# Systematics of the non-geniculate coralline red algae from the South African south coast

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A thesis submitted in fulfillment of the requirements for the degree PhD in the Department of Biodiversity and Conservation Biology, University of the Western Cape.

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August 2015

**I declare that**

***"Systematics of the non-geniculate coralline red algae***

***from the South African south coast"***

**is my own work, that it has not been submitted for any degree or examination at any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.**

**……………………………………………..** **24 August 2015**
**…………………..**

Elizabeth van der Merwe Date

This thesis is dedicated to my family.

To my mother, Beatrix, my brother (Jors), my sisters (Francina and Koekie)
and my children (Dante, Belinda, Amandus and Roland) who never stopped believing in me
and waited with great anticipation and expectation.
All the glory and honor to my heavenly father, the Almighty who kept me always in his hand,
and never deserted me for a moment through all my life.

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## 1.1 Non-geniculate coralline algae versus geniculate coralline algae

Coralline algae are red seaweeds that deposit calcium carbonate (as calcite) in their cell walls (Farr *et al*., 2009). Traditionally coralline algae have been divided into two groups, namely geniculate corallines and non-geniculate corallines, although this division does not constitute a taxonomic grouping (Johansen, 1976). Geniculate coralline algae consist of attached, branched fronds that are made flexible by non-calcified segments (genicula) separating longer calcified segments (intergenicula) (Johansen, 1976; Garbary and Johansen, 1987; Woelkerling and Nelson, 2004; Harvey *et al*., 2005; Harvey and Woelkerling, 2007). Non-geniculate coralline algae are unbranched (or non-articulated or crustose or encrusting), lack the uncalcified segments (genicula) and so are completely calcified, except for the outermost walls of their epithallial cells that are only weakly calcified (Johansen, 1976; Harvey *et al*., 2005; Farr *et al*., 2009). The growth-forms (see Woelkerling *et al*., 1993 for growth-forms in non-geniculate coralline algae) of non-geniculate coralline algae vary over a wide spectrum and a single species may display several different growth morphotypes.

## 1.2 Non-geniculate coralline algae

### 1.2.1 Distribution

Non-geniculate coralline red algae (Rhodophyta, Corallinophycidae) are widespread in all of the world's oceans where they often form the dominant cover on primary rocky substrata and on reefs (Adey, 1973; Adey and MacIntyre, 1973; Littler and Doty, 1975; Adey *et al.*, 1976; Johansen, 1976, 1981; Brattström, 1980; Zaneveld and Sanford, 1980; Steneck, 1982, 1985, 1986; Lubchenco *et al*., 1984; Paine, 1984; Littler *et al*., 1985; 1991; Kamura and Choonhabandit, 1986; Steneck and Paine, 1986; Woelkerling, 1988; Menge and Farrell, 1989; Dethier *et al*., 1991; John and Lawson, 1991; Steneck *et al*., 1991; Brosnan, 1992;

Keats *et al*., 1993; Williams, 1993; Freiwald and Henrich, 1994; Keats and Maneveldt, 1994; Keats *et al*., 1994a, b; Björk *et al*., 1995; Wehrmann *et al*., 1995; Oliveira, 1996; Figueidero, 1997; Kikuchi and Leão, 1997; Littler and Littler, 1997; Payri, 1997; Steneck, 1997; Basso, 1998; Dethier and Steneck, 2001; Irving *et al*., 2004; Schwarz *et al*., 2005; Huisman and Saunders, 2007; Kuffner *et al*., 2007; Nelson, 2009). These algae generally display tolerances to a wide range of environmental factors, including wave energy (Adey and Vassar, 1975) and changing light conditions (Steneck, 1986), allowing them to occupy diverse habitats (Bosence, 1985; Rasser and Piller, 1997; Huisman and Saunders, 2007). Habitats include stable (primary bedrock) and unstable (pebbles, boulders, corals, other non-geniculate corallines or algae) environments from intertidal rock pools (Paine and Vadas, 1969; Dethier, 1984), to exposed intertidal and shallow subtidal zones (Stephenson and Stephenson, 1972; Steneck and Adey, 1976; Branch and Branch, 1981; Paine, 1980, 1984; Moore and Seed, 1986), to the deepest ocean basins (Adey, 1970; James and Ginsburg, 1979; Littler *et al*., 1985; Liddell and Ohlhorst, 1988; Dullo *et al*., 1990; Iryu *et al*., 1995; Steller and Foster, 1995). They are found occurring throughout a broad temperature range from the tropical and subtropical regions (e.g. *Hydrolithon*, *Kvaleya*, *Lithophyllum*, *Porolithon* and *Neogoniolithon* - see Adey and Sperapanie, 1971; Adey and Vassar, 1975; Adey *et al*., 1976; Steneck and Adey, 1976; Adey, 1978, 1979, 1986; Bosence, 1985; Braga and Aguirre, 2001; Aguirre *et al*., 2007), to the temperate (e.g. *Lithophyllum* - see Adey, 1986) and to polar regions (*Clathromorphum* - see Adey, 1966, 1968, 1971, 1973; Adey and MacIntyre, 1973; Lebednik, 1977; Steneck, 1982).

### 1.2.2 Substrate and Habit

Non-geniculate coralline algae generally occur epilithically (on the primary bedrock or other rocky substrates - Adey, 1971; Steneck, 1986), but may also occur epiphytically (on the surfaces of other algae and marine angiosperms - Steneck, 1986; Reyes and Afondso-Carillo, 1995; Kjøsterud, 1997; Beavington-Penney *et al*., 2004; Morcom *et al*., 2005; Nelson, 2009; Browne *et al*., 2013), epizoically (on the shells of marine molluscs - Adey, 1971; Steneck, 1986; Steneck and Paine, 1986; Nelson, 2009); and/or epigenously on various other artificial substrates (Nelson, 2009). These corallines may also occur unattached and free-living and are then generally referred to as rhodoliths (Adey and MacIntyre, 1973; Steneck, 1986; Ballantine *et al*., 2000; Harvey and Woelkerling, 2007; Nelson, 2009; Peña and Bárbara, 2010), rhodolites (Bosellini and Ginsburg, 1971; Montaggioni, 1979; Ballantine *et al*., 2000; Foster, 2001), rhodoids (Ballantine *et al*., 2000), nodules (Bosellini and Ginsburg, 1971; Montaggioni, 1979; Steneck, 1986; Ballantine *et al*., 2000; Lund *et al*., 2000), or maerl (Adey and McKibbin, 1970; Adey and MacIntyre, 1973; Steneck, 1986; Freiwald, 1993; Foster, 2001; Wilson *et al*., 2004; Nelson, 2009; Peña and Bárbara, 2010). The term 'rhodolith' was original coined by Barnes *et al*. (1970) to refer to "… a small nodular mass with a nucleus which is made of a debris, the shape of which can be botryoïd (like a bunch of grapes) or branching". The nucleus of the rhodolith is often covered by one or several species of non-geniculate coralline algae (Foster, 2001; Payri and Cabioch, 2004). Free-living rhodolith beds may occur in shallow areas subjected to increased water agitation (Lund *et al*., 2000; Payri and Cabioch, 2004; Amado-Filho *et al*., 2007, 2010) or may occur in deep water environments (Bosence, 1985; Montaggioni, 1979; Iryu *et al*., 1995; Harris *et al*., 1996; Lund *et al*., 2000; Amado-Filho *et al*., 2007; Bahia *et al*., 2011, 2014).

### 1.2.3 Ecological importance and abundance

Non-geniculate coralline algae are considered a key functional group of organisms on coral reef ecosystems where they are major constituents and maintainers of the reef structure (Adey, 1978; Littler, 1972, 1973; MacIntyre and Aronson, 1997; Camoin *et al*., 1999; Gherardi and Bosence, 2001; Rasser and Riegl, 2002; Webster *et al*., 2009). Not only do they act as reef cementers (Littler and Littler, 1994, 1997, Flamand *et al*., 2008), they are also important contributors to reef sedimentation (Wray, 1977; Braga and Aguirre, 2001; Bassi, 2005; Bassi *et al*., 2009; Braga *et al*., 2010) and act as food for a number of reef inhabitants (Brock, 1979; Borowitzka, 1981; Carpenter, 1981; Hay, 1984; Freiwald, 1993; Johnson and Sutton, 1994; Pitlik and Paul, 1997; Chrisholm, 2003).

In addition to these direct ecological benefits, non-geniculate coralline algae have a number of indirect benefits. Some corallines slough off a surface layer of epithallial cells, which not only serves an important antifouling function, but plays an important role in local biodiversity (Johnson and Mann, 1986; Littler and Littler, 1997). Non-geniculate corallines and their associated bacterial films provide important settlement cues for a variety of marine molluscs (Steneck, 1982). In addition, thick corallines provide important spatial refuges and microhabitats for many invertebrates and their larvae (Kaspar, 1992; Andrew, 1993; Kamenos *et al*., 2004; Fortunato and Schäfer, 2009). On a larger global scale, coralline algae assist in carbon sequestration and are reported to be one of the largest stores of carbon in the biosphere (Martin *et al*., 2007; Chung *et al*., 2011; Amado- Filho *et al*., 2012).

## 1.3 Classification of the non-geniculate coralline algae

Note that the following taxonomic hierarchical classification is provided only for the non-geniculate coralline red algae.

Phylum: Rhodophyta Wettstein, 1901: 46
Subphylum: Eurhodophytina G.W.Saunders & Hommersand, 2004: 1503
Class: Florideophyceae Cronquist, 1960: 438

**Subclass: Corallinophycidae L.Le Gall & G.W.Saunders, 2007: 1129**
**Order: Corallinales P.C.Silva & H.W.Johansen, 1986: 250; emendavit W.A.Nelson, J.E.Sutherland, T.J.Farr & H.S.Yoon, 2015: 464**
**Family: Corallinaceae J.V.Lamouroux, 1812: 185; emendavit A.S.Harvey, Broadwater, Woelkerling & Mitrovski, 2003: 993-994**

**1. Subfamily: Hydrolithoideae A.Kato & M.Baba, 2011: 669**
**Genera:**
1. *Hydrolithon* (Foslie) Foslie

**2. Subfamily: Lithophylloideae Setchell, 1943: 134**
**Genera:**
1. *Ezo* W.H.Adey, T.Masaki & Akioka
2. *Lithophyllum* Philippi
3. *Paulsilvella* Woelkerling, Sartoni & Boddi
4. *Titanoderma* Nägeli

**3. Subfamily: Mastophoroideae Setchell, 1943: 134; emendavit A.Kato & M.Baba, 2011: 669**
**Genera:**
1. *Mastophora* Decaisne
2. *Metamastophora* Setchell

The following genera placed previously under the Mastophoroideae still have to be dealt with appropriately but are considered here under the Mastophoroideae as per Harvey *et al*. (2003).

3. *Lesueuria* Woelkerling & Ducker
4. *Lithoporella* (Foslie) Foslie
5. *Pneophyllum* Kützing
6. *Spongites* Kützing

**4. Subfamily: Neogoniolithoideae A.Kato & M.Baba, 2011: 669**
**Genera:**
1. *Neogoniolithon* Setchell & L.R.Mason

**5. Subfamily: Porolithoideae A.Kato & M.Baba, 2011: 669**
**Genera:**
1. *Porolithon* (Foslie) Foslie

**Order: Hapalidiales W.A.Nelson, J.E.Sutherland, T.J.Farr & H.S.Yoon, 2015: 464**
**Genus:**
1. *Corallinapetra* T.J.Farr, W.A.Nelson & J.E.Sutherland[1]

**Family: Hapalidiaceae J.E.Gray, 1864: 22; emendavit A.S.Harvey, Broadwater, Woelkerling & Mitrovski, 2003: 995**

**1. Subfamily: Austrolithoideae A.S.Harvey & Woelkerling, 1995: 363**
**Genera:**
1. *Austrolithon* A.S.Harvey & Woelkerling
2. *Boreolithon* A.S.Harvey & Woelkerling
3. *Epulo* R.A.Townsend & Huisman

**2. Subfamily: Choreonematoideae Woelkerling, 1987: 125**
**Genus:**
1. *Choreonema* F.Schmitz

**3. Subfamily: Melobesioideae Bizzozero, 1885: 109**
**Genera:**
1. *Clathromorphum* Foslie
2. *Exilicrusta* Y.M.Chamberlain
3. *Kvaleya* W.H.Adey & Sperapani
4. *Lithothamnion* Heydrich
5. *Mastophoropsis* Woelkerling
6. *Melobesia* J.V.Lamouroux
7. *Melyvonnea* Athanasiadis & D.L.Ballantine
8. *Mesophyllum* Me.Lemoine
9. *Phymatolithon* Foslie
10. *Synarthrophyton* R.A.Townsend

**Order: Sporolithales L.Le Gall & G.W.Saunders, 2010: 305**
**Family: Sporolithaceae E.Verheij, 1993: 195**
**Genera:**
1. *Heydrichia* R.A.Townsend, Y.M.Chamberlain & Keats
2. *Sporolithon* Heydrich

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[1] The genus *Corallinapetra* has yet to be assigned to a family and subfamily.

## 1.4 Characterisation of the non-geniculate coralline algae

### 1.4.1 Subclass: Corallinophycidae L.Le Gall & G.W.Saunders, 2007: 1129

1. Pit plug with two cap layers at cytoplasmic faces, outer dome-shaped, membrane absent.
2. Carpogonial branches two-celled.
3. Tetrasporangia zonately or cruciately divided.
4. Calcification in the form of calcite.

### 1.4.1.1 Order: Corallinales P.C.Silva & H.W.Johansen, 1986: 250, emendavit W.A.Nelson, J.E.Sutherland, T.J.Farr & H.S.Yoon, 2015: 464

With the characteristcs of the Corallinophycidae (Le Gall and Saunders, 2007), and possessing:

1. multiple tetrasporangia in uniporate conceptacles;
2. tetrasporangia that are zonately divided;
3. tetrasporangial conceptacles lacking apical pore plugs; and
4. cell fusions or secondary pit connections.

### Family: Corallinaceae J.V.Lamouroux., 1812: 185; emendavit A.S.Harvey, Broadwater, Woelkerling & Mitrovski, 2003: 993-994

With the characteristics of the Corallinales (Nelson *et al*., 2015).

### Subfamily: Hydrolithoideae A.Kato & M.Baba 2011: 669

With the characteristics of the Corallinaceae (Harvey *et al*., 2003), and possessing:

1. thallus non-geniculate;

2. cells of contiguous vegetative filaments joined by cell fusions;
3. basal layer of non-palisade cells;
4. trichocytes absent in large tightly packed horizontal fields;
5. tetra/bisporangial conceptacles formed by filaments peripheral to the fertile area and interspersed among tetra/bisporangial initials; and
6. spermatangia developing on the floor of the male conceptacle.

**Genus: *Hydrolithon* (Foslie) Foslie, 1909: 55; emendavit A.Kato & M.Baba, 2011: 669**

With the characteristics of the Hydrolithoideae (Kato *et al*., 2011).

**Subfamily: Lithophylloideae Setchel, 1943: 134** (as ‘Lithophylleae’) (see Cabioch, 1972; Harvey *et al*., 2003)

With the characteristics of the Corallinaceae (Harvey *et al*., 2003), and possessing:

1. cells of contiguous vegetative filaments joined by secondary pit connections; cell fusions absent rare or absent; and
2. genicula (when present) composed of one or more tiers of cells.

**Genus: *Ezo* W.H.Adey, T.Masaki & Akioka, 1974: 331**

With the characteristics of the Lithophylloideae (Harvey *et al*., 2003), and possessing:

1. thallus non-geniculate and largely epigenous, forming small, applanate, crustose thalli that lack protuberances;
2. anchored to substrate (usually species of *Lithophyllum*) by cell adhesion and by haustoria that penetrate the host surface layers and become appressed to, or fuse with cells of the host; and
3. thallus construction dimerous, possessing a basal layer primarily of non-palisade cells.

**Genus:** ***Lithophyllum* Philippi, 1837: 387** (Chamberlain and Irvine, 1994a; Chamberlain, 1996)

With the characteristics of the Lithophylloideae (Harvey *et al*., 2003), and possessing:

1. thallus non-geniculate and lacking haustoria;
2. thallus construction predominantly dimerous, possessing a basal layer of predominantly non-palisade cells; and
3. no areas of bistratose thallus present, as the thallus begins to thicken immediately behind the primary meristematic cell.

**Genus:** ***Paulsilvella* Woelkerling, Sartoni & Boddi, 2002: 359**

With the characteristics of the Lithophylloideae (Harvey *et al*., 2003), and possessing:

1. thallus non-geniculate and lacking haustoria;
2. possessing protuberant branches that resemble a series of fused beads;
3. core region of protuberances composed of single arching tiers of elongate, columnar cells alternating with two tiers of short, non-columnar cells; and
4. an encrusting basal region which is dimerous while the upright bead-like branches are monomerous.

**Genus:** ***Titanoderma* Nägeli, 1858: 352** (Chamberlain and Irvine, 1994a; Chamberlain, 1996)

With the characteristics of the Lithophylloideae (Harvey *et al*. 2003), and possessing:

1. thallus non-geniculate and lacking haustoria;
2. thalli construction predominantly dimerous, possessing a basal layer of predominantly palisade cells; and

3. thallus partly to entirely bistratose (consisting of basal cell and an epithallial cell, thicker species have bistratose margins).

**Subfamily: Mastophoroideae Setchell, 1943: 134; emendavit A.Kato & M.Baba, 2011: 669**

With the characteristics of the Corallinaceae (Harvey *et al*., 2003), and possessing:

1. thallus non-geniculate;
2. cells of contiguous vegetative filaments joined by cell fusions;
3. basal layer of palisade cells;
4. trichocytes absent in large tightly packed horizontal fields;
5. tetra/bisporangial conceptacles formed from filaments peripheral to the fertile area; and
6. spermatangia developing on the floor of the male conceptacle.

**Genus: *Mastophora* Decaisne., 1842: 365** (Woelkerling, 1988; Womersley, 1996; Harvey *et al*., 2006)

With the characterisitcs of the Mastophoroideae (Kato *et al*., 2011), and possessing:

1. thallus lacking haustoria;
2. thallus construction dimerous;
3. thallus 2-3 (5) cells thick except where localized development or erect filaments occur and where conceptacle initiation is taking place; and
4. tetra/bisporangial conceptacles possessing a central columella.

**Genus: *Metamastophora* Setchell, 1943: 130** (Woelkerling, 1988; Womersley, 1996; Harvey *et al*., 2006)

With the characteristics of the Mastophoroideae (Kato *et al*., 2011), and possessing:

1. thallus lacking haustoria;
2. growth form arborescent (tree-like), thalli anchored to substrate by a holdfast and stipe, branch tips flattened and flabelliform;
3. thallus construction dimerous thallus; and
4. tetra/bisporangial conceptacles possessing a central columella.

The precise phylogenetic positions of *Lesueuria*, *Lithoporella*, *Pneophyllum* and *Spongites* still need to be confirmed (Kato *et al*., 2011).

**Genus: *Lesueuria* Woelkerling & Ducker, 1987: 193** (Woelkerling, 1988; Womersley, 1996; Harvey *et al*., 2006)

With the characteristics of the Mastophoroideae (Harvey *et al*., 2006), and possessing:

1. thallus endophytic, possessing haustoria;
2. thallus lacking a basal layer of palisade cells;
3. vegetative filaments that lack epithallial cells; and
4. tetra/bisporangial conceptacle pore canals lined by cells that arise from peripheral roof filaments; these cells are oriented more or less parallel.

**Genus: *Lithoporella* (Foslie) Foslie, 1909: 58** (Woelkerling, 1988; Womersley, 1996; Harvey *et al*., 2006)

With the characteristics of the Mastophoroideae (Harvey *et al*., 2006), and possessing:

1. thallus non-endophytic, lacking haustoria;

2. vegetative filaments that possess epithallial cells;
3. thallus possessing a basal layer of predominantly palisade cells; and
4. tetra/bisporangial conceptacle pore canals lined cells that arise from filaments interspersed among and surrounding the sporangial initials; these cells are orientated more-or less perpendicularly to the roof surface.

**Genus: *Pneophyllum* Kützing, 1943: 385** (Woelkerling, 1988; Womersley, 1996; Harvey *et al*., 2006)

With the characteristics of the Mastophoroideae (Harvey *et al*., 2006), and possessing:

1. thallus non-endophytic and lacking haustoria;
2. vegetative filaments that possess epithallial cells;
3. thallus lacking a basal layer of palisade cells; and
4. tetra/bisporangial roofs that develop from filaments interspersed among, as well as from peripheral filaments surrounding the sporangial initials;
5. tetra/bisporangial conceptacle pore canals lined by cells that arise from filaments interspersed among, as well as from filaments peripheral to the sporangial initials; these cells are oriented more or less parallel to the conceptacle roof surface.

**Genus: *Spongites* Kützing, 1841:30** (Woelkerling, 1988; Womersley, 1996; Harvey *et al*., 2006)

With the characteristics of the Mastophoroideae (Harvey *et al*., 2006), and possessing:

1. thallus non-endophytic and lacking haustoria;
2. vegetative filaments that possess epithallial cells;
3. thallus lacking a basal layer of palisade cells; and

4. tetra/bisporangial conceptacle pore canals lined by cells that arise from peripheral roof filaments; these cells are oriented more or less parallel to conceptacle roof surface.

**Subfamily: Neogoniolithoideae A.Kato & M.Baba, 2011: 669**

With the characteristics of the Corallinaceae (Harvey *et al*., 2003) and possessing:

1. thallus non-geniculate;
2. cells of contiguous vegetative filaments joined by cell fusions;
3. basal layer lacking palisade cells;
4. trichocytes absent in large tightly packed horizontal fields;
5. tetra/bisporangial conceptacles formed by filaments peripheral to the fertile area and interspersed among tetra/bisporangial initials; and
6. spermatangia developing on the floor and roof of the male conceptacle.

**Genus: *Neogoniolithon* Setchell & L.R.Mason, 1943: 89** (Woelkerling, 1988; Womersley, 1996; Harvey *et al*., 2006)

1. With the characteristics of the Neogoniolithoideae (Kato *et al*., 2011).

**Subfamily: Porolithoideae A.Kato & M.Baba, 2011: 669**

With the characteristics of the Corallinaceae (Harvey *et al*., 2003), and possessing:

1. thallus non-geniculate;
2. cells of contiguous vegetative filaments joined by cell fusions;
3. basal layer lacking palisade cells;
4. trichocytes present in large tightly packed horizontal fields;
5. tetra/bisporangial conceptacles formed by filaments peripheral to the fertile area and interspersed among tetrasporangial/bisporangial initials; and

6. spermatangia developing on the floor of the male conceptacle.

**Genus: *Porolithon* (Foslie) Foslie 1909: 57; emendavit A.Kato & M.Baba, 2011: 669**

With the characteristics of the Porolithoideae (Kato *et al*., 2011).

### 1.4.1.2 Order: Hapalidales W.A.Nelson, J.E.Sutherland, T.J.Farr & H.S.Yoon, 2015: 464

With the characteristics of the Corallinophycidae (Le Gall and Saunders, 2007), and possessing:

1. multiple tetrasporangia in multiporate conceptacles;
2. tetrasporangia that are zonately divided;
3. tetrasporangial conceptacles bearing apical pore plugs;
4. thallus non-geniculate; and
5. thallus lacking secondary pit connections

**Family: Not ascertained** (see Nelson *et al*., 2015)

**Subfamily: Not ascertained** (see Nelson *et al*., 2015)

**Genus: *Corallinapetra* T.J.Farr, W.A.Nelson & J.E.Sutherland, 2015: 459**

With the characteristics of the Hapalidiales (Nelson *et al*., 2015), and possessing:

1. flared epithallial cells;
2. cells of contiguous vegetative filaments joined by cell fusions;
3. gametangia in uniporate conceptacles;
4. tetra/bisporangia in individual compartments grouped in shallow depressions;

5. small tetra/bisporangial pores visible on thallus surface giving appearance of multiporate conceptacles;
6. stalk cells present.

