (tree-like) and flabelliform (fan-shaped) in growth form, and anchored to the substratum by a distinct holdfast and stipe . *Metamastophora flabellatum*

Thallus not arborescent and flabelliform, but encrusting 2

2. Pore canals of tetra/bisporangial conceptacles lined by a ring of conspicuously enlarged cells orientated perpendicular to the roof surface 3

Pore canals of tetra/bisporangial conceptacles lined by small papillate cells that protrude more or less laterally into the canal and are initially orientated parallel to the roof surface but may also produce an elaborate crown of filaments later 7

3. Plants thin, epiphytic, with dimerous internal construction 4

Plants thin to thick, epilithic, with predominantly monomerous internal construction 5

4. Plants up to 150 μm thick, reproductively mature thalli no more than 2-5 cells thick ..... *Hydrolithon farinosum*

Plants to 370 μm thick, reproductively mature thalli more than 5 cells thick ..... *Hydrolithon pellire*

5. Plants becoming very thick, surface granular due to the presence of abundant, large, horizontally arranged pustulose trichocyte fields that also become buried in the thallus ..... *Hydrolithon onkodes*

Plants thin, lacking large horizontal pustulose trichocyte fields throughout the thallus 6

6. Mature conceptacles occurring in a superficial, lightly calcified layer above the thallus that is shed upon senescence; conceptacle roofs comprising an elongate meristematic cell that is 1.5-2 times the length of the epithallial cell ..... *Hydrolithon superficiale*

Thallus gleaming dark red, mature conceptacles evident as small 'pinpricks' at thallus surface and shed individually or in small groups upon senescence; conceptacle roofs comprising an elongate meristematic cell that is 2.5-5 times the length of the epithallial cell ..... *Hydrolithon samöense*

7. Male conceptacles containing simple spermatangial systems that are restricted to the conceptacle floor, gonimoblast filaments of carposporangial conceptacles arising only from the margins of the fusion cell 8

Male conceptacles containing simple spermatangial systems that are found on the floor, walls and roof of the conceptacle, gonimoblast filaments of carposporangial conceptacles arising dorsally from fusion cells ..... *Neogoniolithon brassica-florida*

8. Thallus forming thick, trumpet-shaped adjoining thalli encircling seagrass and green algal stalks ..... *Pneophyllum amplexifrons*

Thallus thin to thick, epiphytic, epilithic, or epizoic 9

9. Epiphytic, flat thalli on *Ecklonia maxima* stipes and/or holdfasts and various red algae 10

Epilithic or epizoic 12

10. With very prominent raised conceptacles, only known on *Ecklonia* ..... *Pneophyllum coronatum*
With flat conceptacles 11
11. Known only on *Ecklonia*, with up to 4 layers of epithallial cells, subepithallial initials markedly elongate ..... *Pneophyllum keatsii*
On *Ecklonia* and red algal hosts, with a single layer of epithallial cells, subepithallial initials only slightly elongate ..... *Pneophyllum fragile*
12. Forming a band on the mid-shore, thallus surface wrinkled like an elephant's skin, crusts becoming thick and flat, margins often growing back-to-back to form convoluted crests, yellowish to beige in colour ..... *Spongites impar*
Thalli thin and flat to protuberant, margins not growing back-to-back to form convoluted crests, but merging 13
13. Crusts pink, forming thin, flat thalli that give rise to thick, discoid to crested thalli on top of thin thalli ..... *Spongites discoideus*
Crusts greyish to beigish to blueish mauve, forming thin to protuberant thalli, predominant on mid- to low shore, especially together with the limpet *Scutellastra cochlear* ..... *Spongites yendoi*

Key to Choreonematoideae
This subfamily is characterised by the monotypic genus *Choreonema* that in turn possesses only one species, *C. thuretii*. The features diagnostic of the subfamily and genus therefore can be used to distinguish this species from others (see above). ..... *Choreonema thuretii*