**Family: Hapalidiaceae Gray, 1864: 22; emendavit A.S.Harvey, Broadwater, Woelkerling & Mitrovski, 2003: 995**

With the characteristics of the Hapalidiales (Nelson *et al*., 2015).

**Subfamily: Austrolithoideae A.S.Harvey & Woelkerling, 1995: 363**

With the characteristics of the Hapalidiaceae (Harvey *et al*., 2003), and possessing:

1. tetra/bisporangial conceptacle pore plate of cellular construction; and
2. cells of contiguous vegetative filaments not joined by either secondary pit connections or cell fusions.

**Genus: *Austrolithon* A.S.Harvey & Woelkerling, 1995: 363**

With the characteristics of the Australithoideae (Harvey *et al*., 2003), and possessing:

1. thallus endophytic, haustoria absent or unknown;
2. thallus composed partly or largely of unconsolidated filaments; and
3. thallus construction diffuse to partly monomerous.

**Genus: *Boreolithon* A.S.Harvey & Woelkerling, 1995: 374**

With the characteristics of the Australithoideae (Harvey *et al*., 2003), and possessing:

1. thallus non-endophytic
2. thallus no composed of unconsolidated filaments; and
3. thallus construction dimerous.

**Genus:** ***Epulo*** **R.A.Townsend & Huisman, 2004: 289**

With the characteristics of the Australithoideae (Harvey *et al*., 2003), and possessing:

1. thallus endophytic and possessing haustoria;
2. thallus composed partly or largely of unconsolidated filaments; and
3. thallus construction diffuse to monomerous.

**Subfamily: Choreonematoideae Woelkerling, 1987: 125** (Harvey *et al*., 2003)

With the characteristics of the Hapalidiaceae (Harvey *et al*., 2003), and possessing:

1. tetra/bisporangial conceptacle pore plate acellular at maturity, composed only of a calcium carbonate matrix; and
2. cells of contiguous vegetative filaments joined by neither secondary pit connections nor cell fusions.

**Genus:** ***Choreonema*** **F.Schmitz, 1889: 455** (Woelkerling, 1987)

With the characteristics of the Choreonematoideae (Woelkerling, 1987).

**Subfamily: Melobesioideae Bizzozero, 1885: 109** (as 'Melobesieae') (Womersley, 1996; Harvey *et al*., 2003)

With the characteristics of the Hapalidiaceae (Harvey *et al*., 2003), and possessing:

1. tetra/bisporangial conceptacle pore plate of cellular construction.

**Genus:** ***Clathromorphum*** **Foslie, 1898:4** (Woelkerling, 1988)

With the characteristics of the Melobesioideae (Harvey *et al*., 2003), and possessing:

1. thallus lacking haustoria;
2. growth-form not arborescent;

3. thallus construction monomerous throughout;
4. outermost walls of terminal epithallial cells rounded or flattened, but not flared;
5. subepithallial initials usually as long as or longer than cells immediately subtending them;
6. spermatangial conceptacle roofs formed vertically by continued meristematic activity in the filaments that form spermatangial initials; and
7. simple (unbranched) spermatangial systems confined to the floor, walls and roof of male conceptacle chambers.

**Genus: *Exilicrusta* Y.M.Chamberlain., 1992: 185**

With the characteristics of the Melobesioideae (Harvey *et al*., 2003), and possessing:

1. thallus lacking haustoria;
2. growth-form not arborescent;
3. thallus construction dimerous;
4. flared epithallial cells;
5. spermatangial conceptacle roof development uncertain; and
6. simple (unbranched) spermatangial systems confined to the floor of male conceptacle chambers.

**Genus: *Kvaleya* W.H.Adey & Sperapani, 1971:31** (Woelkerling, 1988)

With the characteristics of the Melobesioideae (Harvey *et al*., 2003), and possessing:

1. thallus possessing haustoria;
2. growth-form not arborescent;
3. thallus construction monomerous;

4. epithallial cells commonly absent, but when present the outermost walls are rounded or flattened, but not flared;
5. subepithallial initials as short as or shorter than the cells immediately subtending them;
6. spermatangial conceptacle roofs formed from groups of filaments peripheral to the fertile area; and
7. simple (unbranched) spermatangial systems confined to the floor, walls and roof of male conceptacle chambers.

**Genus: *Lithothamnion* Heydrich, 1897: 412** (Womersley, 1996)

With the characteristics of the Melobesioideae (Harvey *et al*., 2003), and possessing:

1. thallus lacking haustoria;
2. growth-form not arborescent;
3. thallus construction monomerous;
4. flared epithallial cells;
5. subepithallial initials usually as long as or longer than cells immediately subtending them;
6. spermatangial conceptacle roofs formed from groups of filaments peripheral to the fertile area; and
7. both simple (unbranched) and dendroid (branched) spermatangial systems confined to the floor, walls and roof of male conceptacle chambers.

**Genus: *Mastophoropsis* Woelkerling, 1978: 210** (Woelkerling, 1988; Womersley, 1996)

With the characteristics of the Melobesioideae (Harvey *et al*., 2003), and possessing:

1. thallus lacking haustoria;

2. growth-form arborescent, composed of a distinct holdfast with a stipe that bears flattened branches;
3. thallus construction monomerous;
4. outermost walls of terminal epithallial cells rounded or flattened, but not flared;
5. subepithallial initials as short as or shorter than the cells immediately subtending them;
6. spermatangial conceptacle roof development uncertain; and
7. simple (unbranched) spermatangial systems confined to the floor, walls and roof of the male conceptacle chamber.

**Genus: *Melobesia* J.V.Lamouroux, 1812: 186** (Wilks and Woelkerling, 1991)

With the characteristics of the Melobesioideae (Harvey *et al*., 2003), and possessing:

1. thallus lacking haustoria;
2. growth-form not arborescent;
3. thallus construction dimerous;
4. outermost walls of terminal epithallial cells rounded or flattened, but not flared;
5. subepithallial initials cell elongation characteristics uncertain;
6. spermatangial conceptacle roof development uncertain; and
7. simple (unbranched) spermatangial systems confined to the floor, walls and roof of male conceptacle chambers.

**Genus: *Melyvonnea* Athanasiadis & D.L.Ballantine, 2014: 391**

With the characteristics of the Melobesioideae (Harvey *et al*., 2003), and possessing:

1. thallus lacking haustoria;
2. growth-form not arborescent;
3. thallus construction monomerous;

4. outermost walls of terminal epithallial cells rounded or flattened, but not flared;
5. subepithallial initials usually as long as or longer than cells immediately subtending them;
6. spermatangial conceptacle roof development unknown;
7. simple (unbranched) spermatangial systems confined to the floor, walls and roof of male conceptacle chambers.
8. erect cortical protuberances that may branch and dominate over the basal thallus;
9. monoecious gametophytes with conceptacles occasionally formed in sequence (superimposition);
10. spheroid carposporangial chambers (lacking a central pedestal); and
11. filaments lining the pores of tetra/bisporangial conceptacles composed of 3-5 cells (the basal cells being elongate).

**Genus: *Mesophyllum* Me.Lemoine, 1928: 251; emendavit Athanasiadis & D.L.Ballantine, 2014: 418**

With the characteristics of the Melobesioideae (Harvey *et al*., 2003), and possessing:

1. thallus lacking haustoria;
2. growth-form not arborescent;
3. thallus construction monomerous throughout.
4. outermost walls of terminal epithallial cells rounded or flattened, but not flared;
5. subepithallial initials usually as long as or longer than cells immediately subtending them;
6. spermatangial conceptacle roofs formed from groups of filaments peripheral to the fertile area;

7. simple (unbranched) spermatangial systems confined to the floor, walls and roof of male conceptacle chambers;
8. absence of cortical protuberances;
9. gametophytes dioecious;
10. carposporangial chambers with a distinctive central pedestal that supports the fertile area; and
11. filaments lining the pores of tetra/bisporangial conceptacles are non-differentiated and composed of more than 5 cells.

**Genus: *Phymatolithon* Foslie, 1898: 4** (Woelkerling, 1988)

With the characteristics of the Melobesioideae (Harvey *et al*., 2003), and possessing:

1. thallus lacking haustoria;
2. growth-form not arborescent;
3. thallus construction monomerous;
4. outermost walls of terminal epithallial cells rounded or flattened, but not flared;
5. subepithallial initials usually as short as or shorter than cells immediately subtending them;
6. spermatangial conceptacle roofs formed from groups of filaments peripheral to the fertile area; and
7. both simple (unbranched) and dendroid (branched) spermatangial systems confined to the floor, walls and roof of male conceptacle chambers

**Genus: *Synarthrophyton* R.A.Townsend, 1979: 252** (May and Woelkerling, 1988)

With the characteristics of the Melobesioideae (Harvey *et al*., 2003), and possessing:

1. thallus lacking haustoria;

2. growth-form not arborescent;
3. thallus construction monomerous throughout;
4. outermost walls of terminal epithallial cells rounded or flattened, but not flared;
5. subepithallial initials usually as long as or longer than cells immediately subtending them;
6. dendroid (branched) or both dendroid and simple (unbranched) spermatangial systems confined to the floor, walls and roof of male conceptacle chamber.

#### 1.4.1.3 Order: Sporolithales L.LeGall & G.W.Saunders, 2010: 305

With the characteristics of the Corallinophycidae (Le Gall and Saunders, 2007), and possessing:

1. tetrasporangia borne individually in calcified compartments;
2. tetrasporangia which are cruciately divided;
3. tetrasporangial compartments bearing apical pore plugs; and
4. both cell fusions and secondary pit connections present.

**Family: Sporolithaceae E.Verheij, 1993: 195** (Le Gall *et al*., 2010; Townsend *et al*. 1995)

With the characteristics of the Sporolithales (Le Gall and Saunders, 2010):

**Genus: *Heydrichia* R.A.Townsend., Y.M.Chamberlain & Keats, 1994: 178**

With the characteristics of the Sporolithaceae (Le Gall and Saunders, 2010; Townsend *et al*. 1995), and possessing:

1. outermost walls of terminal epithallial cells flattened and flared at their corners;
2. tetrasporangia borne on multiple stalk cells that result from the production of successive sporangia; and

3. tetrasporangial compartments surrounded by an involucre of narrow, elongate cells that differ from the ordinary vegetative cells.

**Genus: *Sporolithon* Heydrich, 1897: 66** (Le Gall and Saunders, 2010; Townsend *et al*., 1995)

With the characterisitcs of the Sporolithaceae (Verheij, 1993), and possessing:

1. outermost walls of terminal epithallial cells flattened and flared at their corners;
2. tetrasporangia borne on a single stalk cell that does not produce successive sporangia; and
3. tetrasporangial compartments not surrounded by an involucre.

## 1.5 South Africa's non-geniculate coralline algae

The South African rocky intertidal and subtidal habitats are rich in diversity and abundance of non-geniculate coralline algae (Maneveldt *et al*., 2008). Few scattered records of coralline algae were published prior to 1993, but these are now treated with caution since many taxa have undergone major taxonomic review since then. Reference to these older records as well as works published between 1993 and 2007 were gathered in a single publication (Maneveldt *et al*., 2008) as a catalogue with keys to the then known South African non-geniculate coralline algae.

Maneveldt *et al*. (2008) reported that the non-geniculate coralline algal diversity for South Africa was comparable to other regions (e.g. British Isles, southern Australia) where similar research investment had been made, and even more so than in still other regions (e.g. central New Zealand). The South African diversity is notably higher on a per area basis when one considers that the coastlines of these comparative regions far exceed the South African coastline of roughly 3000 km. The number of species for South Africa (and other regions where the non-geniculate coralline algae is receiving much attention) is no doubt a function of the sampling effort and more than likely would reveal a number of new records and possibly species new to science.

## 1.6 Aim of this study

The account by Maneveldt *et al*. (2008) represents the most up to date assimilated account of the non-geniculate coralline algae for South Africa. Maneveldt *et al*. (2008) concluded that the true diversity of the South African non-geniculate coralline algae could not be decisively stated and suggested that some of the reasons were the fact that many species were very cryptic and still others often occurred locally in very low abundance. In addition, while Maneveldt *et al*. (2008) sampled around the entire South African coastline, a huge gap exists in our knowledge of the South African south coast (see Maneveldt *et al*., 2008: 558 map of their sampling locations). Ongoing global taxonomic changes as well as the lack of complete records for South Africa have meant that the inventory of the South African non-geniculate coralline algae (let alone the host of geniculate coralline algae that are equally abundant) is incomplete.

The aim of this study was therefore to document the intertidal and shallow subtidal species of non-geniculate coralline red algae from the South Africa south coast. The main emphasis of the study are encompassed in four research chapters and one concluding chapter focusing on: 1) the documentation of the non-geniculate coralline red algae occurring along the South Africa south coast; 2) revisiting the *Leptophytum-Phymatolithon* complex in order to resolve the taxonomic status of species previously ascribed to the genus *Leptophytum* from South African; 3) starting to prepare modern monographic accounts of the higher taxa; and 4) the production of updated keys to all the currently recognised taxa of non-geniculate coralline algae for South Africa. Although nowhere near complete, here we present our findings and report on the current biodiversity status of the non-geniculate coralline red algae after a further four years of extensive sampling.

## 1.7 NAMES OF JOURNALS

### 1.7.1 *Phycologia*

### 1.7.2 *South African Journal of Botany*

## 1.8 List of Papers

### 1.8.1 Paper 1.

Maneveldt G.W. & Van der Merwe E. 2012. *Heydrichia cerasina* sp. nov. (Sporolithales, Corallinophycidae, Rhodophyta) from the southernmost tip of Africa. *Phycologia* 51(1): 11–21.

### 1.8.2 Paper 2.

Van der Merwe, E., Maneveldt, G.W. 2014. The genus *Phymatolithon* (Hapalidiaceae, Corallinales, Rhodophyta) in South Africa, including species previously ascribed to *Leptophytum*. *South African Journal of Botany* 90:170–192.

### 1.8.3 Paper 3.

Van der Merwe E., Miklasz K., Channing A., Maneveldt G.W. & Gabrielson P.W. 2015. DNA sequencing resolves species of *Spongites* (Corallinales, Rhodophyta) in the Northeast Pacific and South Africa, including *S. agulhensis* sp. nov. *Phycologia* 54(5), in press.

### 1.8.4 Paper 4.

Van der Merwe, E. & Maneveldt, G.W. 2015. A modern account of the South African non-geniculate Lithophylloideae (Corallinales, Corallinophycidae, Rhodophyta). *South African Journal of Botany*: in press.

# Chapter 2: Paper 1

## *Heydrichia cerasina* sp. nov. (Sporolithales, Corallinophycidae, Rhodophyta) from the southernmost tip of Africa

This Chapter has been published as:

Maneveldt G.W. & Van der Merwe E. 2012. *Heydrichia cerasina* sp. nov. (Sporolithales, Corallinophycidae, Rhodophyta) from the southernmost tip of Africa. *Phycologia* 51(1): 11–21.

# ***Heydrichia cerasina* sp. nov. (Sporolithales, Corallinophycidae, Rhodophyta) from the southernmost tip of Africa**

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Running Head: *Heydrichia cerasina* sp. nov.

Keywords: *Heydrichia*; *H. cerasina*; non-geniculate coralline algae; South Africa; Sporolithales; taxonomy.

## ABSTRACT

A new species of *Heydrichia* (Sporolithales), *H. cerasina* sp. nov., is described, found only on pebbles in the low intertidal zone along a 10 km stretch of the South African south coast from Cape Agulhas to Struisbaai. The species is characterized by the following suite of features that distinguish it from the other two species of *Heydrichia* found in South Africa: 1) unusual cherry-red colour when freshly collected; 2) uniformly warty growth from; 3) relatively thin crust (to 1400 µm thick); 4) tetra/bisporangial sori comprised of mostly single sporangial chambers; and 5) unbranched spermatangial structures distributed on the floor, walls and roof of the mature male conceptacle. The species appears to be most closely related to *H. homalopasta* from Australia. This study has affirmed that the distribution of spermatangial structures within male chambers is a feature that cannot be used to separate *Heydrichia* from *Sporolithon*, the only other genus in Sporolithales, although features of thallus construction and tetra/bisporangia continue to distinguish the genera. A key to the southern African species from the order Sporolithales is provided.

## INTRODUCTION

Non-geniculate coralline red algae are widespread in all of the world's oceans (Adey & MacIntyre 1973; Johansen 1981; Littler & Littler 2000; 2003), where they often form the dominant cover on primary rocky substrata (Lee 1967; Adey 1978; Littler 1973; Adey *et al*. 1982; Steneck 1986; Keats & Maneveldt 1994; Maneveldt & Keats 2008). Despite their ubiquity, they are a comparatively poorly known group of marine organisms. Much of this lack of knowledge stems from a legacy of poor quality taxonomic work (summarised in Woelkerling & Lamy 1998). Over the past few decades though, great strides have been made in redressing this lack of taxonomic understanding (e.g., Penrose & Woelkerling 1988; 1992; Harvey *et al*. 2003).

In keeping with the trend to document and understand the world's non-geniculate coralline red algae, studies are being made of the taxonomy of South African species, and many are now known in a modern context. Although Maneveldt *et al*. (2008) gathered together all the information on non-geniculate coralline red algae from recent references and other earlier but dubious records from South Africa into a single publication, there still exists a gap in our knowledge of this group from South Africa. During investigations, a non-geniculate coralline red alga attributable to the genus *Heydrichia* R.A.Townsend, Y.M.Chamberlain & Keats was commonly found on small pebbles (ranging from 10-40 mm along the long axis) at the low-water mark of spring tides along a 10 km stretch of coastline. This paper presents the formal description of the new species, compares it against all previously documented species found to conform to the generic description of *Heydrichia*, and provides a key to the known species of the order Sporolithales L.Le Gall & G.W.Saunders (Le Gall *et al.* 2010) from southern Africa, to which this genus belongs.

## MATERIAL AND METHODS

Field collections were made in the low intertidal zone of the Western Cape Province, South Africa. Pebbles bearing the algae were collected. Plants were examined as far as possible when fresh; otherwise they were air-dried or fixed in neutralized 10% commercial formalin seawater (4% formaldehyde) and stored in a 70% ethanol : 10% glycerol : 20% distilled water solution.

For scanning electron microscopy (SEM), air-dried material was fractured using either forceps, diagonal cutters, or a small hammer and cold chisel. The fractured pieces were mounted on stubs, using adhesive tabs (Agar Scientific Ltd., M11 Business Link, Parsonage Lane, Stansted, Essex CM24 8GF, UK), stored in a desiccator for at least 24 h prior to examination, coated with gold for 4-6 min in an Edwards S150B sputter coater, and examined with a Hitachi X650 scanning electron microscope at an accelerating voltage of 25 kV.

For light microscopy, formalin preserved specimens were first decalcified in 10 % nitric acid. Thereafter, specimens were immersed in 70 %, 90 % and 100 % ethanol solutions respectively for a minimum of 60 mins each in order to displace any water and acid in the specimens. Thereafter, each specimen was removed from the 100 % ethanol and allowed to air dry for no more than a few seconds. Specimens were then immersed in Leica Historesin filtration medium for several hours until completely infiltrated. A hardening solution was then added to the infiltration medium and the specimens orientated in this final solution until set. Gelling of the hardener usually occurred within 15 - 25 mins; for more rapid hardening, specimens were placed immediately in an oven at 60 °C for approximately 5 - 10 mins.

Specimens were then sectioned at 6 - 12 µm thickness using a Bright 5030 microtome. Sequential sections were removed from the microtome blade using a fine sable hair brush and transferred to a slide covered with distilled water. In this way, multiple sections were orientated on a single slide. Slides were then left to air dry for at least 24 hrs so that sections could stick. Once dried, slides bearing the sections were stained with toluidine blue (0.25 g borax 100 ml$^{-1}$ and 0.06 g toluidine blue 100 ml$^{-1}$), again left to air dry, and later covered with cover slips using DPX Mountant for microscopy (BDH Laboratory Supplies, The Birches, Willard Way, Imberhorne Industrial Estate, East Grinstead, West Sussex RH19 1XZ, UK).

In cell measurements, length donates the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. Conceptacle measurements follow Adey and Adey (1973). Thallus anatomical terminology follows Chamberlain (1990). Morphological (growth forms) terminology follows Woelkerling *et al*. (1993). Herbarium codes are those used in *Index Herbariorum*, previously in print (Holmgren *et al.* 1990) and now electronically online (Thiers 2011, continuously updated).

## OBSERVATIONS

### *Heydrichia cerasina* Maneveldt & E.van der Merwe, sp. nov.

(Figs 1-27)

Thalli firme ad parvos calculos affixi, proprie cerasini. Plantae verruculosae propter superficiem protuberationibus numerosis, crebrissimis, brevibus, obtusis obtectam. Thalli dorsiventrales. Medulla tenuis et plumosa (non-coaxialis). Cellulae et medullae et corticis aeque globulosae, cellulis filorum contiguorum conjunctionibus cellularum conjunctis. Cellulae epithalliales complanatae et in angulis dilatatae. Conceptacula spermatangialia (mascula) structurae spermatangiales simplices ferentia quae trans solum, parietes et tectum cubiculi maturi conceptaculae crescent. Conceptacula carposporangialia (foeminea) cellula centrali conjungenti carentia, filamentis bicellularibus gonimoblastorum dorsaliter per solum et parieties cubiculi conceptacularis orientibus. Sori tetra/bisporangiales plerumque systema sporangialia singula cubiculis uniporatis supra superficiem ambientis thalli elevatis, poris singularibus cellulis 6–10 rosularibus ad canalem pori depressis circumcinctis. Cubicula tetra/bisporangialia singula involucro 1–3 filamentorum quorum cellulae tenues sunt circumcincta, pro parte maxima tetrasporangia cruciate divisa, stipite aliquot (1–4) cellularum subtenta, ferentes.

Thalli firmly attached to small pebbles; thalli characteristically cherry-red in colour. Plants warty in appearance due to the surface covered by numerous densely crowded short, blunt protuberances. Thalli dorsiventral. Medulla thin and plumose (non-coaxial). Cells of both medulla and cortex uniformly bead-like, with cells of contiguous filaments joined by cell fusions. Epithallial cells flattened and flared at their corners. Spermatangial (male) conceptacles bear unbranched spermatangial structures that develop across the floor, walls and roof of the mature conceptacle chamber. Carposporangial (female) conceptacles lack a central fusion cell and short, 2-celled gonimoblast filaments arise dorsally across the floor and walls of the conceptacle chamber. Tetra/bisporangial sori mostly as single sporangial complexes displaying uniporate chambers that are raised above the surrounding thallus surface, with the individual pores surrounded by 6-10 rosette cells that are sunken toward the pore canal. Individual tetra/bisporangial chambers surrounded by an involucre of 1-3 thin-celled filaments, and bear mostly cruciately divided tetrasporangia subtended by multiple (1-4) stalk cells.

HOLOTYPE: L 0821464, 16.vi.2010, *leg. G.W. Maneveldt, E. van der Merwe, C. van Gass & O. van Gass*, on small pebble at the low-water mark of spring tide in sandy gully flanked by rugged rocky outcrops, Fig. 2.

ISOTYPES: L 0821455-63, Fig. 3, and UWC 10/144.

TYPE LOCALITY: South Africa. Western Cape Province, Cape Agulhas: L'Agulhas (S 34° 49,609´; E 20° 01,783´).

ETYMOLOGY: *cerasina* from the Latin *cerasinus* referring to the characteristic cherry-red colour of fresh, living plants.

DIAGNOSIS: The new species differs from all previously described species of *Heydrichia* by possessing a uniformly warty growth form and occurring only on pebbles. Similar to *H. homalopasta* R.A.Townsend & Borowitzka, the tetra/bisporangial sori of *H. cerasina* are comprised of mostly single (but also clusters of 2-5) chambers whereas those of *H. groeneri* Keats & Y.M.Chamberlain and *H. woelkerlingii* R.A.Townsend, Y.M.Chamberlain & Keats are composed of numerous sporangial complexes. Also similar to *H. homalopasta*, *H. cerasina* displays unbranched spermatangial structures distributed across the floor, walls and roof of mature male conceptacle chambers as opposed to the branched ones found only on the floor of the male conceptacle chambers, so far known for the type species of the genus.

REPRESENTATIVE SPECIMENS EXAMINED: Eight sets of samples totalling 250 pebbles (including the holotype and isotypes) were examined, these representing our entire collection for this taxon.

South Africa. Western Cape Province: Struisbaai (S 34° 48,847´; E 20° 02,975´), in low shore tidepools and sandy gullies at the low-water mark of spring tide, 07.vii.2009, *G.W. Maneveldt & E. van der Merwe*, UWC 09/116 ; Cape Agulhas, L'Agulhas, in sandy gullies at the low-water mark of spring tide (S 34° 49,461´; E 20° 01,196´, 08.vii.2009, *G.W. Maneveldt & E. van der Merwe*, UWC 09/137); (S 34° 49,433´; E 20° 01,814´, 15.vi.2010, *G.W. Maneveldt & E. van der Merwe*, UWC 10/134); (S 34° 49,609´; E 20° 01,783´, 16.vi.2010, *G.W. Maneveldt, E. van der Merwe, C. van Gass & O. van Gass*, L 0821464); (S 34° 49,609´; E 20° 01,783´, 16.vi.2010, *G.W. Maneveldt, E. van der Merwe, C. van Gass & O. van Gass*, L 0821455-63); (S 34° 49,609´; E 20° 01,783´, 16.vi.2010, *G.W. Maneveldt, E. van der Merwe, C. van Gass & O. van Gass*, UWC 10/144); (S 34° 49,615´; E 20° 01,753´, 23.x.2010, *G.W. Maneveldt, A.J. Maneveldt & J.D. Maneveldt*, UWC 10/300); (S 34° 49,653´; E 20° 00,748´, 24.x.2010, *G.W. Maneveldt & C. van Gass*, UWC 10/301).

DISTRIBUTION: Known only from South Africa; Western Cape Province, Struisbaai westward to L'Agulhas (Cape Agulhas). The species has a remarkably limited distribution of only about 10 km. Despite extensive collections either side of the recorded distribution, no other specimens were found.

HABIT: Plants are non-geniculate and grow on small pebbles (29.57 ± 0.63 mm in length by 19.68 ± 0.39 mm in width; values as means ± se, N = 250 pebbles) (Figs 1-3). Crusts are firmly adherent and when freshly collected, living plants are characteristically cherry-red in colour (Fig. 1). Thalli measure up to 1400 µm thick and have a distinctly warty appearance resulting from the numerous densely crowded short, blunt, sometimes fused protuberances that measure 360-810 µm in height and 350-1340 µm in diameter (Fig. 4).

VEGETATIVE ANATOMY: The thallus is dorsiventrally organised, and haustoria are absent (Fig. 5). The medulla is extremely thin and plumose (non-coaxial) (Figs 5-6, 8-9), composed of 1-5 filaments aligned more or less parallel to the substratum and measuring 5-20 µm thick. Cells of medullary filaments are rectangular to elongate with cell lumens often uniformly bead-like (Figs 8-9), measuring 7-15 µm in length and 2-6 µm in diameter. Fusions between cells of contiguous medullary filaments are abundant and frequently occupy most of the adjoining cell wall. Secondary pit connections have not been observed in either the medulla or cortex. The cortex comprises the bulk of the thallus thickness (Figs 5-6) and after decalcification, is rather loosely coalescent (Fig. 6). Cells of cortical filaments are rectangular to square with cell lumens also often uniformly bead-like, measuring 5-10 µm in length and 4-9 µm in diameter. Fusions between cells of contiguous cortical filaments are abundant and frequently occupy most of the adjoining cell wall. Subepithallial initials are square to rectangular, measure 5-11 µm in length and 5-10 µm in diameter, and are similar in size to the subtending cells. Epithallial cells occur in a single layer, are flattened with flared corners (Fig. 7) and measure 2-5 µm in length and 5-10 µm in diameter.

REPRODUCTIVE ANATOMY: Gametangial plants are dioecious. Spermatangial (male) conceptacles are conical, raised above the surrounding thallus surface and measure 196-294 (368) µm in external diameter and 37-110 µm in external height (Figs 10-11). Their chambers are transversely elliptical and measure 147-198 µm in diameter and 74-105 µm high, with the roof no more than 61 µm thick and nearly three times as thick along the pore canal. The roof is formed from filaments that arise peripheral to the fertile area, the terminal initials of which are more elongate than the surrounding cells. As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate and projecting into the pore in fully developed conceptacles (Fig. 12). Terminal initials near the pore opening are broader and more elongate and project slightly out of the pore. A mucilage plug often occludes the pore (Figs 11-12). Unbranched spermatangial structures develop across the floor, walls and roof of the mature male conceptacle (Figs 13-15). Male conceptacles and tetra/bisporangial chambers are commonly observed to occur on the same specimens (Fig. 6). Senescent male conceptacles appear to be shed from the thallus surface as no buried conceptacles have been observed.

Female plants with carpogonia have not been observed, but after presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles. Carposporangial conceptacles are larger than male conceptacles and are raised above the surrounding thallus surface measuring 281-870 (960) µm in external diameter and 37-74 (117) µm in external height (Figs 16-18). These conceptacles are broad, low-domed structures with a prominent raised central pore canal. This latter feature gives a false impression of the conceptacle diameter which is slightly buried in the thallus (Figs 16, 18). Their chambers are transversally elliptical and measure 220-280 µm in diameter and 100-140 (170) µm high, with the roof no more than 98 µm thick. Roof formation is similar to that of male conceptacles. Unlike male conceptacles, however, female conceptacles appear to be produced successively in the cortex directly above, and in the same area as the modified cortex of an earlier generation (Figs 17-19). A central fusion cell is absent, and short, 2-celled gonimoblast filaments, including a terminal carposporangium that at maturity measures 32-69 µm in length and 15-34 µm in diameter, arise dorsally across the floor and walls of conceptacle chambers (Figs 17-18, 20). Senescent female conceptacles appear to be shed from the thallus surface as no buried conceptacles have been observed.

Tetra/bisporangial sori are formed in a superficial, raised layer above the surrounding thallus surface (Fig. 23). Individual tetra/bisporangial chambers are uniporate (Figs 21-26) and occur either singly and isolated (Figs 21, 24-25), or in clusters of 2-5 chambers (Fig. 26). Chambers are transversely elliptical to rounded, measure 32-51 µm in diameter and 34-51 µm high, and are surrounded by an involucre of 1-3 thin-celled filaments. Chamber pores measure 7-15 µm in diameter and are surrounded by 6-10 rosette cells (Fig. 22) that are sunken toward the pore opening. Entire senescent tetra/bisporangial sori are sloughed off (Fig. 23) from the outer thallus and secondary cortical growth commonly occurs to infill individual old sporangial lumens (Fig. 27). Within sori, each chamber bears only one tetra/bisporangium in which the planes of division are mostly either in the same plane, or at right angles to one another. Consequently either zonately arranged bisporangia measuring 25-42 µm in length and 27-47 µm in diameter (Fig. 26), or cruciately divided tetrasporangia (with a '+'-shaped pattern of division) measuring 25-42 µm in length and 27-49 µm in diameter (Fig. 25), are formed. Incompletely cruciately divided tetrasporangia (with a 'T'-shaped pattern of division) are common. Occasionally, however, the planes of division vary and result in tetrasporangia having a tetrahedral ('Y'-shape) pattern of division (Fig. 24). Tetra/bisporangia bear apical pore plugs and are borne on multiple (1-4) stalk cells that result from the production of successive sporangia (Figs 24-26).

## DISCUSSION

At present, the following characters collectively delimit *Heydrichia* (Townsend *et al*. 1994): 1) tetrasporangia are cruciately divided and borne in sori (i.e. in uniporate sporangial chambers that bear only one sporangium); 2) tetra/bisporangia bear apical pore plugs; 3) thalli are non-geniculate and lack haustoria; 4) outermost walls of terminal epithallial cells are flattened and flared at their corners; 5) cells of contiguous filaments commonly and mostly joined by cell fusions with secondary pit connections being very rare; 6) tetra/bisporangia borne on multiple stalk cells that result from the production of successive sporangia; and 7) tetra/bisporangial sori are surrounded by an involucre of narrow, elongate cells that differ from ordinary vegetative cells. All of the above characters are present in *H. cerasina*, and clearly it fits within the generic delimitation of *Heydrichia*. The first four characters place the taxon within the order Sporolithales, family Sporolithaceae Verheij (1993). The last three characters separate the taxon from *Sporolithon* Heydrich (Townsend *et al*. 1994), the only other genus in Sporolithaceae. In *Sporolithon*: 1) cells of contiguous filaments are commonly joined by both cell fusions and secondary pit connections; 2) tetra/bisporangia are borne on only a single stalk cell that does not produce successive sporangia; and 3) tetra/bisporangial sori are not surrounded by an involucre of narrow, elongate cells, but rather by cells that do not differ from other vegetative cells.

Only three other species of *Heydrichia* have been described. Table 1 records the differences and similarities between the species. *Heydrichia cerasina* is anatomically similar to the Australian *H. homalopasta* (see Townsend & Borowitzka 2001; Harvey *et al*. 2002) and while morphology and substrata preference are known to be very plastic characters, the characteristically warty growth form and habitat preference of the new species for small pebbles, distinguishes *H. cerasina* from *H. homalopasta*. Furthermore, Townsend *et al*. (1994) regarded the dendroid (branched) spermantangial structures and their restriction to the floor of male conceptacles in *H. woelkerlingii,* to be diagnostic of the genus. Keats and Chamberlain (1995, see also their key) re-affirmed the distribution of spermatangial structures within the male conceptacle chamber to be one of the diagnostic characters separating South African species of

*Heydrichia* (only on the floor, but not seen in *H. groeneri*) from those of *Sporolithon* (on the floor, walls and roof, see also Verheij 1993; Townsend *et al*. 1994). Later Harvey *et al.* (2002) found male plants of *H. homalopasta* and showed that, unlike the generitype, this species has unbranched spermatangial structures that develop across the floor, walls and roof of the mature male conceptacle. Although Harvey *et al*. (2002) did comment on this difference, they did not challenge the use of spermatangial structure type and their distribution within mature male conceptacles to differentiate *Heydrichia* from *Sporolithon*. *Heydrichia cerasina* is like *H. homalopasta*, with unbranched spermatangial structures distributed across the floor, walls and roof of mature male conceptacles. Thus, both spermatangial structure type (unbranched versus branched) and notably, distribution of spermatangial structures within male conceptacles, cannot be considered diagnostic characters of *Heydrichia*.

Similarly, while not presently regarded as diagnostic features, gametangial conceptacle placement and carposporangial conceptacle development appear unique in *H. cerasina*. For both *H. woelkerlingii* and *H. groeneri* gametophyte conceptacles are sunken in the thallus and roofs are flush with the surrounding thallus surface; conceptacles are only discernable in surface view by their pores (Townsend *et al*. 1994; Keats & Chamberlain 1995). *Heydrichia cerasina* has gametangial conceptacles that are raised well above the surrounding thallus surface (and are flush to only slightly raised in *H. homalopasta*; see Harvey *et al.* 2002) and are easy to observe under a dissecting microscope. The apparent successive production of carposporangial conceptacles in the cortex directly above, and in the same area as the modified cortex of an earlier generation seen in *H. cerasina*, has not been reported for any other species in the genus.

A key to the southern African species belonging to the order Sporolithales (modified from Keats & Chamberlain 1995 and Maneveldt *et al*. 2008) is provided below.

## Key to the southern African Sporolithales

This key is designed for southern African specimen identification only, and the characters used in the key are not necessarily diagnostic of the species to which they pertain.

1. Plants distributed along warm temperate to subtropical shores; sporangia in tetra/bisporangial chambers borne on a single stalk cell .....………..………................... 2
   Plants distributed along cold temperate to warm temperate shores; sporangia in tetra/bisporangial chambers borne on multiple (up to 5) stalk cells ..…………………… 3
2. Old tetra/bisporangial chambers buried in rows in the thallus ……………………………………………………………………..…... *Sporolithon ptychoides*
   Old tetra/bisporangial chambers shed, not becoming buried in the thallus …………………………………………………………………….…... *Sporolithon episporum*
3. Plants mostly encrusting (smooth), but also lumpy, generally occurring on boulders and the primary bedrock ……………………………………………...………..……..……… 4
   Plants warty, occurring only on small (ranging from 10-40 mm along the long axis) pebbles ……………………………………..……………............ *Heydrichia cerasina*
4. Thallus thin, less than 1 mm thick …………………………....…….. *Heydrichia groeneri*
   Thallus very thick (up to 15 mm) and generally massively discoid in appearance ……………………………………………………………..…. *Heydrichia woelkerlingii*

*Heydrichia cerasina* is the fourth species reported in *Heydrichia*, and South Africa is now home to three of the four known congeners. The new species re-affirms South Africa as a region rich in coralline algal diversity (see also Maneveldt *et al*. 2007; 2008). The new species appears to be a range restricted endemic. Although very rare, such phenomena are not unfamiliar to South Africa. Awad *et al*. (2002) for example showed that range restricted endemics among South African marine invertebrates tend to occur in biogeographical transition regions. Similarly, Anderson *et al*. (2009) showed that narrow distribution seaweed endemics also occur around transitions between biogeographical marine provinces. The Cape Agulhas region is a well-documented biogeographical marine province transition zone (Bolton & Anderson 1990; Bolton *et al*. 2004), and so it is perhaps not surprising that even among the coralline algae there might be a species endemic to a narrow section of the South African coastline. What is perhaps so very unusual is the extremely restricted geographic distribution of this species occurring along a stretch of coastline no greater than 10 km at the southernmost tip of the African continent.

In conclusion, the new species differs in habit from all previously described species of *Heydrichia* by possessing a uniformly warty growth form as opposed to a smooth to lumpy growth form in the congeners. Moreover, *H. cerasina* grows as a relatively thin crust (to 1400 µm thick), similar to *H. homalopasta* (to 1000 µm thick) from Australia and to *H. groeneri* (to 800 µm thick) from Namibia and South Africa, but differing from the very thick (to 15 mm thick), massively discoid plants found in *H. woelkerlingii* from South Africa. Similar to *H. homalopasta*, the tetra/bisporangial sori of *H. cerasina* occur as mostly single sporangial chambers whereas those of *H. groeneri* and *H. woelkerlingii* are composed of numerous sporangial chambers. Again similar to *H. homalopasta*, *H. cerasina* displays unbranched spermatangial structures distributed across the floor, walls and roof of mature male conceptacle chambers (male plants unknown for *H. groeneri*) as opposed to the branched ones found only on the floor of the male conceptacle chambers, so far known for the type species, *H. woelkerlingii*.

## ACKNOWLEDGEMENTS

We thank the Department of Biodiversity and Conservation Biology at the University of the Western Cape for providing funding and research equipment, and the South African National Research Foundation (NRF) for a research grant to GWM. Adrian Josephs and Dawn Faroe provided assistance with the operation of the SEM and digital imagery microscope respectively. We are most grateful to Alex George (Murdoch University, Australia) for rendering the Latin translation of the description. John Bolton (University of Cape Town, South Africa) and Paul Gabrielson (University of North Carolina, Chapel Hill, USA) are thanked for invaluable comments. The reviewers are gratefully thanked for their contributions in strengthening the manuscript.

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## TABLE

**Table 1.** Comparison of the four species of *Heydrichia* based on selected characters (after Townsend *et al*. 1994; Keats & Chamberlain 1995; Townsend & Borowitzka 2001; Harvey *et al.* 2002; this paper). ND = no data.

| Character | *H. woelkerlingii* | *H. groeneri* | *H. homalopasta* | *H. cerasina* |
|---|---|---|---|---|
| Substrate | epilithic on primary substratum (bedrock) and boulders | epilithic on primary substratum (bedrock) | epilithic on primary substratum (bedrock) | epilithic only on small (mostly 10-40 mm in length) pebbles |
| Growth form | mostly encrusting (smooth), but also lumpy | Encrusting (smooth) | encrusting (smooth) | warty |
| Thallus thickness | to 15 mm | to 800 µm | to 1000 µm | to 1400 µm |
| Type of cell connection | cell fusions (mostly) and secondary pit connections (rare) | cell fusions only | cell fusions (mostly) and secondary pit connections (rare) | cell fusions only |
| Cortical coalescence after decalcification | loosely coalescent | compact and cohesive | compact and cohesive | loosely coalescent |
| Gametangial plants | monoecious | dioecious ?[2] | dioecious | dioecious |
| Gametangial conceptacles | buried, roofs flush with surrounding thallus surface | buried, roofs flush with surrounding thallus surface | not buried, roofs flush to only slightly raised above surrounding thallus surface | not buried, roofs raised well above surrounding thallus surface |
| Spermatangial structure type and distribution | branched, restricted to conceptacle floor | ND | unbranched, on conceptacle floor, walls and roof | unbranched, on conceptacle floor, walls and roof |
| Tetra/bisporangial chamber arrangement | large groups | large groups | individual | mostly individual |
| Tetra/bisporangial chamber roof | sunken | flush | flush to raised | flush to raised |
| Tetrasporangial pattern of division | tetrahedral (‘Y’-shaped) | tetrahedral (‘Y’-shaped) | cruciate (‘+’-shaped) | mostly cruciate (‘+’-shaped) |

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[2] Keats & Chamberlain (1995) did not find male plants, but presumed the species to be dioecious.

## FIGURE CAPTIONS

**Fig. 1.** Individuals of *H. cerasina* in their common habitat from L'Agulhas, Cape Agulhas, Western Cape Province, growing on small pebbles in low shore surge channels. South African one Rand coin in photograph is 20 mm in diameter.

**Fig. 2.** Holotype specimen (tetrasporangial) of *H. cerasina* (L 0821464). Scale bar = 20 mm.

**Fig. 3.** Isotype specimens (tetra/bisporangial and gametangial) of *H. cerasina* (L 0821455-63). Scale bar = 20 mm.

**Figs 4-9.** Vegetative morphology and anatomy of *H. cerasina* (L 0821455-63).

**Fig. 4.** Characteristically warty thallus surface. Scale bar = 3 mm.

**Fig. 5.** Vertical section of monomerous thallus showing thin, plumose (non-coaxial) medulla (m), outer cortex (c) and single epithallial layer (arrow). Scale bar = 60 µm.

**Fig. 6.** Vertical section showing rather loosely coalescent (*) thallus that results after decalcification.  Tetra/bisporangial complexes (arrow) and male conceptacles (arrowheads) commonly present on the same specimens. Scale bar = 300 µm.

**Fig. 7.** Magnified view of outer thallus showing subepithallial initials (arrows) and a single layer of flattened epithallial cells (arrowheads) with flared corners. Scale bar = 15 µm.

**Fig. 8.** Magnified view of inner thallus showing both dimerous (uni-axial) (arrow) and monomerous (multi-axial) (m) portions. Note cell fusions (arrowheads) between contiguous filaments. Scale bar = 30 µm.

**Fig. 9.** Magnified view of inner thallus showing predominantly monomerous (multi-axial) thallus. Note cell fusions (arrowheads) between contiguous filaments. Scale bar = 30 µm.

**Figs 10-15.** Spermatangial morphology and anatomy of *H. cerasina* (UWC 10/144).

**Fig. 10.** Dorsal view of male plant showing raised conical conceptacles between protuberances (p). Scale bar = 500 µm.

**Fig. 11.** Vertical section through spermatangial conceptacle. Note mucilage plug (arrow) occluding pore. Scale bar = 100 µm.

**Fig. 12.** Vertical section through pore of spermatangial conceptacle showing papillate cells (arrows) lining pore canal (p) and elongate initials terminating in mucilage plug (m) that occludes pore opening. Scale bar = 30 µm.

**Fig. 13.** Magnified view of spermatangial conceptacle chamber showing spermatangial structures (arrows) distributed across floor (f), walls (w) and roof (r) of the chamber. Scale bar = 30 µm.

**Fig. 14.** Magnified view of floor of spermatangial conceptacle chamber showing elongated, unbranched spermatangial mother cells (white arrowheads) bearing spermatia (black arrow) distally. Scale bar = 15 µm.

**Fig. 15.** Magnified view of roof of spermatangial conceptacle chamber showing elongated, unbranched spermatangial mother cells (white arrowheads) bearing spermatangia (black arrowheads) distally. Note spermatangia borne from floor of chamber (black arrow). Scale bar = 15 µm.

**Figs 16-20.** Carposporangial morphology and anatomy of *H. cerasina* (UWC 10/144).

**Fig. 16.** Dorsal view of female plant showing broadly, low-domed, raised, conical carposporangial conceptacles.  Arrows highlight external conceptacle diameters; arrowheads demarcate centrally raised pore canal structure. Scale bar = 500 µm.

**Fig. 17.** Vertical section through carposporangial conceptacle showing centrally raised pore canal structure (p) and gonimoblast filaments (g) borne across floor and walls of

conceptacle chamber. Note pattern of secondary growth (black arrows). Scale bar = 75 µm.

**Fig. 18.** Vertical section of thallus showing broadly, low-domed carposporangial conceptacle ( ⊓ ) with centrally elevated pore canal structure (between black arrows). Note pattern of secondary growth (white arrows) suggesting successive production of this female conceptacle in same area of previous reproductive event. Scale bar = 200 µm.

**Fig. 19.** Magnified view of conceptacle in fig. 18 showing successive reproductive event highlighted by dramatic change in filament alignment (arrows). Scale bar = 100 µm.

**Fig. 20.** Magnified view of carposporangial conceptacle floor showing absence of central fusion cell and gonimoblast filaments arising dorsally across conceptacle floor and walls; short 2-celled gonimoblast filaments (arrowheads) terminate in tear-shaped carposporangia (c). Scale bar = 30 µm.

**Figs 21-27.** Tetra/bisporangial morphology and anatomy of *H. cerasina* (UWC 10/144).

**Fig. 21.** SEM surface view of tetra/bisporangial sori showing uniporate chambers with slightly raised roofs. Scale bar = 200 µm.

**Fig. 22.** SEM of tetra/bisporangial chamber pore bearing nine rosette (r) cells. Scale bar = 20 µm.

**Fig. 23.** Surface view of tetra/bisporangial plant showing numerous chambers embedded in a superficial layer; some sori (arrows) already have been shed. Scale bar = 500 µm.