Key to Melobesioideae
1. Thalli thin, with dimerous construction, usually epiphytic ..... *Melobesia membranacea*
Thalli thin to thick, with monomerous construction 2
2. Epithallial cells with flared outer cell walls 3
Epithallial cells with flattened, squarish or domed outer cell walls but not flared 4
3. Cortex with some areas of extra large angular cells, mature tetra/bisporangial pore plate appearing spiny in surface view due to shedding of rosette cells surrounding the pores ..... *Lithothamnion superpositum*
Cortex lacking areas of large cells, pore plate with smooth (not spiny) surface ..... *Lithothamnion muelleri*
4. Thalli only known to be epiphytic 5
Thalli epilithic and/or epizoic, but not epiphytic 8

5. Epiphytic, only known on *Amphiroa*, tetra/bisporangial conceptacle roof minute, slightly sunken, conceptacle chamber 59-73 µm in diameter ..... *Clathromorphum tubiforme*

Epiphytic on *E. maxima, Gelidium* and other red algae, not known on *Amphiroa* 6

6. Only known as epiphytic on *E. maxima*, thalli thin and flat, tetra/bisporangial conceptacle roofs flush to somewhat sunken, with slightly raised rim ..... *Synarthrophyton eckloniae*

Not epiphytic on *Ecklonia* 7

7. Epiphytic mainly on *Gelidium* spp., plants discoid, conceptacle roof raised and dome-like, 750-1300 µm in diameter ..... *Synarthrophyton patena*

Epiphytic on *Gelidium capense*, conceptacles truncated conical with sunken pore plate, 450-900 µm in diameter ..... *Mesophyllum capense*

8. Thalli thin and flat, surface pitted with sunken conceptacles 9

Thalli thick and flat, or protuberant, or layered 10

9. Thallus bright pink, occurring on intertidal pebbles, medullary cells about twice as long as in diameter, cortical cells squarish ..... *"Leptophytum" acervatum*

Thallus brownish-pink with numerous pale, imbricate margins running more-or-less parallel to the primary margin; medullary cells very long and thin, cortical cells elongate ..... *"Leptophytum" foveatum*

10. Thalli mauvish grey, flat or with flat-topped protuberances either entire or composed of back-to-back thalli, conceptacles slightly raised, rimless, 140-280 µm in diameter ..... *"Leptophytum" ferox*

Thalli reddish to brownish to purplish brown, not with back-to-back thalli 11

11. Tetra/bisporangial conceptacles with raised rim and depressed pore plate 12

Tetra/bisporangial conceptacles domed or flattened, not with depressed pore plate 13

12. Thalli thin with minute, low, irregularly domed papillae fused into scroll-like patterns, conceptacles 185-330 µm in diameter, with shallowly depressed pore plate ..... *Synarthrophyton robbenense*

Thallus flat to occasionally warty, conceptacles 475-990 µm in diameter, volcano-like with high rim and deeply depressed pore plate .... *Synarthrophyton munimentum*

13. Tetra/bisporangial conceptacles arising adventitiously from groups of vegetative cells within the thallus, subepithallial cells as short as or shorter than subtending cells, crescent-shaped scars seen throughout thallus in vertical section ..... *Phymatolithon repandum*

Tetra/bisporangial conceptacles arising in subepithallial initials, subepithallial initials as long as or longer than subtending cells 14

14. Male conceptacles with only simple spermatangial systems, medulla usually coaxial ... 15

Male conceptacles with some branched spermatangial systems at least on the floor 17

15. Tetra/bisporangial conceptacle pores lined by cells not differing from surrounding roof filaments 16

Tetra/bisporangial conceptacle pores lined by cells differing from those of surrounding roof filaments in having a long basal cell ..... *Mesophyllum erubescens*

16. Tetra/bisporangial conceptacles very large (up to 1.2 mm), roof filaments composed of filaments 7-10 cells long ..... *Mesophyllum funafutiense*

Tetra/bisporangial conceptacles rarely exceeding 600 µm in diameter (just visible with the naked eye), roof composed of filaments 4-6 cells long ..... *Mesophyllum engelhartii*

17. Tetra/bisporangial conceptacles domed, thalli adherent with pale rims and minute, pale-topped papillate protuberances, usually found on intertidal polychaete worm tubes ..... *Synarthrophyton papillatum*