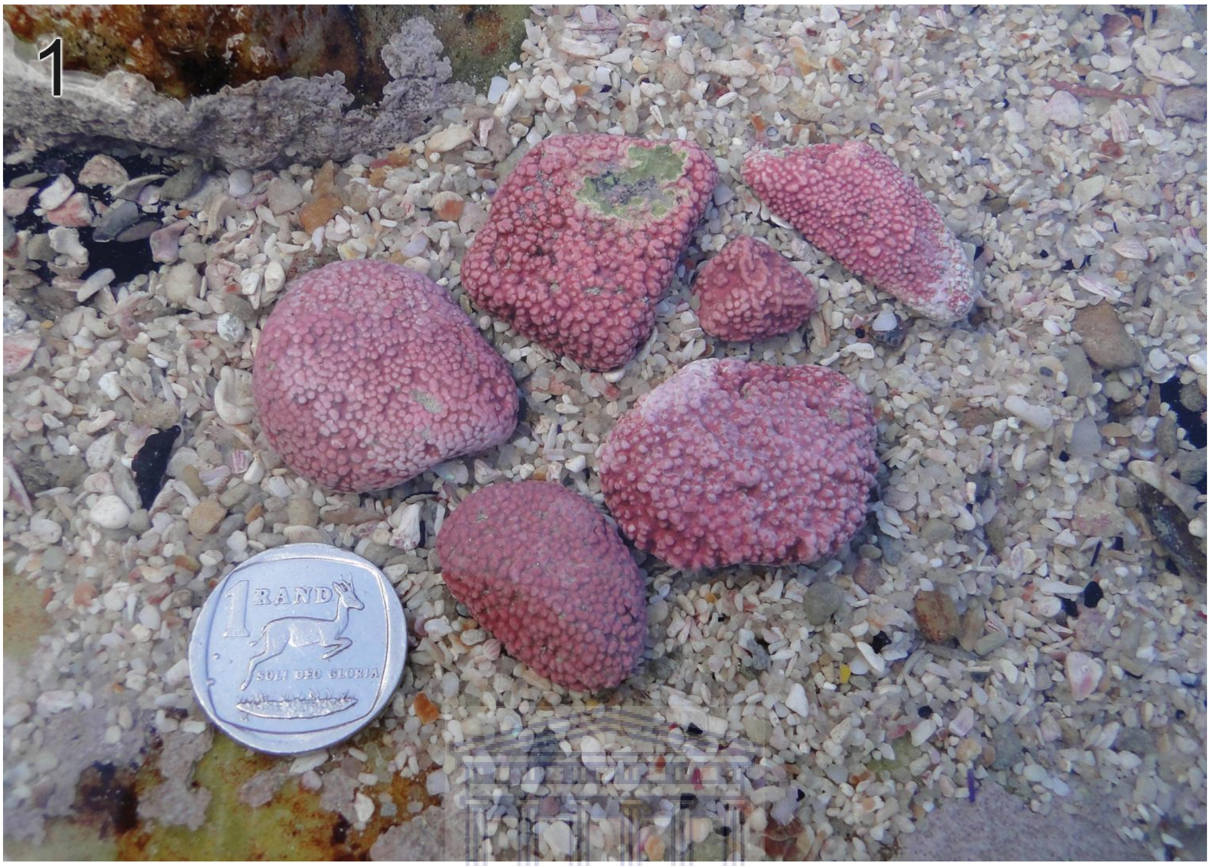
**Fig. 24.** Single tetrasporangial chamber showing tetrasporangium with tetrahedral (‘Y’-shaped) division pattern. Note pore plug (p), involucre (white arrowheads) of narrow elongated cells lining chamber, and subtending stalk cells (black arrowheads). Scale bar = 30 µm.

**Fig. 25.** Single tetrasporangial chamber showing tetrasporangium with characteristic cruciate (‘+’-shaped) pattern of division. Note pore plug (p), involucre (white arrowheads) of

narrow elongated cells lining chamber, and subtending stalk cells (black arrowheads). Scale bar = 30 µm.

**Fig. 26.** Outer thallus section showing group of three sporangial chambers bearing bisporangia. Scale bar = 30 µm.

**Fig. 27.** Saucer-shaped scars (arrowheads) in outer thallus representing secondary cortical growth that has infilled senescent tetra/bisporangial lumens shed during previous reproductive event. Scale bar = 50 µm.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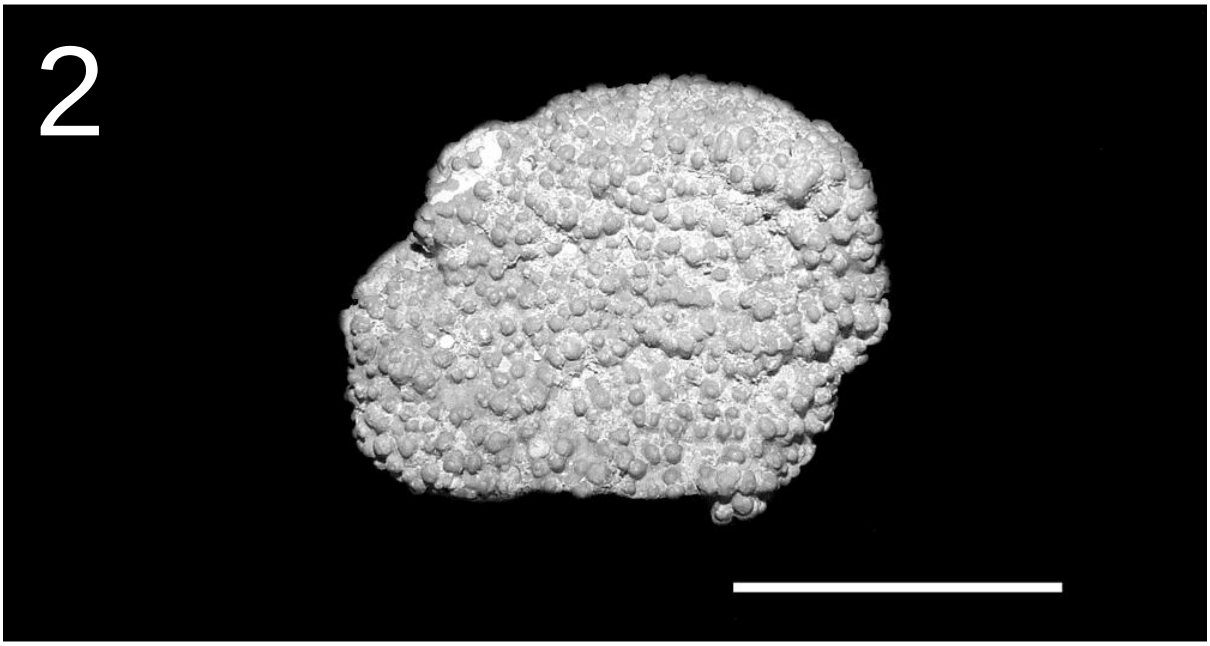
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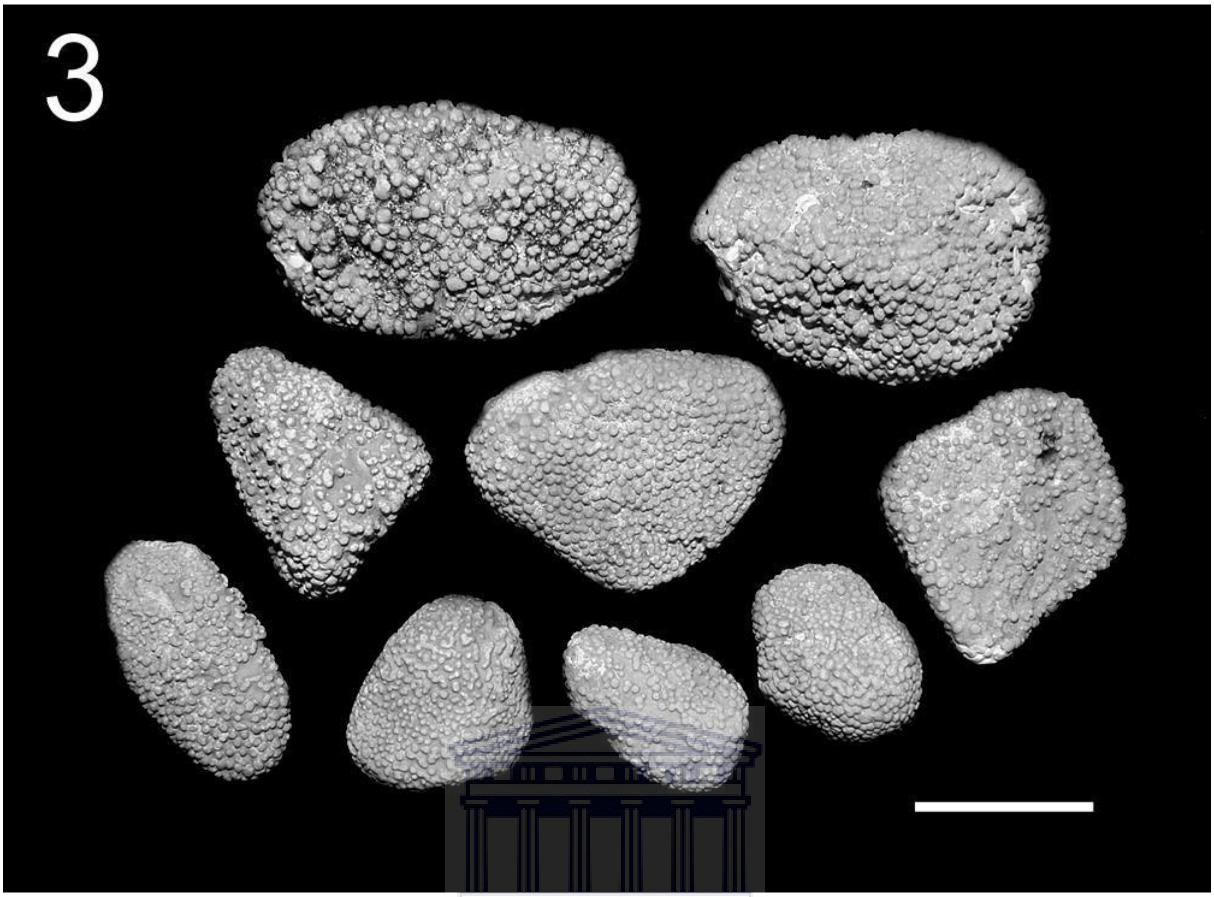
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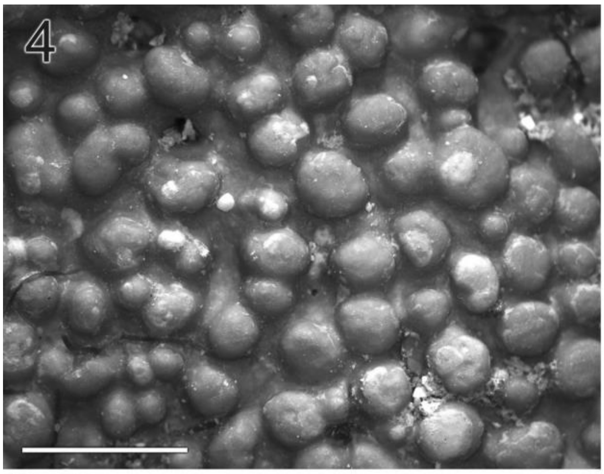
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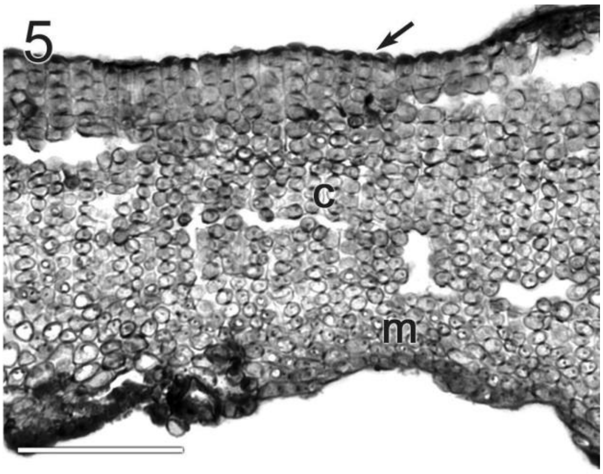
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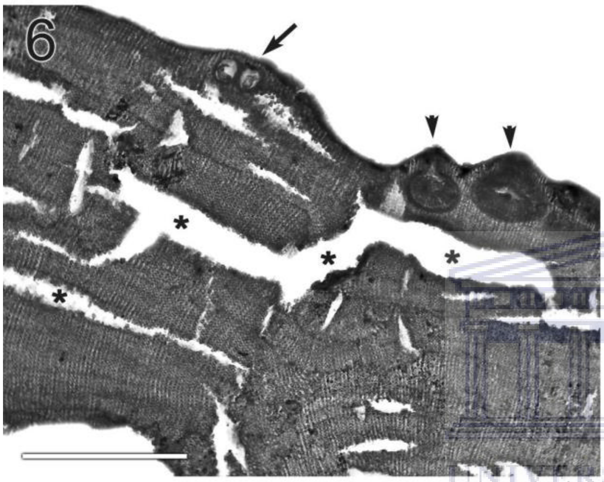
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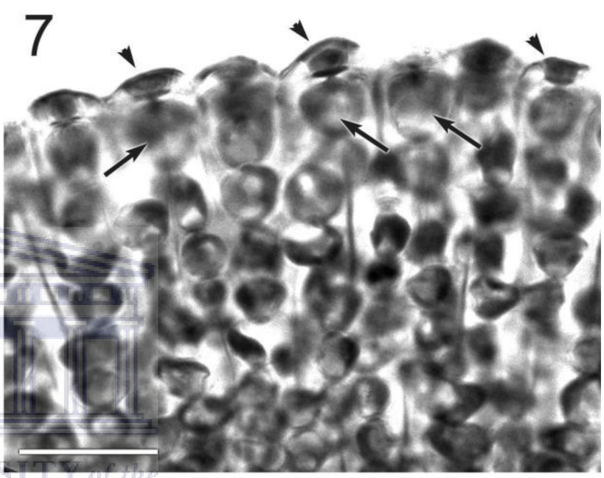
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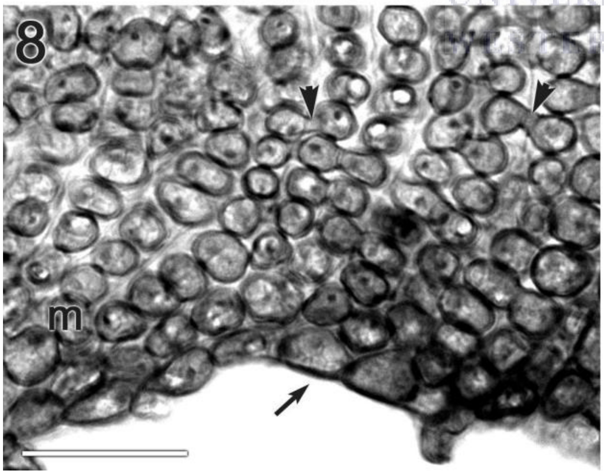
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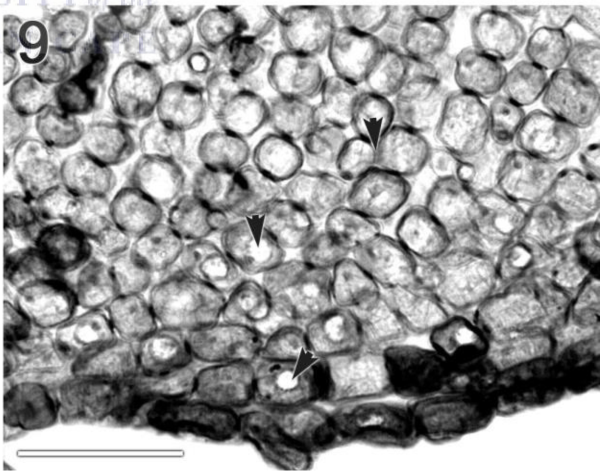
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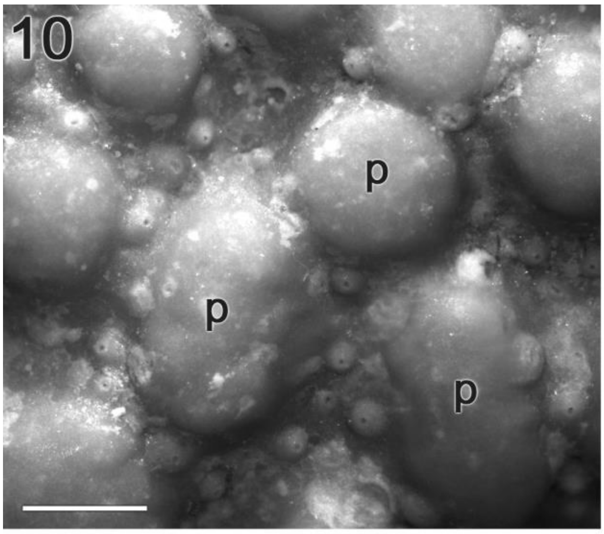
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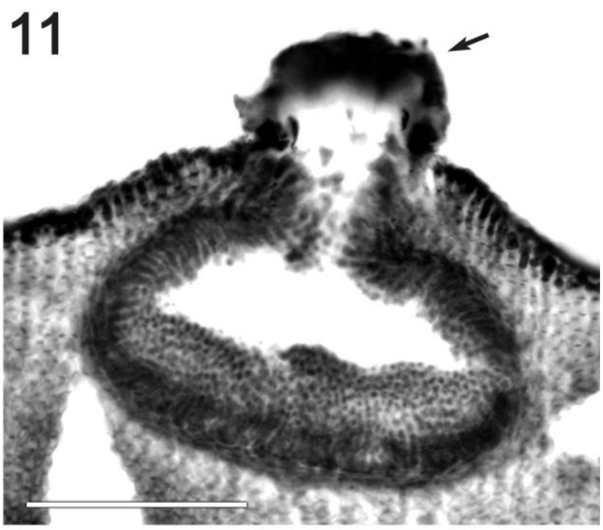
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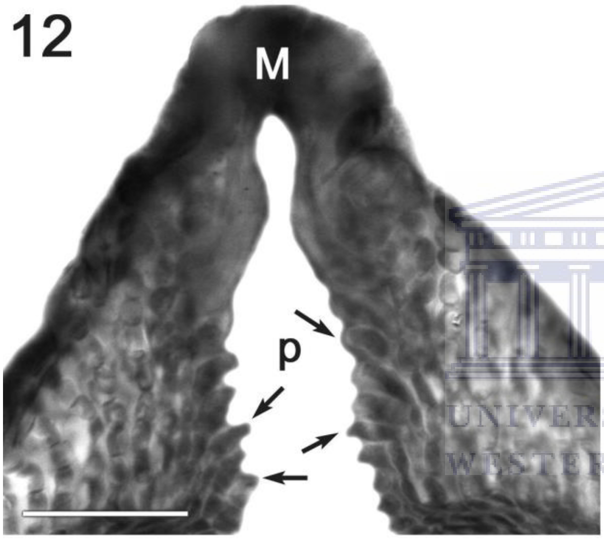
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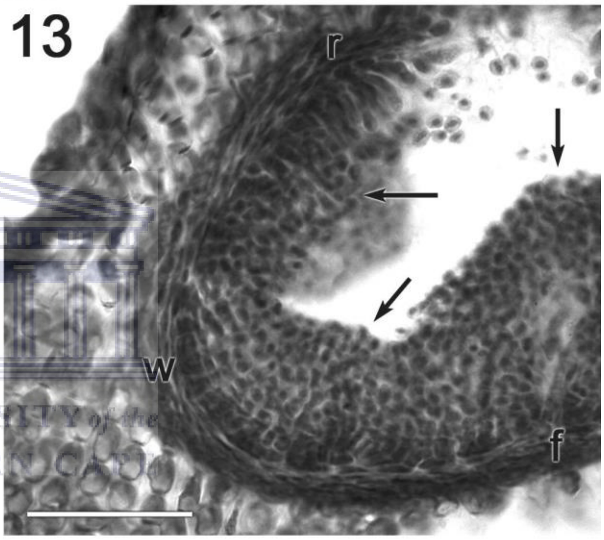
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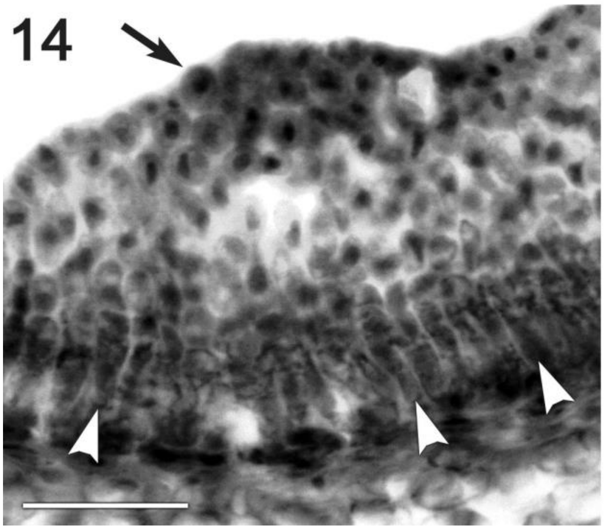
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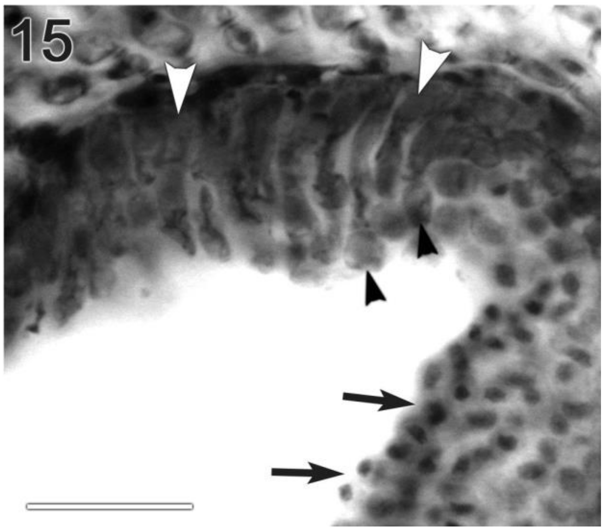
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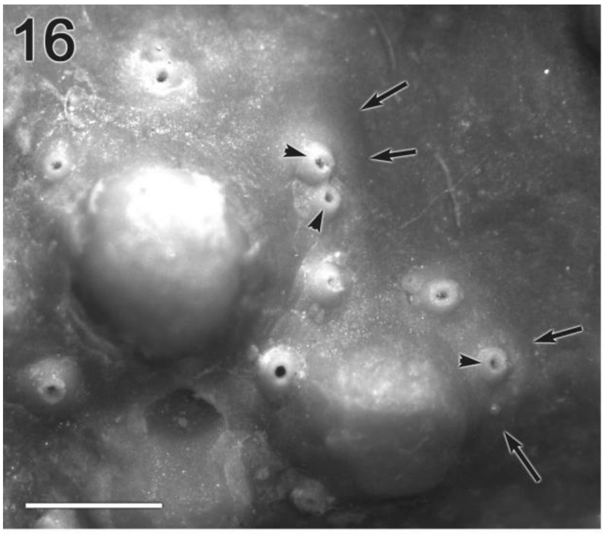
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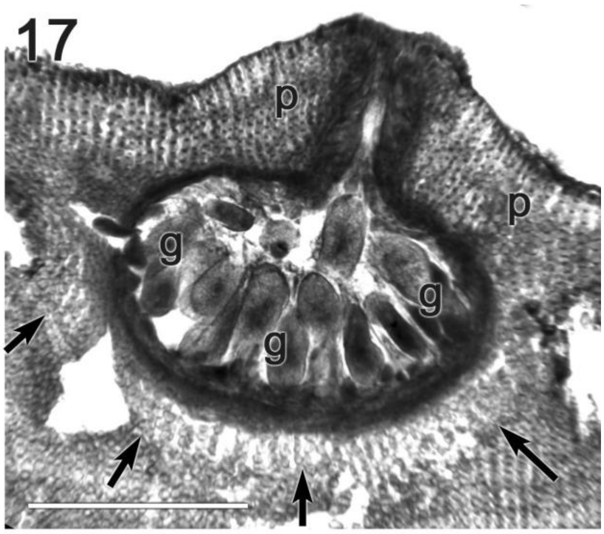
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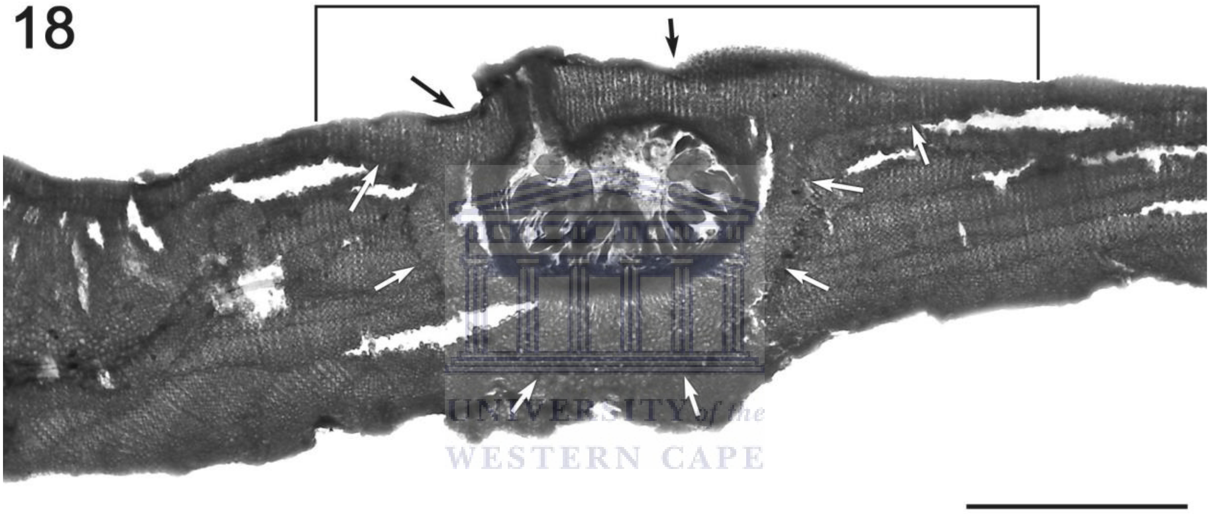
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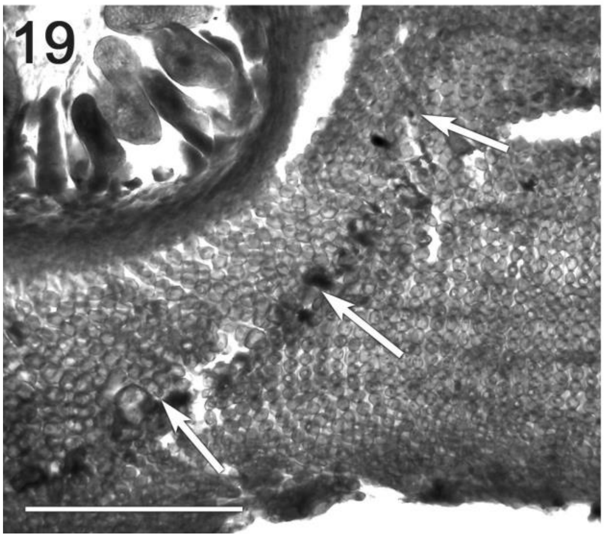
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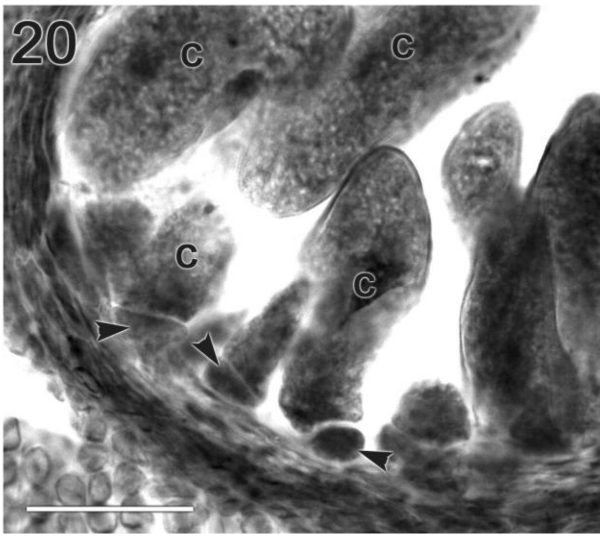
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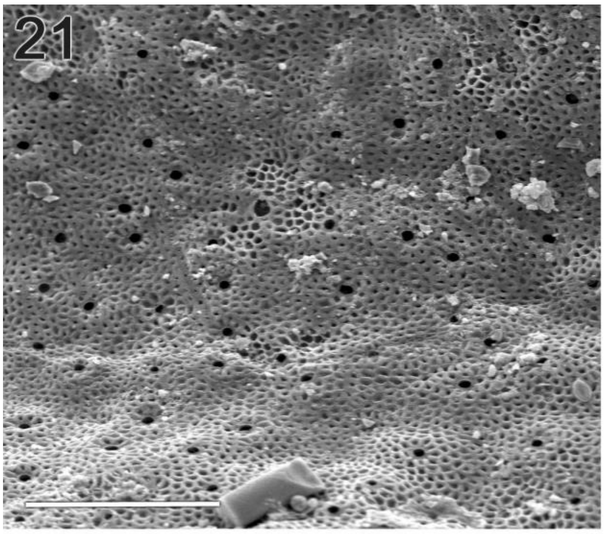
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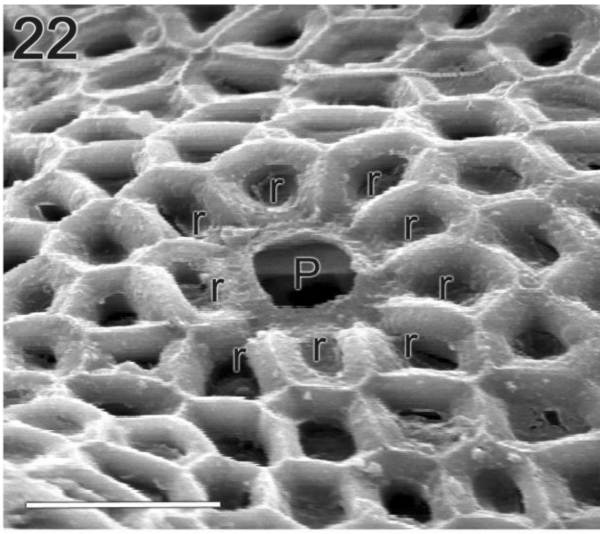
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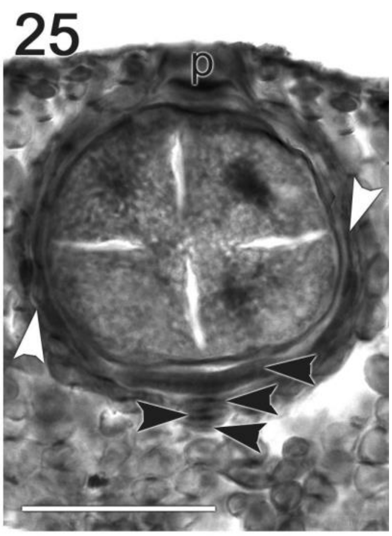
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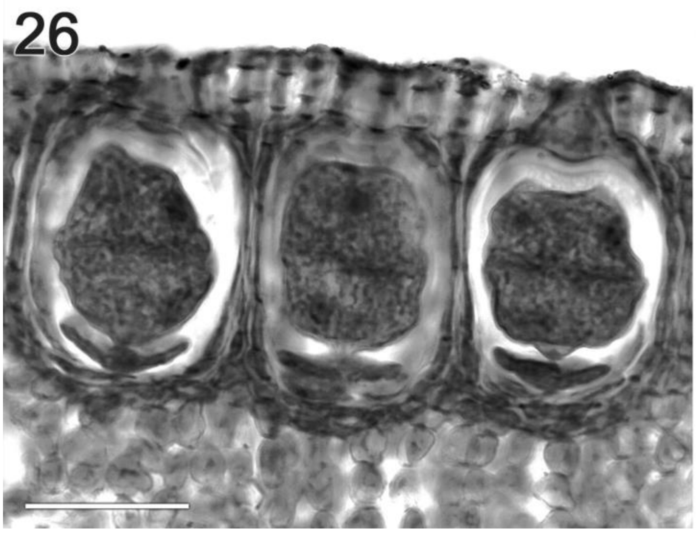
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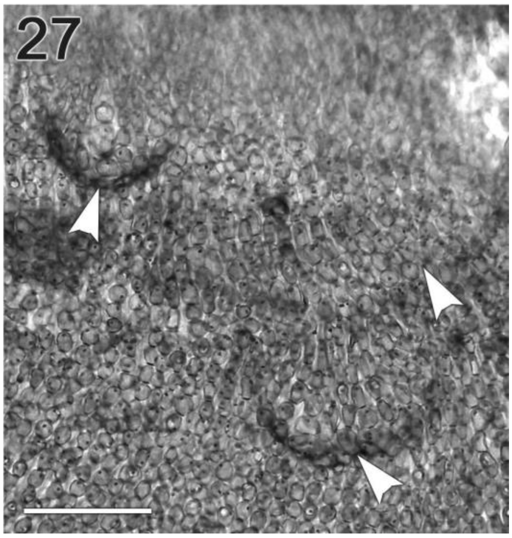
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## Chapter 3: Paper 2

# The genus *Phymatolithon* (Hapalidiaceae, Corallinales, Rhodophyta) in South Africa, including species previously ascribed to *Leptophytum*

This Chapter has been published as:

Van der Merwe, E., Maneveldt, G.W. 2014. The genus *Phymatolithon* (Hapalidiaceae, Corallinales, Rhodophyta) in South Africa, including species previously ascribed to *Leptophytum*. *South African Journal of Botany* 90,170–192.

# The genus *Phymatolithon* (Hapalidiaceae, Corallinales, Rhodophyta) in South Africa, including species previously ascribed to *Leptophytum*

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Running Head: The genus *Phymatolithon* (Hapalidiaceae, Corallinales, Rhodophyta) in South Africa

## Abstract

Of the genera within the coralline algal subfamily Melobesioideae, the genera *Leptophytum* Adey and *Phymatolithon* Foslie have probably been the most contentious in recent years. In recent publications, the name *Leptophytum* was used in quotation marks because South African taxa ascribed to this genus had not been formally transferred to another genus or reduced to synonymy. The status and generic disposition of those species (*L. acervatum*, *L. ferox*, *L. foveatum*) have remained unresolved ever since Düwel and Wegeberg (1996) determined from a study of relevant types and other specimens that *Leptophytum* Adey was a heterotypic synonym of *Phymatolithon* Foslie. Based on our study of numerous recently collected specimens and of published data on the relevant types, we have concluded that each of the above species previously ascribed to *Leptophytum* represents a distinct species of *Phymatolithon*, and that four species (incl. *P. repandum*) of *Phymatolithon* are currently known to occur in South Africa.

Here we present detailed illustrated accounts of each of the four species, including: new data on male and female/carposporangial conceptacles; ecological and morphological/anatomical comparisons; and a review of the information on the various features used previously to separate *Leptophytum* and *Phymatolithon*. Southern African species ascribed to the genus *Phymatolithon* may be separated from one another in the field by their growth forms, the substrata on which they are generally found, and the colour of living thalli. A key for identifying southern African specimens in the field is included. Our data support the conclusion that the characters upon which *Leptophytum* is based are unreliable for generic delimitation from *Phymatolithon.*

**Keywords:** Non-geniculate coralline algae; *Phymatolithon acervatum*; *Phymatolithon ferox; Phymatolithon foveatum; Phymatolithon repandum*; South Africa; taxonomy.

## 1. Introduction

This paper contains an account of South African representatives of the coralline red algal genus *Phymatolithon* (Hapalidiaceae, Corallinales, Rhodophyta), including three species based on South African types that had previously been referred to the genus *Leptophytum*. The status and generic disposition of those species (*L. acervatum*, *L. ferox, L. foveatum*) have remained unresolved ever since Düwel and Wegeberg (1996) determined from a study of relevant types and other specimens that *Leptophytum* Adey was a heterotypic synonym of *Phymatolithon* Foslie. The complex nomenclatural history of *Leptophytum* has been reviewed by Woelkerling (1988: 217-218), Düwel and Wegeberg (1996), Woelkerling et al. (2002) and Teichert et al. (2013: footnote 1), and comments on this genus from the Nomenclature Committee for Algae appear in Compère (2004) and in Prud'homme van Reine (2011).

Based on our study of numerous recently collected specimens and of published data on the relevant types, we have concluded that each of the above species hitherto ascribed to *Leptophytum* represents a distinct species of *Phymatolithon*, and that four species of *Phymatolithon* are currently known to occur in South Africa. Detailed illustrated accounts of each species are presented, including data on synonymy and types, etymology, specimens examined, distribution, habit, and vegetative and reproductive anatomy. New data on male and female/carposporangial conceptacles are provided; ecological and morphological/anatomical comparisons of the four species are summarized; various features used previously to separate *Leptophytum* and *Phymatolithon* are reviewed; and a key for identifying South African specimens in the field is included.

## 2. Materials & Methods

Field collections were made from the high to low intertidal and shallow subtidal zones of Southern Africa from Namibia, South Africa and Mozambique (Inhaca Island). Thalli were examined as far as possible when fresh; otherwise they were air-dried or fixed in neutralized 10 % commercial formalin seawater (4 % formaldehyde) and stored in a 70 % ethanol: 10 % glycerol: 20 % distilled water solution.

Specimens for microscopy were prepared following Maneveldt and van der Merwe (2012). For scanning electron microscopy, air-dried material was fractured using forceps, diagonal cutters, or a small hammer and chisel. Fractures perpendicular to a leading edge was used to determine internal anatomy. The fractured pieces were mounted on stubs, using adhesive tabs (Agar Scientific, 66a Cambridge Rd., Stanstead, Essex CM24 8DA, UK), stored in a desiccator for at least 24 h prior to examination, coated with carbon in a single cycle for 2 s in an EMITECH K950X Carbon evaporator, and examined with a LEO 1450 scanning electron microscope (SEM) at an accelerating voltage of 20 kV.

For light microscopy, formalin preserved specimens were first decalcified in 10 % nitric acid. Thereafter, specimens were immersed in 70 %, 90 % and 100 % ethanol solutions respectively for a minimum of 60 mins each in order to displace any water and acid in the specimens. Thereafter, each specimen was removed from the 100 % ethanol and allowed to air dry for no more than a few seconds. Specimens were then immersed in Leica Historesin filtration medium for several hours (3-6) until completely infiltrated. A hardening solution was then added to the infiltration medium and the specimens orientated in this final solution until set. Gelling of the hardener usually occurred within 30-45 mins; for more rapid hardening, specimens were placed immediately in an oven at 60 °C for approximately 10-20 mins.

Specimens were then sectioned at 8-10 µm thickness using a Bright 5030 microtome. Individual cut sections were removed from the microtome blade using a fine sable hair brush and transferred to a slide covered with distilled water. In this way, multiple sections were orientated on a single slide. Slides were then left to air dry for at least 24 hrs. Once dried, slides bearing sections were stained with toluidine blue (0.25 g borax/100 ml and 0.06 g toluidine blue/100 ml) that was previously filtered to prevent dye crystal formation, again left to air dry, and later covered with cover slips using DPX Mountant for microscopy (BDH Laboratory Supplies, England).

In cell measurements, length denotes the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. Conceptacle measurements follow Adey and Adey (1973). Thallus anatomical terminology follows Chamberlain (1990). Morphological (growth forms) terminology follows Woelkerling et al. (1993). Typification data follow Woelkerling (1993). Herbarium abbreviations follow Thiers (2013, continuously updated).

Collection data are presented firstly according to geographic location from north to south along the South African west coast and then from west to east, followed by date of collection within a region, and finally by collection number on a particular day.

## 3. Generic Concept and Species Accounts

### 3.1 *Phymatolithon* Foslie

*Phymatolithon*, as delimited by Harvey et al. (2003), is the only known genus in the family Hapalidiaceae (subfamily Melobesioideae): 1) possessing subepithallial initials that are as short as or shorter than the cells immediately subtending them; and 2) producing both branched (dendroid) and unbranched (simple) spermatangial filaments in male conceptacles. Two other genera of Melobesioideae (*Kvaleya*; *Mastophoropsis*) also have subepithallial initials that are as short as or shorter than subtending cells, but these genera produce only unbranched spermatangial filaments in their male conceptacles. Furthermore, *Kvaleya* differs in possessing haustoria (which are lacking in *Phymatolithon* and *Mastophoropsis*), while *Mastophoropsis* is arborescent and flabelliform, a growth-form that is absent in *Phymatolithon* and *Kvaleya*. Harvey et al. (2003: 676) provide a synoptic description of the genus, and Harvey et al. (2003: 653, Table 2) summarise diagnostic characters and character states separating all nine currently recognized extant genera of Melobesioideae.

Like all members of the Corallinales, *Phymatolithon* bears tetra/bisporangia in conceptacles and produce tetra/bisporangia that are zonately divided. Like all members of the Hapalidiaceae, thalli are entirely non-geniculate and tetra/bisporangia are produced in multiporate conceptacles that bear apical pore plugs. Also, like all members of the Melobesioideae, contiguous vegetative filaments are joined by cell fusions and the multiporate conceptacle roofs are composed of cells rather than a calcified sieve-like matrix.

*Phymatolithon* is typified by *P. calcareum* (Pallas) W.H.Adey & D.L.McKibbin. Spencer et al. (2009: 253) recently updated the nomenclature of that name; an account of the type is provided by Woelkerling and Irvine (1986).

Le Gall et al. (2010: 305, Table 1) list characters that distinguish the Corallinales from the other two orders (Rhodogorgonales, Sporolithales) of the subclass Corallinophycidae and Le Gall and Saunders (2007: 1129) provide the characterisation of Corallinophycidae. A synoptic description of the Hapalidiaceae and further data on included subfamilies occurs in Harvey et al. (2003: 648-649).

## 3.2 Identification key of southern African species of *Phymatolithon* based on diagnostic characters

1. Thalli encrusting (smooth) only …......……...……..……………………….……........... 2

   Thalli mostly warty to lumpy to fruticose ……………………………….……………...…. 3

2. Thalli mostly epilithic on pebbles and small boulders, surface with a pitted appearance ……………………….. ……………...……………………........... *Phymatolithon acervatum*

   Thalli epilithic on the primary bedrock, surface imbricate in appearance ……………………………………………………………….... *Phymatolithon foveatum*

3. Thalli producing secondary mouth-like margins, gonimoblast filaments peripherally arranged in carposporangial conceptacle chambers ...……………….... *Phymatolithon ferox*

   Thalli without conspicuous secondary margins, gonimoblast filaments peripherally arranged or scattered across the floor in carposporangial conceptacle chambers ……………..……………………………………………………… *Phymatolithon repandum*

## 3.3 Field identification key to the southern African species of *Phymatolithon*

By all accounts, the southern African species now ascribed to the genus *Phymatolithon* may be separated from each other in the field by their growth forms, the substrata on which they are generally found, and the colour of the living specimens. A key (modified from Maneveldt et al. 2008), to the southern African species of *Phymatolithon* is presented below. This key is designed for southern African specimen identification only and the characters used in the key are not necessarily diagnostic of the species to which they pertain.

1. Thalli encrusting (smooth) only ….......……...…….……………………….……........... 2
   Thalli mostly warty to lumpy to fruticose …….……….……………….………………...… 3
2. Thalli mostly epilithic on pebbles and small boulders in intertidal rock pools, living specimens bright pink in colour (Fig. 75), thallus surface matt-like with a pitted appearance (Fig. 1 and 2) …………..…………………….......... *Phymatolithon acervatum*
   Thalli epilithic on the primary bedrock in the low intertidal zone, living specimens brownish-pink in colour (Fig. 77), thallus surface glossy and covered in secondary margins (Fig. 39) giving the thallus an imbricate appearance ...... *Phymatolithon foveatum*
3. Thalli loosely adherent on the primary bedrock on the exposed intertidal zone and on worm tubes, living specimens mauvish grey (Fig. 76), thalli mostly warty to lumpy and producing numerous secondary margins that form mouth-like structures (Fig. 76) where they meet ...…………………………...…………………………………….... *Phymatolithon ferox*
   Thalli firmly adherent on the primary bedrock in intertidal rock pools, living specimens variable in colour from dull pinkish to reddish to brownish to purplish brown (Fig. 78), thalli warty to fruticose without conspicuous secondary margins
   ……………..……………………………………………………… *Phymatolithon repandum*

## 3.4 ***Phymatolithon acervatum*** (Foslie) Adey, 1970: 28

(Fig. 1-21 and 75)

Basionym: *Lithothamnion acervatum* Foslie, 1907: 4.

Synonyms: *Leptophytum acervatum* (Foslie) Y.M.Chamberlain & Keats, 1994: 111.

Lectotype: TRH, B1-1607. Natal, South Africa, A. Weber van Bosse. Foslie slide 702; Printz 1929, pl. 1, fig.15 (as *Lithothamnion*).

Syntype: TRH, B1-1608. Knysna, Cape Province, South Africa A. Weber van Bosse. Foslie slide 704; Printz 1929, pl. 1, fig. 14.

Adey (1970: 28, as *Phymatolithon*) referred to the above specimens as cotypes. Woelkerling (1993: 16) did not distinguish between the two specimens and designated them jointly as holotypes although the labels show the specimens to come from Natal and Knysna respectively. Chamberlain and Keats (1994: 112) subsequently designated the Natal specimen as lectotype and the Knysna specimen as syntype.

Etymology: *acervatum*, heaped up, crowded together. Foslie (1907) did not explain the origin of the epithet. According to Chamberlain and Keats (1994: 112) this may refer to the raised mounds of thallus surrounding the sunken conceptacles or to the presence of crowded thalli on small stones.

### *3.4.1 Specimens examined*

In total, forty three (43) specimens were examined, these currently representing our entire collection for this taxon.

South Africa. Northern Cape Province: Groenriviermond, epilithic on pebbles and small boulders tide pools (17.vii.1993, *D.W. Keats*, UWC 93/172).