Conceptacles low-domed, thalli adherent, but later producing free, overlapping lamellae, usually epilithic subtidally ..... *Synarthrophyton magellanicum*

Discussion

South Africa has similar numbers of non-geniculate coralline algal species to regions where comparable research investment has been made (e.g. the British Isles with 43 species [see Irvine and Chamberlain, 1994]; southern Australia with 40 species [see Womersley, 1996; Woelkerling, 1997]) and even more so than in other regions (e.g. central New Zealand with 20 species [see Harvey et al., 2005]). Our numbers appear particularly high when one considers that the aforementioned regions have coastlines of considerably longer lengths (British Isles – 13,877 km; southern Australia – 5,067 km; central New Zealand – ±6,000 km) than South Africa (2,789 km) (see CIA, 2005). The question of whether South Africa has a more diverse flora than any other country cannot be answered with any degree of certainty though, particularly as the non-geniculate coralline red algae as a whole are a relatively poorly studied group of marine organisms. The recorded number of taxa for South Africa (and other countries where this group of algae is receiving much attention) is no doubt a function of the renewed interest in this important group of algae. Additionally, many more species have yet to be discovered or studied, particularly the less common ones.

Chamberlain (1991) commented that modern studies (see e.g. Womersley, 1996; Woelkerling, 1997) would lead to the conclusion that there will be a considerable reduction in the number of accepted species once the type specimens are compared with modern collections. Chamberlain (1991) argued that this would become particularly true when one considers the vast number of previously poorly described taxa. While Woelkerling and Lamy (1998) cite examples of such poorly described works from older literature (see also Woelkerling, 1984; Chamberlain et al., 1991), many of the problems persist in modern research despite continued calls (e.g. Keats, 1997; Keats et al., 1997) to describe as many characters in sufficient detail to allow future researchers to assess specimens without having to resort to an analysis of already dwindling type specimens. Earlier, Seagrief (1984) noted that close to two thirds

of the specific names given to the seaweed flora of South Africa at that time (including the non-geniculate coralline algae) represented synonyms rather than valid names. Similarly, the coralline algal biodiversity of southern Australia was overestimated by 80% (Woelkerling, 1997), all of this attesting to Chamberlain's (1991) earlier remarks.

The proliferation of species has mostly been due to the fact that throughout his career, Foslie (and others) had erected a large number of taxa based largely or even solely on apparent differences in 1) external morphology, 2) sporangial conceptacle size and shape, and 3) internal vegetative anatomy (see Woelkerling, 1984). While Foslie (1905) concluded that many of his earlier taxa were probably synonymous (stating that he "... had partly laid too great a stress on the shape and size of conceptacles ..." and that "... a considerable reduction was necessary ..."), he continued in subsequent papers to distinguish species largely on differences in their external morphology (see Woelkerling, 1984). Nonetheless, the non-geniculate coralline algal publications and herbarium collections of Mikael Foslie arguably constitute the single most important resource for coralline taxonomists globally (Woelkerling, 1984; Woelkerling et al., 2005).

In conclusion, while South Africa appears to have a high diversity of non-geniculate coralline algae, this cannot be stated conclusively. This is so largely for two reasons. First, the taxonomy of the non-geniculate coralline algae on a global scale has undergone significant revision in recent years and consequently all species lists world-wide are in need of revision. Second, as a group, the non-geniculate coralline algae are often very cryptic (appearing like other encrusting organisms such as corals, sponges, bryozoans, etc) with many taxa often occurring locally in very low abundance. Many of the recent advances in the taxonomy of this group have largely been focused on the more abundant species. In order to remedy the situation, it is therefore imperative that (besides ongoing taxonomic revision and species descriptions) we continue to revisit and construct modern-day species lists, popular guides and keys of this so-called "problematic" group of marine algae.

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[i] Seagrief (1984) catalogues a list of 1567 specific names that have been applied to South African green, brown and red (including non-geniculate coralline algae) marine algae, roughly two thirds of which are synonyms. But, whether or not each of these synonyms actually relates to a sampled specimen from South Africa is unclear. Cross-referencing many of Seagrief's citations suggests that the latter has not been the case. The above table therefore comprises only names of taxa known to have been sampled from South Africa under these names.