South Africa. Western Cape Province: Yzerfontein, epilithic on low shore bedrock, and epizoic on low shore limpet (*Scutellastra argenvillei* and *S. cochlear*) shells (18.ii.1992, *D.W. Keats*, UWC 92/73); Robben Island, epilithic on bedrock at depths of 9-12 m (17.xi.1993, *D.W. Keats*, UWC 93/228; 24.ii.1994, *D.W. Keats*, UWC 94/24); Cape Point, epilithic on pebbles and small boulders in low shore tide pools (27.x.1991, *D.W. Keats*, UWC 91/95; 27.x.1991, *D.W. Keats*, UWC 91/96); False Bay, Partridge Point, epilithic on bed rock at a depth of 10-14 m (06.viii.1993, *D.W. Keats* & *G.W. Maneveldt*, UWC 93/95; 25.viii.1993, *D.W. Keats*, UWC 93/216); Fish Hoek Nature Reserve, epilithic on subtidal pebbles (13.vi.1990, *D.W. Keats*, UWC Cor-32; 13.vi.1990, *D.W. Keats*, UWC Cor-33; 13.vi.1990, *D.W. Keats*, UWC Cor-34; 13.vi.1990, *D.W. Keats*, UWC Cor-35); Kalk Bay, epilithic on small boulders in mid shore tide pools (16.i.2002, *G.W. Maneveldt*, UWC 2002/01; 24.viii.2002, *G.W. Maneveldt*, UWC 2002/08; 17.vii.2003, *G.W. Maneveldt* & *S.T. Dlaza*, UWC 2003/10; 13.viii.2003, *G.W. Maneveldt* & *S.T. Dlaza*, UWC 2003/11A; 13.viii.2003, *G.W. Maneveldt* & *S.T Dlaza*, UWC 2003/13; 13.viii.2003, *G.W. Maneveldt* & *S.T. Dlaza*, UWC 2003/14; 13.viii.2003, *G.W. Maneveldt* & *S.T. Dlaza*, UWC 2003/16; 13.viii.2003, *G.W. Maneveldt* & *S.T. Dlaza*, UWC 2003/17; 13.viii.2003, *G.W. Maneveldt* & *S.T. Dlaza*, UWC 2003/19; 10.x.2003, *S.T. Dlaza*, UWC 2003/26); Holbaaipunt, epizoic on limpet (*S. cochlear*) and whelk (*Crepidula porcellana*) shells, and epilithic on pebbles and small boulders in low to midshore tide pools (23.vi.1990, *D.W. Keats* & *I. Matthews*, UWC Cor-25; 25.x.1991, *D.W. Keats*, UWC 91/75; 25.x.1991, *D.W. Keats*, UWC 91/76; 27.x.1991, *D.W. Keats*, UWC 91/95; 26.xi.1991, *D.W. Keats*, UWC 91/251; 26.xi.1991, *D.W. Keats*, UWC 91/252; 21.vi.1993, *D.W. Keats* & *G.W. Maneveldt*, UWC 93/72; 26.v.1994, *D.W. Keats*, UWC 94/129; 16.vi.1995, *D.W. Keats*, UWC 95/28); Betty's Bay, epilithic on pebbles and small boulders in low to midshore tide pools (03.i.1994, *D.W. Keats*, UWC 94/36); Cape Agulhas, L'Agulhas, epilithic on pebbles in low to midshore tide pools and sandy gullies (08.vii.2009, *G.W. Maneveldt* & *E. van der Merwe*, UWC 09/135;

15.vi.2010, *G.W. Maneveldt* & *E. van der Merwe*, UWC 10/129); Struisbaai, epilithic on pebbles and small boulders in low shore tide pools and sandy gullies (07.vii.2009, *G.W. Maneveldt* & *E. van der Merwe*, UWC 09/116); De Hoop Nature Reserve, epilithic on pebbles in midshore tide pools (10.xii.1991, *D.W. Keats*, UWC 91/313); Stilbaai, Skulpiesbaai, epilithic on pebbles and small boulders in low shore tide pool (12.vi.2010, *G.W. Maneveldt* & *E. van der Merwe*, UWC 10/103); Knysna Heads, epilithic on pebbles and small boulders in high to midshore tide pools (08.xii.1991, *Y.M. Chamberlain*, UWC 91/271; 07.iv.2008, *G.W. Maneveldt* & *U. van Bloemestein*, UWC 08/26); Nature's Valley, epilithic on pebbles and small boulders in high to midshore tide pools (05.iv.2008, *G.W. Maneveldt* & *U. van Bloemestein*, UWC 08/14).

South Africa. Eastern Cape Province: Tsitsikamma, Grootbank, dominant coralline epilithic on the bedrock in the low shore *cochlear* zone (10.iv.2008, *G.W. Maneveldt* & *U. van Bloemestein*, UWC 08/37); Port Elizabeth, near Noordhoek, epilithic on pebbles and small to large boulders in intertidal surge pools (20.v.1992, *D.W. Keats*, UWC 92/122); Kei Mouth, epilithic on small boulder in high shore tide pools (11.vii.2010, *G.W. Maneveldt* & *E. van der Merwe*, UWC 10/217).

### *3.4.2 Distribution*

Known only from South Africa. Distributed from the Northern Cape Province (Groenriviermond), to at least the Kei Mouth in the Eastern Cape Province.

### *3.4.3 Habit*

Thalli are non-geniculate, epilithic on the primary bedrock on the low shore intertidal zone, but more so on pebbles and small boulders (Fig. 75) in high to low shore intertidal rock pools and gullies, and occasionally epizoic on mollusc (limpets and whelks) shells. Thalli are firmly adherent, conforming to the substrate and are difficult to remove. Freshly collected living specimens are bright pink in colour, are encrusting (smooth) with a matt-like appearance, and have a visibly pitted appearance due to the sunken nature of the conceptacles (Fig. 1 and 2). Thalli are thin, measure up to 500 µm thick and lack protuberances.

### *3.4.4 Vegetative anatomy*

The thallus is dorsiventrally organised and monomerous, and haustoria are absent. The medulla is plumose (non-coaxial) (Fig. 4), comprising 5-10 cell layers, and measures 20-74 µm in thickness. Cells of the medullary filaments are elongate with rounded corners and are 2-4 times as long as wide. The cortex comprises the bulk of the thallus and comprise cells that are small, rounded to square and are uniformly bead-like in appearance. Fusions between cells of contiguous medullary and cortical filaments are abundant and frequently occupy most of the wall of adjoining cells; secondary pit connections have not been observed. Subepithallial initials are rounded to square to slightly flattened and in length are as short as or shorter than the cells immediately subtending them (Fig. 3). Epithallial cells occur in a single layer (up to 2 when shedding) and are rounded to oval to elliptical to flattened. Data on measured vegetative characters are summarised in Table 1.

### *3.4.5 Reproductive anatomy*

Gametangial thalli are dioecious. Spermatangial (male) conceptacles occur sunken in depressions that measure 370 - 450 µm in diameter (Fig. 5). Within depressions, conceptacles have raised (domed) roofs that extend above the immediately surrounding thallus surface (Figs 5-6). Mature male conceptacle chambers are elliptical. Conceptacle initiation occurs deep (adventitious, 10 cell layers or more) in the dorsal region of the thallus (Fig. 7). The roof is formed from filaments that arise peripheral to the fertile area, the terminal initials of which are more elongate than their inward derivatives. As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate. These cells project into the pore canal and are orientated more or less parallel to the conceptacle roof surface in fully developed conceptacles. Throughout the early development a protective layer of epithallial and cortical cells surrounds the conceptacle primordium (Fig. 8); this protective layer is shed once the pore canal is fully developed. The pore opening in fully developed conceptacles is often occluded by a mucilage plug (Fig. 6). Branched (dendroid) and unbranched (simple) spermatangial systems develop across the floor, walls and roof of mature male conceptacles (Fig. 6, 8-10). Senescent male conceptacles appear to be shed as no buried conceptacles were observed.

A single mature carpogonial (female) conceptacle was observed to occur in a depression 441 µm in diameter (Fig. 11). Within the depression, the conceptacle has a raised (domed) roof that extends above the immediately surrounding thallus surface. The carpogonial conceptacle chamber is elliptical. The conceptacle floor is located several (more than 20) cells below the thallus surface. The conceptacle pore canal cells project into the pore as papillae and are orientated more or less parallel to the conceptacle roof surface. The conceptacle pore is also occluded by a mucilage plug. Carpogonial branches develop across the floor of the conceptacle chamber, and comprised a single support cell and a hypogynous cell bearing a carpogonium extended into a trichogyne. Sterile cells are also present on the hypogynous cell.

After presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles (Fig. 12). Carposporangial conceptacles are comparatively large and occur in depressions that measure 368-515 µm in diameter. Carposporangial conceptacle chambers are elliptical, but with flattened bottoms presumably caused by the growth of the expanding carpospores. The pore is unoccluded and the canal is similarly structured to carpogonial conceptacles (Fig. 12 and 13), but noticeably wider. A large central fusion cell is absent; instead a discontinuous fusion cell is present and several-celled gonimoblast filaments (incl. a terminal carposporangium) develop along the periphery of the conceptacle chamber (Fig. 14). The remains of unfertilized carpogonia persist across the dorsal surface of the fusion cell. Senescent carposporangial conceptacles appear to be shed as no buried conceptacles were observed.

Tetrasporangial conceptacles are slightly to deeply sunken below the thallus surface in depressions measuring 274-490 µm in diameter (Fig. 15, 16 and 19). Conceptacle initiation occurs deep (adventitious, 10 cell layers or more) in the dorsal region of the thallus (Fig. 17). Tetrasporangial conceptacles are multiporate (Fig. 18) with roofs that are formed from filaments peripheral to and interspersed among the developing tetrasporangia. The lower segments of these interspersed filaments degenerate, creating the conceptacle chamber and leaving a roof 15-25 µm thick composed of 3-5 cells (including an epithallial cell) (Fig. 19 and 21). Conceptacle chambers are rounded to elliptical. Zonately divided tetrasporangia are scattered across the chamber floor (Fig. 20). Tetrasporangial conceptacle roofs bear apical pore plugs (Fig. 21). Pores are surrounded by 5-8 rosette cells with the pore opening slightly raised above the surrounding rosette cells (Fig. 18). Cells of the filaments lining the pore canal are squarish to slightly elongate and increase in size towards the conceptacle chamber (Fig. 19 and 21). Pore canal cells are, however, not markedly different (in shape, size or staining intensity) from the cells that make up the rest of the roof. Senescent tetrasporangial conceptacles appear to be shed as no buried conceptacles were observed. Data on measured reproductive characters are summarised in Table 2.

## 3.5 ***Phymatolithon ferox*** (Foslie) Maneveldt & E.van der Merwe, comb. nov.

(Fig. 22-38 and 76)

Basionym: *Lithothamnion ferox* Foslie, 1907: 7.

Synonyms: *Leptophytum ferox* (Foslie) Y.M.Chamberlain & Keats, 1994: 119; *Lithothamnion falsellum* f. *genuina* Foslie, 1900: 10; *Lithothamnion falsellum* f. *plicata* Foslie, 1900: 10; *Lithothamnion ferox* Foslie, 1907: 7; *Lithothamnion prolixum* Foslie, 1908: 9; *Mesophyllum ferox* (Foslie) W.H.Adey, 1970: 24; *Mesophyllum prolixum* (Foslie) Adey, 1970: 24.

Holotype: TRH, B15-2357. Natal, South Africa, A. Weber van Bosse, undated. Foslie slide 706. Printz 1929: pl. 4. Fig. 9 (as *Lithothamnion*).

Etymology: *ferox*, fierce or spiny, possibly referring to the horn-like shape of a tubeworm encrusted with this species in the type specimen (see Printz 1929: pl. 4, fig. 9) (Chamberlain and Keats, 1994: 119).

### *3.5.1 Specimens examined*

In total, thirty two (32) specimens were examined, these representing our entire collection for this taxon.

Namibia. Luderitz, Grossebuct, epilithic on bedrock on low shore and in mid to low shore tide pools (13.vii.1992, *D.W. Keats*, UWC 92/306).

South Africa. Northern Cape Province: Groenriviermond, epilithic on bedrock in the mid shore and epizoic on worm tubes (08.v.1993, *D.W. Keats* & *G.W. Maneveldt*, UWC 93/47; 27.ii.1994, *D.W. Keats*, UWC 94/34).

South Africa. Western Cape Province: Oudekraal, epilithic on bedrock on the mid shore (27.i.1994, *D.W. Keats*, UWC 94/20). Kommetjie, epiphytic on *Spongites yendoi* (23.xi.1991, *D.W. Keats*, UWC 91/235). Cape of Good Hope, epilithic on bedrock on the mid shore

(27.x.1991, *D.W. Keats*, UWC 91/98). Kalk Bay, epizoic on barnacles on the mid shore (16.i.2002, *G.W. Maneveldt*, UWC 2002/02). Dalebrook, epiphytic on *Spongites yendoi* on the lower intertidal zone (21.xi.1991, *D.W. Keats*, UWC 91/203). Holbaaipunt, epilithic on bedrock and epizoic on worm tubes on the mid to lower intertidal zone (10.vi.1990, *D.W. Keats* & *I. Matthews*, UWC Cor-14; 10.vi.1990, *D.W. Keats*, UWC Cor-15; 23.vi.1990, *D.W. Keats* & *I. Matthews*, UWC Cor-18; 23.vi.1990, *D.W. Keats* & *I. Matthews*, UWC Cor-23; 17.xi.1990, *D.W. Keats*, UWC Cor-93; 20.xi.1990, *D.W. Keats*, UWC Cor-95); (20.xi.1990, *D.W. Keats*, UWC Cor-96; 16.ii.1991, *D.W. Keats*, UWC Cor-182; 29.v.1991, *D.W. Keats*, UWC Cor-225; 26.xi.1991, *D.W. Keats*, UWC 91/253; 22.xii.1991, *D.W. Keats*, UWC 91/335; 05.v.1992, *D.W. Keats*, UWC 92/89; 16.vi.1992, *D.W. Keats*, UWC 92/154; 26.v.1994, *D.W. Keats*, UWC 94/126). Brandfontein, epilithic on bedrock in the high intertidal zone (09.vii.2009, *G.W. Maneveldt* & *E. van der Merwe*, UWC 09/146). Struisbaai, epilithic on bedrock and epizoic on worm tubes in mid intertidal gullies (06.vii.2009, *G.W. Maneveldt* & *E. van der Merwe*, UWC 09/109; 06.vii.2009, *G.W. Maneveldt* & *E. van der Merwe*, UWC 09/111). Stilbaai, Jongensfontein, epizoic on worm tubes on exposed mid-shore flats (13.vi.2010, *G.W. Maneveldt* & *E. van der Merwe*, UWC 10/125). Knysna Heads, epilithic on bedrock and epizoic on worm tubes on the high shore (07.iv.2008, *G.W. Maneveldt* & *E. van der Merwe*, UWC 08/27).

South Africa. Eastern Cape Province: Tsitsikamma National Park, Storms River Mouth, epizoic on worm tubes on the lower intertidal zone (12.vii.1991, *D.W. Keats*, UWC 91/273). Port Elizabeth, near Noordhoek, epilithic on bedrock on the mid-shore (20.v.1992, *D.W. Keats*, UWC 92/120). Kei Mouth, epilithic on bedrock and epizoic on worm tubes on the high shore (11.vii.2010, *G.W. Maneveldt* & *E. van der Merwe*, UWC 10/203; 11.vii.2010, *G.W. Maneveldt* & *E. van der Merwe*, UWC 10/204).

Mozambique. Inhaca Island, habitat unknown (01.vii.1991, *G. Branch*, UWC 91/260).

### *3.5.2 Distribution*

Known from Namibia, South Africa and Mozambique, but most common from the Northern Cape Province (Groenriviermond) to the Western Cape Province (Cape Agulhas).

### *3.5.3 Habit*

Thalli are non-geniculate, epilithic on the primary bedrock and epizoic on worm tubes and barnacles. Thalli are loosely adherent, thin and fragile and are easily removed from the substratum. Freshly collected living specimens are mauvish grey in colour, varying from being encrusting (smooth) to warty to lumpy. Warty to lumpy thalli bear abundant flat-topped protuberances that are unbranched and measure up to 10 mm in length and up to 3 mm in diameter. The thallus surface is often heavily grazed. Margins appear whitish. Secondary margins form characteristic mouth-like structures where they meet (Fig. 76). Thalli are thin and measure up to 500 µm thick.

### *3.5.4 Vegetative anatomy*

The thallus is dorsiventrally organized and monomerous, and haustoria are absent. The medulla is plumose (non-coaxial) (Fig. 22), comprising several cell layers that measure 74-172 µm in thickness. Cells of the medullary filaments are square to elongate with rounded corners. The cortex comprises roughly half the thallus. Cells of cortical filaments are square to oval to rectangular (Fig. 23). Fusions between cells of contiguous medullary and cortical filaments are abundant and frequently occupy most of the wall of adjoining cells; secondary pit connections have not been observed. Subepithallial initials are square to flattened and in length are as short as or shorter than the cells immediately subtending them (Fig. 23). Epithallial cells occur in a single layer and are squarish to oval to flattened. Data on measured vegetative characters are summarised in Table 1.

### *3.5.5 Reproductive anatomy*

Gametangial thalli are dioecious. Spermatangial (male) conceptacles are comparatively large and raised above the surrounding thallus surface (Fig. 24). Their chambers are elliptical. Male conceptacle primordia have not been observed. Conceptacle roof filaments project into the pore canal as papillae in fully developed conceptacles (Fig. 25). The pore opening is often occluded by a mucilage plug (Fig. 24). Both branched (dendroid) and unbranched (simple) spermatangial systems develop across the floor (weakly branched), walls and roof of the mature male conceptacle (Fig. 24, 26 and 27). Senescent male conceptacles appear to be shed from the thallus surface as no buried conceptacles were observed.

Of all carpogonial conceptacles observed, only one was fully developed and was raised above the thallus surface (Fig. 28). The conceptacle chamber is roundish. Carpogonial conceptacle primordia have not been observed. In young conceptacles, the roof is formed from filaments that arise peripheral to the fertile area, the terminal initials of which are more elongate than their inward derivatives (Fig. 29). As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate (Fig. 30). These cells project into the pore canal and are orientated more or less parallel to the conceptacle roof surface in fully developed conceptacles. Throughout the early development a protective layer of epithallial and cortical cells surrounds the conceptacle primordium (Fig. 29 and 30); this protective layer is shed once the pore canal is fully developed. The pore canal in fully developed conceptacles is occluded by a mucilage plug (Fig. 28).

After presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles. Carposporangial conceptacles are comparatively large and raised well above the surrounding thallus (Fig. 31). Chambers are roundish. The pore canal is lined by papillate cells that protrude into the pore canal (Fig. 32). The conceptacle pore is occluded by a mucilage plug (Fig. 31 and 32). A large central fusion cell is absent; instead a discontinuous fusion cell is present and several-celled gonimoblast filaments (incl. a terminal carposporangium) develop along the periphery of the conceptacle chamber (Fig. 31 and 33). Senescent carposporangial conceptacles appear to be shed from the thallus surface as no buried conceptacles were observed.

Tetrasporangial conceptacles are raised well above the surrounding thallus surface (Fig. 34 and 35), and vary greatly in external diameter. Conceptacle initiation occurs mostly deep (adventitious, 10 cell layers or more) in the dorsal region of the thallus (Fig. 36). Tetrasporangial conceptacles are multiporate (Fig. 35, 37 and 38) with roofs that are formed from filaments peripheral to and interspersed among the developing tetrasporangial (Fig. 38). The lower segments of these interspersed filaments degenerate, creating the conceptacle chamber and leaving a roof 22- 42 μm thick composed of 4-6 cells (including an epithallial cell that is sometimes missing). Conceptacle chambers are elliptical. Zonately divided tetrasporangia are scattered across the chamber floor (Fig. 35). Tetrasporangial conceptacle roofs bear apical pore plugs (Fig. 35 and 38). Pores are surrounded by 5-7 (mostly 6) rosette cells that are flush toward the pore opening (Fig. 37). The cells of the filaments lining the pore canal are rectangular to elongate and not markedly different (in shape, size or staining intensity) from the cells that make up the rest of the roof. Senescent tetrasporangial conceptacles appear to be shed from the thallus surface as no buried conceptacles were observed. Data on measured reproductive characters are summarised in Table 2.

## 3.6 ***Phymatolithon foveatum*** (Y.M.Chamberlain & Keats) Maneveldt & E.van der Merwe, comb. nov.

(Fig. 39-53 and 77)

Basionym: *Leptophytum foveatum* Y.M.Chamberlain & Keats, 1994: 115-119, figs 32-48.

Synonyms: None.

Holotype: L, 993.052 539. Yzerfontein, west coast of the Western Cape Province, South Africa. Y.M. Chamberlain & D.W. Keats.

Etymology: *foveatum* after the Latin *foveatus* meaning pitted. The epithet makes reference to the pitted nature of the thallus surface (Chamberlain and Keats, 1994: 115).

### *3.6.1 Specimens examined*

In total, twelve (12) specimens were examined, these representing our entire collection for this taxon.

Namibia. Swakopmund, epilithic on the primary bedrock in low shore tide pools and epizoic on mollusc shells in the low shore and upper sublittoral zone (05.vii.1993, *D.W. Keats, G.W. Maneveldt & Y. Chamberlain*, UWC 93/150; 05.vii.1993, *D.W. Keats, G.W. Maneveldt & Y. Chamberlain*, UWC 93/153B).

South Africa. Northern Cape Province: Port Nolloth, epilithic on the primary bedrock on the low shore, sublittoral fringe and subtidal zone to 2 m deep, and epizoic on the low shore on shells of the limpet *S. argenvillei* (07.v.1993, *D.W. Keats*, UWC 93/23; 07.v.1993, *D.W. Keats*, UWC 93/30; 17.vii.1993, *D.W. Keats & G.W. Maneveldt*, UWC 93/164; 26.ii.1994, *D.W. Keats*, UWC 94/30). Groenriviermond, epilithic on the primary bedrock on the low shore and in tide pools, and epizoic on limpet (*S. argenvillei* and *S. cochlear*) shells in the low shore (08.v.1993, *D.W. Keats & G.W. Maneveldt*, UWC 93/46).

South Africa. Western Cape Province: Kalk Bay, epizoic on winkle (*Oxystele sinensis*) shells in the subtidal zone (19.viii.2008, *G.W. Maneveldt & R. Eager*, UWC 08/53). Holbaaipunt, epilithic on the primary bedrock and epizoic on limpet (*S. cochlear*) shells on the low shore (03.iii.1995, *D.W. Keats*, UWC 95/05). Struisbaai, epilithic on bedrock in low shore tide pools (06.vii.2009, *G.W. Maneveldt & E. van der Merwe*, UWC 09/114). Stilbaai, Jongensfontein, epilithic on the primary bedrock and epizoic on worm tubes in low shore tide pools (13.vi.2010, *G.W. Maneveldt & E. van der Merwe*, UWC 10/123). Tsitsikamma, Nature's Valley, epilithic on the primary bedrock on the low shore (06.iv.2008, *G.W. Maneveldt & U. van Bloemestein*, UWC 08/21).

### *3.6.2 Distribution*

Distributed from Namibia (Swakopmund) to at least Tsitsikamma (Nature's Valley) in the Western Cape Province.

### *3.6.3 Habit*

Thalli are non-geniculate, epilithic on the primary bedrock, and epizoic on worm tubes and mollusc (limpet and winkle) shells. Freshly collected living specimens are brownish-pink in colour, are matt, encrusting (smooth) and firmly adherent (Fig. 77), and sometimes appear uneven and nodular as a result of conforming to the substrate. The surface has a pitted appearance due to the sunken nature of the conceptacles. Their primary margins are slightly raised and abundant secondary margins occur throughout the thallus surface, giving the thallus an imbricate appearance (Fig. 39). Thalli are thin, measure up to 500 µm thick and lack protuberances.

### *3.6.4 Vegetative anatomy*

The thallus is dorsiventrally organised and monomerous, and haustoria are absent. The medulla is plumose (non-coaxial) (Fig. 40), comprising 2-7 cell layers, and measures 10-49 µm in thickness. Cells of the medullary filaments are rectangular to elongate with rounded corners and are 2-5 times as long as wide. The cortex comprises the bulk of the thallus thickness. Cells of cortical filaments vary from square to elongate (Fig. 41). Fusions between cells of contiguous medullary and cortical filaments are abundant and frequently occupy most of the wall of adjoining cells; secondary pit connections have not been observed. Solitary trichocytes occur throughout the cortex (Fig. 41). Subepithallial initials are square to oval to squat and in length are as short as or shorter than the cells immediately subtending them. An epithallial cell layer is often not intact, but when it is it occurs in a single layer (Fig. 41). Epithallial cells are rounded to elliptical. Data on measured vegetative characters are summarised in Table 1.

### *3.6.5 Reproductive anatomy*

Gametangial thalli are dioecious. Spermatangial (male) conceptacles are comparatively large and occur sunken in depressions that measure 220-550 µm in diameter. In depressions, conceptacles roofs are slightly raised above the surrounding depressed thallus (Fig. 42). Mature male conceptacles chambers are elliptical. Conceptacle initiation occurs deep (adventitious, 10 cell layers or more) in the dorsal region of the thallus (Fig. 43). The roof is formed from filaments that arise peripheral to the fertile area (Fig. 44), the terminal initials of which are more elongate than their inward derivatives. As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate. These cells project into the pore canal in fully developed conceptacles. Throughout the early development a protective layer of epithallial and cortical cells surrounds the conceptacle primordium (Fig. 43 and 44); this protective layer is shed once the pore canal is fully developed. The pore opening in fully developed conceptacles is often occluded by a mucilage plug (Fig. 42). Branched (dendroid) and unbranched (simple) spermatangial systems develop across the floor (Fig. 45 and 46), while those on the walls and roof of the mature male conceptacles are unbranched only (Fig. 45 and 47). The central region of the conceptacle floor often contains different-looking spermatangial structures that we were unable to classify (Fig. 46). Senescent male conceptacles appear to be shed as no buried conceptacles were observed.

Neither carpogonial (female) nor carposporangial thalli were observed.

Tetrasporangial conceptacles are flush with the surrounding thallus surface, to deeply sunken in depressions that measure 290-500 µm in diameter (Fig. 48 and 51). Conceptacle initiation occurs mostly deep (adventitious, 10 cell layers or more) in the dorsal region of the thallus (Fi. 49). Tetrasporangial conceptacles are multiporate (Fig. 8 and 50) with roofs that are formed from filaments peripheral to and interspersed among the developing tetrasporangia (Fig. 52). The lower segments of these interspersed filaments degenerate, creating the conceptacle chamber and leaving a roof 25-42 µm thick composed of 4-5 cells (including an epithallial cell that is sometimes missing) (Fig. 52 and 53). Conceptacle chambers are elliptical. Zonately divided tetrasporangia are scattered across the chamber floor (Fig. 51). Tetrasporangial conceptacle roofs bear apical pore plugs (Fig. 51 and 52). Pores are surrounded by 6-8 rosette cells and the pore opening is slightly raised above the surrounding rosette cells (Fig. 50). Cells of the filaments lining the pore canal are rectangular to elongate with the basal cell the longest (Fig. 52 and 53); the cells are, however, not markedly different (in shape, size or staining intensity) from the cells that make up the rest of the roof. Senescent tetrasporangial conceptacles appear to be shed as no buried conceptacles were observed. Data on measured reproductive characters are summarised in Table 2.

## 3.7 ***Phymatolithon repandum*** (Foslie) Wilks & Woelkerling, 1994: 190-192

(Fig. 54-74 and 78)

Basionym: *Lithothamnion repandum* Foslie, 1904: 4.

Synonyms: *Leptophytum absonum* (Foslie) Adey, 1970: 29; *Leptophytum asperulum* (Foslie) Adey, 1970: 29; *Leptophytum repandum* (Foslie) Adey, 1970: 30; *Lithothamnion absonum* Foslie, 1907: 6-7; *Lithothamnion asperulum* (Foslie) Foslie, 1907: 6; *Lithothamnion lenormandii* f. *australe* Foslie, 1901: 8; *Lithothamnion repandum* f. *asperulum* Foslie, 1906: 5. Additional information on these binomials and information on synonymy are provided by Wilks & Woelkerling (1994).

Lectotype: TRH, unnumbered; Half Moon Bay, Port Phillip Bay, Victoria, Australia; J. Gabriel, 14 January 1899. Designated by Adey in Adey & Lebednik (1967: 83). Additional data are provided by Woelkerling (1993: 189).

Etymology: Foslie (1904) did not explain the origin of the epithet. Presumably it is derived from the Latin *repandus*, which means having a slightly uneven and waved margin (Stearn 1973).

### *3.7.1 Specimens examined*

In total, nine (9) specimens were examined, these representing our entire collection for this taxon.

South Africa. Northern Cape Province: Groenriviermond, epilithic on boulders in low shore tide pools (17.vii.1993, *D.W. Keats*, UWC 93/171).

South Africa. Western Cape Province: Oudekraal, epilithic on the primary bedrock and on boulders in subtidal (to 10 m) sand inundated channels among kelp (19.i.1994, *D.W. Keats & G.W. Maneveldt*, UWC 94/16; 27.i.1994, *D.W. Keats & G.W. Maneveldt*, UWC 94/18). Cape

Hangklip, epilithic on the primary bedrock and on boulders in subtidal zone. Common at 8-10 m depth (19.viii.1993, *D.W. Keats*, UWC 93/200; UWC 93/201). Holbaaipunt, epilithic on the primary bedrock and on boulders in shallow subtidal sand inundated channels (21.v.1993, *D.W. Keats*, UWC 93/52; 21.vi. 1993, *D.W. Keats*, UWC 93/63; UWC 93/68; 26.v.1994, *D.W. Keats*, UWC 94/128).

### *3.7.2 Distribution*

Distributed from Groenriviermond (Northern Cape) to Holbaaipunt in the Western Cape Province.

### *3.7.3 Habit*

Thalli are non-geniculate, epilithic on the primary bedrock and on boulders, mostly in the subtidal where it has been collected to depths of 10 m. Freshly collected living specimens are variable in colour from dull pinkish to reddish to brownish to purplish brown, are matt, and thalli are encrusting to warty to lumpy to fruticose (Fig. 78). Thalli are thick and measure up to 1860 µm with protuberances that measure up to 3 mm in length.

### *3.7.4 Vegetative anatomy*

The thallus is dorsiventrally organised and monomerous, and haustoria are absent. The medulla is mostly plumose (non-coaxial) (Fig. 54), but sometimes also coaxial (Fig. 55) comprising several cell layers. In young coaxial thalli, the medulla comprises up to 70% of the thallus thickness. Cells of the medullary filaments are rectangular to elongate with rounded corners and are 2-4 times as long as wide. In plumose thalli, the cortex comprises the bulk of the thallus thickness. Cells of cortical filaments vary from being square to elongate (Fig. 56). Fusions between cells of contiguous medullary and cortical filaments are abundant and frequently occupy most of the wall of adjoining cells; secondary pit connections have not been observed in either the medullary or the cortical filaments. Trichocytes have not been observed. Subepithallial initials are square to oval to squat and in length are as short as or shorter than the cells immediately subtending them (Fig. 56). Epithallial cells are rounded to elliptical, are dark-staining, and occur in a single layer. Data on measured vegetative characters are summarised in Table 1.

### *3.7.5 Reproductive anatomy*

Gametangial thalli are monoecious or dioecious. Spermatangial (male) conceptacles are variable in size and occur raised above the surrounding thallus surface (Fig. 57). Mature male conceptacles chambers are rounded to elliptical. Conceptacle initiation occurs deep (adventitious, 7 cell layers or more) in the dorsal region of the thallus (Fig. 58 and 59). The roof is formed from filaments that arise peripheral to the fertile area (Fig. 60), the terminal initials of which are more elongate than their inward derivatives. As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate. These cells project into the pore canal in fully developed conceptacles. Throughout the early development a protective layer of epithallial and cortical cells surrounds the conceptacle primordium (Fig. 59 and 60); this protective layer is shed once the pore canal is fully developed. The pore opening in fully developed conceptacles is often occluded by a mucilage plug (Fig. 57). Branched (dendroid) and unbranched (simple) spermatangial systems develop across the floor, walls and roof of the mature male conceptacles (Fig. 57, 61 and 62). Senescent male conceptacles appear to be shed as no buried conceptacles were observed, but infilling is evident as crescent-shaped scars (Fig. 63).

Carpogonial (female) conceptacles are raised above the thallus surface (Fig. 64). The conceptacle chamber is roundish to elliptical to flattened. Conceptacle initiation occurs deep (adventitious) in the dorsal region of the thallus (Fig. 65). The pore canal cells project into the pore as papillae, and are orientated more or less parallel to the conceptacle roof surface. Throughout the early development a protective layer of epithallial and cortical cells surrounds the conceptacle primordium (Fig. 65 and 66); this protective layer is shed once the pore canal is fully developed. The pore canal in fully developed conceptacles is occluded by a mucilage plug (Fig. 64). Carpogonial branches develop across the floor of the female conceptacle and comprise at least one support cell and a hypogynous cell bearing a carpogonium extended into a trichogyne. A sterile cell may also be present on the hypogynous cell.

After presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles. Carposporangial conceptacles are comparatively large and raised well above the surrounding thallus (Fig. 67). Chambers are roundish to elliptical. The pore canal is lined by papillate cells that protrude into the pore canal. The conceptacle pore is occluded by a mucilage plug (Fig. 67). A large central fusion cell is absent; instead a discontinuous fusion cell is present and 3-5 celled gonimoblast filaments (incl. a terminal carposporangium) develop either along the periphery of the conceptacle chamber (Fig. 67 and 69) or are scattered across the floor (Fig. 68). Senescent carposporangial conceptacles appear to be shed as no buried conceptacles were observed, but infilling is evident as crescent-shaped scars (Fig. 63).

Tetrasporangial conceptacles are flush to mostly raised above the surrounding thallus surface and are variable in size (Fig. 70). Conceptacle initiation occurs deep (adventitious, 7 cell layers or more) in the dorsal region of the thallus and the young developing tetrasporangial initials are overlain by a layer of protective cortical and epithallial cells (Fig. 71) that eventually become shed. Tetrasporangial conceptacles are multiporate (Fig. 70, 72 and 73) with roofs that are formed from filaments peripheral to and interspersed among the developing tetrasporangia (Fig. 74). The lower segments of these interspersed filaments degenerate, creating the conceptacle chamber and leaving a roof 20-27 µm thick composed of 3-5 (mostly 4) cells (including an epithallial cell). Conceptacle chambers are roundish to elliptical. Zonately divided tetrasporangia are scattered across the chamber floor (Fig. 73). Tetrasporangial conceptacle roofs bear apical pore plugs (Fig. 74). Pores are surrounded by 6-9 rosette cells and the pore opening is slightly raised above the surrounding rosette cells (Fig. 72). Cells of the filaments lining the pore canal are squarish to slightly elongate with the basal cell the longest (Fig. 74); the cells are, however, not markedly different (in shape, size or staining intensity) from the cells that make up the rest of the roof. Senescent tetrasporangial conceptacles appear to be shed as no buried conceptacles were observed, but infilling is evident (Fig. 73). Data on measured reproductive characters are summarised in Table 2.

*Phymatolithon repandum* from South Africa compares favourably to specimens reported from Australia, which is home to the type locality (Table 3). See Table 4 for a synopsis of the characters considered diagnostic of the four species of *Phymatolithon* now known to exist in South Africa.

## 4. Discussion

*Phymatolithon*, as delimited by Harvey et al. (2003), is the only known genus in the family Hapalidiaceae that: 1) possesses subepithallial initials that are as short as or shorter than the cells immediately subtending them; and 2) produces both branched (dendroid) and unbranched (simple) spermatangial filaments in male conceptacles. In addition to the other family characteristics, *P. acervatum*, *P. ferox* and *P. foveatum* reported here, possess these characters currently considered diagnostic of *Phymatolithon* and so rightly belong in the genus. Furthermore, *P. repandum* presented here is described in detail for the first time from South Africa and is found to compare favourably to specimens reported from Australia, home to the type locality.

Until this study, except for *P. foveatum*, no carpogonial (female) thalli had been reported for the taxa presented here. In their reporting of carposporangial thalli in *L. acervatum*, Chamberlain and Keats (1994) reported the absence of a central fusion cell although they did report discontinuous fusion cells for both *L. ferox* and *L. foveatum*. We confirm the absence of a (solid) central fusion cell, but have found a discontinuous fusion cell to exist that was often visible only in serial sections. The absence of a (solid) central fusion cell does therefore not necessarily mean the absence of a fusion cell altogether.

Most importantly, our research shows that features used to segregate the genus *Leptophytum* from *Phymatolithon* do not stand up to scrutiny. Among other features (see summaries by Düwel and Wegeberg, 1996; Woelkerling et al., 2002), the genus *Leptophytum* was previously separated from *Phymatolithon* by the presence of branched spermatangial systems only on the centre of the floor of the male conceptacle in the former as opposed to branched systems across the entire male conceptacle floor in *Phymatolithon* (Adey, 1966; Lebednik, 1978; Chamberlain, 1990; Chamberlain and Irvine, 1994; Chamberlain and Keats, 1994; Adey et al., 2001). Both *L. acervatum* and *L. ferox* where reported by Chamberlain and Keats (1994) to possess this feature i.e. unbranched spermatangial systems on the floor, walls and roof of the male conceptacles, but branched spermatangial systems restricted to the centre of the floor of the male conceptacle. While no male thalli were previously observed and thus reported on for *L. foveatum*, Chamberlain and Keats (1994: 118) made the assumption that the latter species possessed the same spermatangial (male) characteristics said to be diagnostic of the genus *Leptophytum*. However, during our investigations on an extensive collection of material, we have found all three species to conform to the diagnostic characterisation of *Phymatolithon*. Düwel and Wegeberg (1996) suggested that the different elaborations of the spermatangial systems previously reported as diagnostic for both *Leptophytum* and *Phymatolithon* possibly represent various stages of development. We support this suggestion.

Another feature previously used to separate *Leptophytum* from *Phymatolithon*, was the depth of the tetrasporangial conceptacle initiation. In *Leptophytum*, tetrasporangial conceptacle initiation was reported to be shallow (no more than 3-5 cells below the thallus surface), while in *Phymatolithon* it was reported to be adventitious or 'deep' (several cells) within the dorsal region of the thallus (Adey, 1964, 1966, 1970; Chamberlain 1990; Chamberlain and Irvine 1994; Wilks and Woelkerling, 1994; Womersley 1996; Adey et al., 2001; Athanasiadis and Adey 2006). For the majority of material observed during this study, both gametangial and tetrasporangial conceptacle initiations were generally deep (more than 10 cells) within the dorsal region of the thallus.

As a consequence of the data presented here, we question the continued use and availability of the name *Leptophytum*. Firstly, it is important to note why, in much of the recent literature, the name has been placed in quotation marks. Maneveldt et al. (2008) used the name "*Leptophytum*" in quotation marks because South African taxa ascribed to this genus had not been formally transferred to *Phymatolithon* or reduced to synonymy. This usage was first proposed by Bailey and Chapman (1998: 694 [footnote to table 1]; 700) as a result of the unresolved taxonomy of those taxa ascribed to '*Leptophytum*' and for similar reasons mentioned by Maneveldt et al. (2008). This practice (of placing the name in quotation marks) has been adopted by other authors, notably in molecular studies (e.g. Broom et al., 2008; Bittner et al., 2011).

On the basis of anatomical studies of the relevant types and other specimens, Düwel and Wegeberg (1996) determined that *Leptophytum* Adey is a heterotypic synonym of *Phymatolithon* Foslie. Düwel and Wegeberg (1996: 482), however, did not preclude the possibility of a genus separate from *Phymatolithon* and as noted by Bailey and Chapman (1998: 700), "it is conceivable, but by no means certain, that a new genus may have to be erected to include some species once classified in '*Leptophytum*'. Presently there appears to be no reliable morphological/anatomical features that can be used to establish such a new genus (Woelkerling et al., 2002). If future research does show that a genus separate from *Phymatolithon* is warranted, it should, however, be based on well-defined morphological/anatomical characters and not solely on molecular evidence (Bailey and Chapman, 1998; Woelkerling et al., 2002), a sentiment strongly iterated by Guiry (2012: 1059). Our data and interpretation support this view. Ironically, recent molecular data (e.g. Broom et al., 2008: 970; Bittner et al., 2011; 705 [fig 1]) has shown a closer affinity between *P. repandum* from New Zealand and South African '*Leptophytum' acervatum* and '*Leptophytum' ferox* than with congeners from *Phymatolithon*, providing molecular support for our findings.

In conclusion, not only are we the first to present a description of *P. repandum* for South Africa, previously only reported for the country (see Maneveldt et al., 2008: 560), we are the first to demonstrate that all taxa from South Africa previously classified under the name *Leptophytum*, indeed belong within the genus *Phymatolithon*. Our data supports previous conclusions that the characters upon which *Leptophytum* is based are unreliable for generic delimitation from *Phymatolithon*. We reiterate that the name *Leptophytum* is not available for use as a result of the study of Düwel and Wegeberg (1996). The only exception would be if *P. lenormandii*, with which the type of *Leptophytum* Adey is conspecific (see Düwel and Wegeberg 1996: 481), were determined not to belong to *Phymatolithon* and were also chosen as the type species of a separate genus.

## Acknowledgements

We thank the Department of Biodiversity and Conservation Biology at the University of the Western Cape (UWC) for providing funding and research equipment, and the South African National Research Foundation (NRF) for a research grant to GWM. Adrian Josephs provided assistance with the operation of the SEM. We thank Bill Woelkerling and one other anonymous reviewer for invaluable comments to this paper.

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## TABLES

**Table 1.** A comparison of the habit and vegetative features of the four species of *Phymatolithon* now known to exist in South Africa compared against those of previously published records. ND = No data.

| **Character** | ***P. acervatum*** (this study) | ***L. acervatum*** (Chamberlain and Keats 1994) | ***P. ferox*** (this study) | ***L. ferox*** (Chamberlain and Keats 1994) | ***P. foveatum*** (this study) | ***L. foveatum*** (Chamberlain and Keats 1994) | ***P. repandum*** (this study) |
|---|---|---|---|---|---|---|---|
| Substrate | mostly epilithic on pebbles and small boulders | epilithic on pebbles and small boulders | epilithic on rock, epizoic on worm tubes | epilithic on rock, epizoic on worm tubes | epilithic on rock, epizoic worm tubes and mollusk shells | epilithic on rock, epizoic worm tubes and mollusk shells | epilithic on rock |
| Growth form | encrusting | encrusting | encrusting to warty to lumpy | encrusting to protuberant (= warty/lumpy) | encrusting | encrusting | encrusting to warty to lumpy to fruticose |
| Thallus thickness | to 500 µm | to 500 µm | to 500 µm, protuberances to 10 mm | to 500 µm, protuberances to 10 mm | to 500 µm | to 500 µm | to 1860 µm, protuberances to 3 mm |
| Thallus construction | monomerous and plumose | monomerous and non-coaxial (= plumose) | monomerous and plumose | monomerous and non-coaxial (= plumose) | monomerous and plumose | monomerous and non-coaxial (= plumose) | monomerous and mostly plumose; some coaxial areas occur |
| Medullary cell length | 4-15 µm | 4-14 µm | 10-22 µm | 9-22 µm | 10-33 µm | 15-50 µm | 7-42 µm |
| Medullary cell diameter | 4-7 µm | 4-6 µm | 2-9 µm | 3-9 µm | 5-10 µm | 4-9 µm | 5-11 µm |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Cortical cell length | 5-10 µm | 4-6 µm | 5-10 µm | 2-10 µm | 4-13 µm | 4-10 µm | 6-16 µm |
| Cortical cell diameter | 4-7 µm | 4-6 µm | 4-7 µm | 2-5 µm | 2-10 µm | 4-5 µm | 4-9 µm |
| Subepithallial cell length | 3-5 µm | ND | 4-5 µm | ND | 2-7 µm | ND | 4-7 µm |
| Subepithallial cell diameter | 4-6 µm | ND | 5-6 µm | ND | 2-9 µm | ND | 4-8 µm |
| Epithallial cell length | 2-6 µm | 2-4 µm | 4-5 µm | 2-4 µm | 2-4 µm | 2-4 µm | 4-5 µm |
| Epithallial cell diameter | 3-6(10) µm | 4-6 µm | 4-7 µm | 4-5 µm | 4-7 µm | 4-8 µm | 5-6 µm |
| Trichocytes | none observed | ND | none observed | ND | solitary | ND | none observed |
| Trichocyte length | - | - | - | - | 12-22 µm | - | - |
| Trichocyte diameter | - | - | - | - | 5-7 µm | - | - |

**Table 2.** A comparison of the reproductive features of the four species of *Phymatolithon* now known to exist in South Africa compared against those of previously published records. ND = No data.

| **Character** | ***P. acervatum*** (this study) | ***L. acervatum*** (Chamberlain and Keats, 1994) | ***P. ferox*** (this study) | ***L. ferox*** (Chamberlain and Keats, 1994) | ***P. foveatum*** (this study) | ***L. foveatum*** (Chamberlain and Keats, 1994) | ***P. repandum*** (this study) |
|---|---|---|---|---|---|---|---|
| Gametangial thalli | dioecious | dioecious | dioecious | dioecious | presumably dioecious | presumably dioecious | monoecious or dioecious |
| Spermatangial thalli | | | | | | | |
| Conceptacle placement | sunken in depressions, but with raised roofs | sunken in depressions, but with raised roofs | raised above surrounding thallus surface | raised above surrounding thallus surface | slightly sunken in depressions, but with raised roofs | ND | raised above surrounding thallus surface |
| External conceptacle diameter | 370-450 µm | ND | 350-600 µm | ND | 220-550 µm | ND | 320-580 µm |
| Conceptacle chamber diameter | 155-279 µm | 156-260 µm | 135-250 µm | 208-247 µm | 159-277 µm | ND | 186-314 µm |
| Conceptacle chamber height | 50-118 µm | 52-78 µm | 47-127 µm | 47-117 µm | 71-93 µm | ND | 71-137 µm |
| Conceptacle roof thickness | 39-76 µm | 39-58 µm | 37-75 µm | 60-73 µm | 27-59 µm | ND | 27-70 µm |
| Spermatangial systems | branched and unbranched on floor, walls and roof | unbranched on floor, walls and roof; branched at centre of floor | branched and unbranched on floor, walls and roof | unbranched on floor, walls and roof; branched at centre of floor | branched and unbranched on floor; but mostly unbranched on walls and roof | ND | branched and unbranched on floor, walls and roof |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Carpogonial thalli | | | | | | | |
| Conceptacle placement | sunken in a depression, but with a raised roof | ND | raised above surrounding thallus surface | ND | ND | ND | raised above surrounding thallus surface |
| External conceptacle diameter | 441 µm | ND | 400 µm | ND | ND | ND | 400-500 µm |
| Conceptacle chamber diameter | 142 µm | ND | 154 µm | ND | ND | ND | 130-270 µm |
| Conceptacle chamber height | 51 µm | ND | 93 µm | ND | ND | ND | 54-113 µm |
| Conceptacle roof thickness | 88 µm | ND | 118 µm | ND | ND | ND | 83-127 µm |
| Carposporangial thalli | | | | | | | |
| Conceptacle placement | sunken in depressions, but with raised roofs | sunken in depressions, but with raised roofs | raised above the surrounding thallus | raised above the surrounding thallus | ND | sunken in depressions | raised above surrounding thallus surface |
| External conceptacle diameter | 368-515 µm | ND | 400-600 µm | ND | ND | ND | 430-640 µm |
| Conceptacle chamber diameter | 180-287 µm | 182-286 µm | 140-335 µm | 143-330 µm | ND | 169-286 µm | 233-372 µm |
| Conceptacle chamber height | 50-123 µm | 52-91 µm | 80-206 µm | 83-120 µm | ND | 78-117 µm | 75-159 µm |
| Conceptacle roof thickness | 42-108 µm | 47-78 µm | 49-100 µm | 50-100 µm | ND | 65-130 µm | 96-115 µm |
| Type of fusion cell | discontinuous | fusion cell absent | discontinuous | discontinuous | ND | scattered (= | discontinuous |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | | | | | discontinuous) | |
| Distribution of gonimoblast filaments | peripheral | peripheral | peripheral | peripheral | ND | peripheral | peripheral or scattered across the floor |
| No of cells in gonimoblast filament | 4-7 | 4 | 4-7 | 4-5 | ND | 4-5 | 3-5 |
| Carpospore length | 32-47 µm | ND | 27-62 µm | ND | ND | ND | 25-54 µm |
| Carpospore diameter | 44-74 µm | ND | 56-78 µm | ND | ND | ND | 34-74 µm |
| Tetrasporangial thalli | | | | | | | |
| Conceptacle placement | sunken in depressions | sunken in depressions | raised above surrounding thallus | raised above surrounding thallus | flush with the surrounding thallus surface to sunken in depressions | sunken in depressions | raised above to flush with surrounding thallus surface |
| External conceptacle diameter | 274-490 µm | ND | 180-637 µm | ND | 290-500 µm | ND | 270-600 µm |
| Conceptacle chamber diameter | 115-255 µm | 115-208 µm | 127-348 µm | 130-270 µm | 80-289 µm | 86-208 µm | 191-333 µm |
| Conceptacle chamber height | 50-150 µm | 52-143 µm | 60-176 µm | 60-160 µm | 50-115 µm | 52-91 µm | 88-147 µm |
| Conceptacle roof thickness | 15-25 µm | 15-23 (44) µm | 20-42 µm | 21-34 µm | 25-42 µm | 26-34 µm | 20-27 µm |
| No. of cell in conceptacle pore plate | 3-5 | 3-4 | 4-6 | 2-4 | 4-5 | 4-5 | 3-5 |
| No. of pore rosette cells | 5-8 | 5-8 | 5-7 | 6-7 | 6-8 | 7-8 | 6-9 |
| Tetrasporangium length | 65-113 µm | 65-97 µm | 65-135 µm | 65-78 µm | 50-98 µm | 50-65 µm | 81-147 µm |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Tetrasporangium diameter | 12-69 µm | 30-48 µm | 15-86 µm | 21-65 µm | 20-66 µm | 22-33 µm | 22-78 µm |
| Bisporangium length | 69-103 µm | ND | 50-147 µm | 52-109 µm | 74-100 µm | ND | ND |
| Bisporangium diameter | 27-64 µm | ND | 15-76 µm | 18-49 µm | 27-66 µm | ND | ND |

**Table 3.** Comparison of *P. repandum* from South Africa (this study) and Australia based on selected characteristics. ND = No data.

| **Character** | ***P. repandum*** (this study) | ***P. repandum*** (Wilks and Woelkerling, 1994) | ***P. repandum*** (Womersley, 1996) | ***P. repandum*** (Harvey et al., 2003) |
|---|---|---|---|---|
| Substrate | epilithic on rock | mostly epilithic on rock[1] | epilithic on rock | epilithic on rock |
| Growth form | encrusting to warty to lumpy to fruticose | encrusting to warty to fruticose | encrusting to warty to fruticose | encrusting to warty |
| Thallus thickness | to 1860 µm, protuberances to 3 mm | 100 µm – 1.5 mm | 0.1 – 4.0 mm | up to 1 mm, protuberances to 2 mm |
| Gametangial thalli | monoecious or dioecious | ND | monoecious or dioecious | monoecious or dioecious |
| Spermatangial thalli | | | | |
| Conceptacle placement | raised above surrounding thallus surface | raised above surrounding thallus surface | raised above surrounding thallus surface | slightly raised above or flush with surrounding thallus |
| External conceptacle diameter | 320-580 µm | ND | ND | ND |
| Conceptacle chamber diameter | 186-314 µm | 100-250 µm | 100-250 µm | 120-215 µm |
| Conceptacle chamber height | 71-137 µm | 45-150 µm | 45-150 µm | 30-55 µm |
| Conceptacle roof thickness | 27-70 µm | 25-75 µm | 25-75 µm | ND |
| Spermatangial systems | branched and unbranched on floor, walls and roof | branched and unbranched on floor, walls and roof | branched and unbranched on floor, walls and roof | branched only on floor to branched and unbranched on roof |
| Carpogonial thalli | | | | |
| Conceptacle placement | raised above surrounding thallus surface | raised above to flush with surrounding thallus surface | raised above to flush with surrounding thallus surface | raised above surrounding thallus surface |

| | | | | |
|---|---|---|---|---|
| External conceptacle diameter | 400-500 µm | ND | ND | ND |
| Conceptacle chamber diameter | 130-270 µm | 112-300 µm | ND | 95-135 µm |
| Conceptacle chamber height | 54-113 µm | 50-125 µm | ND | 55-80 µm |
| Conceptacle roof thickness | 83-127 µm | 22-100 µm | ND | ND |
| Carposporangial thalli | | | | |
| Conceptacle placement | raised above surrounding thallus surface | raised above to flush with surrounding thallus surface | raised above to flush with surrounding thallus surface | raised above surrounding thallus surface |
| External conceptacle diameter | 430-640 µm | ND | ND | ND |
| Conceptacle chamber diameter | 233-372 µm | 112-300 µm | 112-300 µm | 95-135 µm |
| Conceptacle chamber height | 75-159 µm | 50-125 µm | 50-125 µm | 55-80 µm |
| Conceptacle roof thickness | 96-115 µm | 22-100 µm | ND | ND |
| Type of fusion cell | large central fusion cell absent; fusion cell is instead discontinuous | large central fusion cell absent; fusion cell is instead discontinuous[2] | large central fusion cell absent; fusion cell is instead discontinuous[3] | irregularly shaped and discontinuous |
| Distribution of gonimoblast filaments | peripheral or scattered across the floor | peripheral or scattered across the floor | ND | scattered across the floor |
| No of cells in gonimoblast filament | 3-5 | 2- several-celled | several-celled | several-celled |
| Carpospore length | 25-54 µm | 17-63 µm | ND | ND |
| Carpospore diameter | 34-74 µm | 12-75 µm | 12-75 µm | ND |

| | | | | |
|---|---|---|---|---|
| Tetrasporangial thalli | | | | |
| Conceptacle placement | raised above to flush with surrounding thallus surface | raised above to flush with surrounding thallus surface | raised above surrounding thallus surface | raised above to flush with surrounding thallus surface |
| External conceptacle diameter | 270-600 µm | ND | ND | ND |
| Conceptacle chamber diameter | 191-333 µm | 96-300 µm | 96-300 µm | 120-205 µm |
| Conceptacle chamber height | 88-147 µm | 50-150 µm | 50-150 µm | 60-120 µm |
| Conceptacle roof thickness | 20-27 µm | 20-33 (42) µm | ND | ND |
| No. of cells in conceptacle pore plate | 3-5 | 3-5 | 3-5 | 3-4 |
| No. of pore rosette cells | 6-9 | ND | ND | ND |
| Tetra/bisporangium length | 81-147 µm | 32-125 µm | 32-125 µm | 45-95 µm |
| Tetra/bisporangium diameter | 22-78 µm | 15-80 µm | 15-80 µm | 16-70 µm |

[1] Also epigenous on a glass bottle.
[2] Figure 10B shows a discontinuous fusion cell.
[3] Figure 81B (same figure as in Wilks and Woelkerling, 1994), shows a discontinuous fusion cell.

**Table 4.** Comparison of the characters collectively considered diagnostic of the four species of *Phymatolithon* now known to exist in South Africa.

| **Character** | ***P. acervatum*** | ***P. ferox*** | ***P. foveatum*** | ***P. repandum*** |
|---|---|---|---|---|
| Substrate | mostly epilithic on pebbles and small boulders | epilithic on rock, epizoic on worm tubes | epilithic on rock, epizoic on worm tubes and mollusk shells | epilithic on rock |
| Growth form | encrusting | encrusting to warty to lumpy | encrusting | encrusting to warty to lumpy to fruticose |
| Thallus surface | smooth, with a visibly pitted appearance | with secondary mouth-like margins and flat-topped protuberances | smooth, with secondary, imbricate margins | protuberant, without secondary margins |
| Thallus thickness | to 500 µm,<br>not protuberant | to 500 µm,<br>protuberances to 10 mm | to 500 µm,<br>not protuberant | to 1860 µm,<br>protuberances to 3 mm |
| Conceptacle placement | sunken in depressions | raised above surrounding thallus surface | flush with the surrounding thallus surface to sunken in depressions | raised above surrounding thallus surface |
| Gametangial thalli | dioecious | dioecious | dioecious | monoecious or dioecious |
| Distribution of gonimoblast filaments | peripheral | peripheral | peripheral | peripheral or scattered across the floor |

## FIGURE CAPTIONS

**Figs 1-4.** Morphology and vegetative anatomy of *P. acervatum* (UWC 10/129).

**Fig. 1.** View of several abutting individual thalli. Note the pitted nature of the thallus. Scale bar = 5 mm.

**Fig. 2.** Magnified view of the thallus showing sunken conceptacles giving the thallus its pitted appearance. Scale bar = 2 mm.

**Fig. 3.** Vertical section of the dorsal region of the thallus showing subepithallial initials (i), the first cortical cells (c) and a single layer of epithallial cells (arrows). Scale bar = 20 µm.

**Fig. 4.** Vertical section of the ventral region of the thallus showing medullary filaments (m) running more or less parallel to the substrate and giving rise to upward curving cortical filaments (c). Note the cell fusions (arrows) between cells of adjoining filaments. Scale bar = 15 µm.

**Figs 5-10.** Spermatangial (male) anatomy of *P. acervatum*.

**Fig. 5.** SEM of the thallus surface showing conceptacles with raised roofs (arrowheads) sunken in depressions (UWC 10/129). Scale bar = 500 µm.

**Fig. 6.** Vertical section through a conceptacle showing spermatangial systems distributed across the floor (f), walls (w) and roof (r) of the conceptacle chamber. The pore opening is occluded by a mucilage plug (arrow) (UWC 10/129). Scale bar = 50 µm.

**Fig. 7.** Vertical section through a conceptacle primordium showing adventitious development from a group of vegetative cells (arrowheads) within the thallus (UWC 10/129). Scale bar = 150 µm.

**Fig. 8.** Vertical section through an immature conceptacle. Note the remains of the protective layer of epithallial and cortical cells (arrow) (UWC 10/129). Scale bar = 70 µm.

**Fig. 9.** Magnified view of the centre of the conceptacle chamber floor showing branched (arrowheads) spermatangial systems interspersed amongst unbranched spermatangial systems. The pore canal (p) is lined by cells that project into the canal as papillae (UWC 10/129). Scale bar = 25 µm.

**Fig. 10.** Magnified view of the roof of the conceptacle chamber showing a cluster of branched spermatangial systems (arrowheads) (UWC 08/26). Scale bar = 20 µm.

**Figs 11-14.** Female anatomy of *P. acervatum.*

**Fig. 11.** Vertical section through a carpogonial conceptacle showing carpogonial branches (cb) distributed across the conceptacle chamber floor. The pore opening is occluded by a mucilage plug (arrow) (UWC 10/129). Scale bar = 50 µm.

**Fig. 12.** Vertical section through a carposporangial conceptacle showing peripherally arranged gonimoblast filaments terminating in carpospores (C). The central region of the conceptacle chamber floor bears unfertilised carpogonial branches (arrowhead) (UWC 08/14). Scale bar = 50 µm.

**Fig. 13.** Vertical section through the pore of a carposporangial conceptacle showing pore canal cells (arrowheads) projecting into the pore canal (p) as papillae (UWC 08/14). Scale bar = 20 µm.

**Fig. 14.** Magnified view of the floor of a carposporangial conceptacle showing a discontinuous fusion cell (arrowheads) bearing a peripherally arranged gonimoblast filament (1-4) terminating in a carpospore (C). The central region of the conceptacle chamber floor bears unfertilised carpogonial branches (arrow) (UWC 08/26). Scale bar = 20 µm.

**Figs 15-21.** Tetrasporangial anatomy of *P. acervatum* (UWC 10/129).

**Fig. 15.** SEM of the thallus surface showing conceptacles (arrowheads) sunken in depressions. Scale bar = 200 µm.

**Fig. 16.** Fracture of the thallus under SEM showing a conceptacle sunken in a depression. Scale bar = 100 µm.

**Fig. 17.** Vertical section through a sunken conceptacle primordium showing adventitious development from a group of tetrasporangial initials (arrowheads) deep within the thallus. Note the protective layer of epithallial and cortical cells (E). Scale bar = 50 µm.

**Fig. 18.** SEM of a conceptacle pore plate showing multiple pores (p) surrounded by rosette cells (*). Scale bar = 10 µm.

**Fig. 19.** Fracture through a conceptacle pore plate under SEM showing multiple pore canals (p) and the cells lining a pore canal (arrowheads). Scale bar = 10 µm.

**Fig. 20.** Vertical section through a sunken conceptacle showing tetrasporangia (t) distributed across the chamber floor. Scale bar = 50 µm.

**Fig. 21.** Magnified view of the outer surface of a conceptacle showing tetrasporangia (t) bearing apical pore plugs (p) in the pore plate. The cells lining the pore canal (arrowheads) become more elongate as they progress towards the conceptacle chamber. Scale = 20 µm.

**Figs 22-23.** Vegetative anatomy of *P. ferox* (UWC 10/125).

**Fig. 22.** Vertical section of the ventral region of the thallus showing medullary filaments running more or less parallel to the substrate. Note the cell fusions (f) between cells of adjoining filaments. Scale bar = 20 µm.

**Fig. 23.** Vertical section of the dorsal region of the thallus showing subepithallial initials (i), the first cortical cell (c) and a single layer of epithallial cells (arrows). Scale bar = 15 µm.

**Figs 24-27.** Spermatangial (male) anatomy of *P. ferox* (UWC 09/111).

**Fig. 24.** Vertical section through a conceptacle showing spermatangial systems distributed across the floor (f), walls (w) and roof (r) of the conceptacle chamber. The pore opening is occluded by a mucilage plug (arrowhead). Scale bar = 50 µm.

**Fig. 25.** Vertical section through the pore of a conceptacle showing pore canal cells (arrowheads) projecting into the pore canal (p) as papillae. The pore opening is occluded by a mucilage plug (arrow). Scale bar = 20 µm.

**Fig. 26.** Magnified view of the roof (r), wall (w) and floor (f) of a conceptacle chamber showing branched spermatangial systems (arrowheads) interspersed amongst unbranched spermatangial systems. Spermatia (arrows) are clustered at the distal ends of the spermatangial branches. Scale bar = 20 µm.

**Fig. 27.** Magnified view of the floor (f) of a conceptacle chamber showing weakly branched (arrowheads) spermatangial systems interspersed amongst unbranched spermatangial systems. Spermatia (arrows) are clustered at the distal ends of the spermatangial systems. Scale bar = 20 µm.

**Figs 28-33.** Female anatomy of *P. ferox* (UWC 09/111).

**Fig. 28.** Vertical section through a carpogonial conceptacle showing a mass of carpogonial branches (cb). The pore opening is occluded by a mucilage plug (arrowhead). Scale bar = 60 µm.

**Fig. 29.** Vertical section through a very young carpogonial conceptacle showing development from a group of initials (arrowheads). Note the protective layer of epithallial and cortical cells (E). Scale bar = 50 µm.

**Fig. 30.** Vertical section through an immature carpogonial conceptacle showing roof development from the periphery (arrowheads). Scale bar = 50 µm.

**Fig. 31.** Vertical section through a carposporangial conceptacle showing peripherally arranged gonimoblast filaments terminating in carpospores (C). The central region of the conceptacle chamber floor bears unfertilised carpogonial branches (arrow). The pore opening is occluded by a mucilage plug (arrowhead). Scale bar = 100 µm.

**Fig. 32.** Vertical section through the pore of a carposporangial conceptacle showing pore canal cells (arrowheads) projecting into the pore canal (p) as papillae. The pore opening is occluded by a mucilage plug (arrow). Scale bar = 30 µm.

**Fig. 33.** Magnified view of the floor of a carposporangial conceptacle showing a discontinuous fusion cell (arrowheads) bearing a peripherally arranged gonimoblast filament (1-4) terminating in a carpospore (C). The central region of the conceptacle chamber floor bears unfertilised carpogonial branches (g). Scale bar = 20 µm.

**Figs 34-38.** Tetrasporangial anatomy of *P. ferox*.

**Fig. 34.** SEM of the thallus surface showing raised conceptacles (UWC 09/109). Scale bar = 100 µm.

**Fig. 35.** Vertical section through a conceptacle showing mature (T) and incompletely divided (t) tetrasporangia distributed across the chamber floor. Note the raised conceptacle roof (arrow) (UWC 10/125). Scale bar = 90 µm.

**Fig. 36.** Vertical section through a young conceptacle showing adventitious development from a group of tetrasporangial initials (between arrowheads) deep within the thallus. Note the protective layer of epithallial and cortical cells (E) (UWC 09/109). Scale bar = 50 µm.

**Fig. 37.** SEM of a conceptacle pore plate showing multiple pores (p) surrounded by rosette cells (*) (UWC 09/109). Scale bar = 10 µm.

**Fig. 38.** Magnified view of the outer surface of a conceptacle showing tetrasporangia (t) bearing apical pore plugs (p) in the pore plate. The cells lining the pore canal (black

arrowheads) are not different to those from the rest of the pore plate. Note the remains of the interspersed filaments (white arrowheads) that gave rise to the conceptacle roof (UWC 10/125). Scale = 20 µm.

**Figs 39-41.** Morphology and vegetative anatomy of *P. foveatum* (UWC 10/123).

**Fig. 39.** Magnified view of the thallus surface showing secondary margins (white scrolls) scattered across the thallus surface giving it an imbricate appearance. Scale bar = 1.5 mm

**Fig. 40.** Vertical section of the ventral region of the thallus showing a plumose (non-coaxial) medulla with filaments running more or less parallel to the substrate and curving upwards to form cortical filaments. Note the cell fusions (f) between cells of adjoining filaments. Scale bar = 20 µm.

**Fig. 41.** Vertical section of the dorsal region of the thallus showing subepithallial initials (i), the first cortical cell (c) and a single layer of slightly dark-staining epithallial cells (arrows). Note the cell fusions (f) between cells of adjoining filaments and the solitary trichocytes (T). Scale bar = 20 µm.

**Figs 42-47.** Spermatangial (male) anatomy of *P. foveatum* (UWC 10/123).

**Fig. 42.** Vertical section through a conceptacle showing spermatangial systems distributed across the floor (f), walls (w) and roof (r) of the conceptacle chamber. The pore opening is occluded by a mucilage plug (arrowhead). Scale bar = 50 µm.

**Fig. 43.** Vertical section through a young conceptacle showing adventitious development from a group of initials (between arrowheads) deep within the thallus. Note the thick layer of protective epithallial and cortical cells (E). Scale bar = 50 µm.

**Fig. 44.** Vertical section through an immature conceptacle showing roof development (r) from the periphery and a protective layer of epithallial and cortical cells (E). Scale bar = 50 µm.

**Fig. 45.** Magnified view of the periphery of a conceptacle chamber showing branched spermatangial systems (arrowheads) interspersed amongst unbranched spermatangial systems on the conceptacle floor (f), and only unbranched spermatangial systems on the conceptacle wall (w). Scale bar = 20 µm.

**Fig. 46.** Magnified view of the centre of a conceptacle chamber floor (f) bearing different-looking spermatangial structures (arrow) that are surrounded by more conventional-looking unbranched spermatangial structures (arrowheads). Scale bar = 20 µm.

**Fig. 47.** Magnified view of the roof (r) of a conceptacle chamber showing unbranched spermatangial systems. Scale bar = 20 µm.

**Figs 48-53.** Tetrasporangial anatomy of *P. foveatum* (UWC 09/114).

**Fig. 48.** SEM of the thallus surface showing multiporate conceptacles (K) sunken in depressions. Some conceptacles (k) have been partly or entirely shed. Scale bar = 150 µm.

**Fig. 49.** Vertical section through a young developing conceptacle showing adventitious development from a group of tetrasporangial initials (between arrowheads) deep within the thallus. Note the protective layer of epithallial and cortical cells (E). Scale bar = 50 µm.

**Fig. 50.** SEM of a conceptacle pore plate showing multiple pores (p) surrounded by rosette cells (*). Scale bar = 10 µm.

**Fig. 51.** Vertical section through a conceptacle showing tetrasporangia (t) distributed across the chamber floor. Note the multiporate roof (arrow) bearing densely staining pore plugs. Scale bar = 50 µm.

**Fig. 52.** Magnified view of the conceptacle pore plate showing apical pore plugs (p). The cells lining the pore canal (black arrowheads) are not different to those from the rest of the pore plate. Note the remains of the interspersed filaments (white arrowheads) that gave rise to the conceptacle roof. Scale = 10 µm.

**Fig. 53.** Fracture through a conceptacle pore plate under SEM showing multiple pore canals (p). The cells lining the pore canal (black arrowheads) are not different to those from the rest of the pore plate. Note the remains of an interspersed filament (white arrowhead) that gave rise to that portion of the conceptacle roof. Scale = 10 µm.

**Figs 54-56.** Morphology and vegetative anatomy of *P. repandum*.

**Fig. 54.** Vertical section of the ventral region of the thallus showing a plumose (non-coaxial) medulla. Note the cell fusions (f) between cells of adjoining filaments (UWC 93/171). Scale bar = 20 µm.

**Fig. 551.** Vertical section of the thallus showing a coaxial medulla. Note the cell fusions (f) between cells of adjoining filaments (UWC 93/201). Scale bar = 100 µm.

**Fig. 56.** Vertical section of the dorsal region of the thallus showing subepithallial initials (i), the first cortical cell (c) and a single layer of slightly dark-staining epithallial cells (arrows). Note the cell fusions (f) between cells of adjoining filaments (UWC 93/171). Scale bar = 20 µm.

**Figs 57-63.** Spermatangial (male) anatomy of *P. repandum*.

**Fig. 57.** Vertical section through a conceptacle showing spermatangial systems distributed across the floor (f), walls (w) and roof (r) of the conceptacle chamber. The pore opening is occluded by a mucilage plug (arrowhead) (UWC 94/16). Scale bar = 50 µm.

**Fig. 58.** SEM of the thallus surface showing young developing conceptacles (depressions), some of which still bear the protective layer of epithallial and cortical cells (E) (UWC 93/201). Scale bar = 200 µm.

**Fig. 59.** Vertical section through a young developing conceptacle showing adventitious development from a group of initials (between arrowheads) within the thallus. Note the layer of protective epithallial and cortical cells (E) (UWC 93/52). Scale bar = 75 µm.

**Fig. 60.** Vertical section through an immature conceptacle showing the roof development from the periphery (arrowheads). Note the remains of the protective layer of epithallial and cortical cells (arrow) (UWC 94/16). Scale bar = 150 µm.

**Fig. 61.** Magnified view of the conceptacle chamber roof (r) showing branched spermatangial systems (arrowheads) (UWC 94/16). Scale bar = 20 µm.

**Fig. 62.** Magnified view of the conceptacle chamber floor showing branched spermatangial systems (arrowheads) interspersed amongst unbranched spermatangial systems (UWC 94/16). Scale bar = 20 µm.

**Fig. 63.** Vertical section of the thallus showing infilled crescent-shaped scars (UWC 94/16). Scale bar = 200 µm.

**Figs 64-69.** Female anatomy of *P. repandum*.

**Fig. 64.** Vertical section through a carpogonial conceptacle showing carpogonial branches (arrowheads) across the conceptacle chamber floor. The pore opening is occluded by a mucilage plug (arrow) (UWC 93/200). Scale bar = 50 µm.

**Fig. 65.** Vertical section through a conceptacle primordium showing adventitious development from a group of vegetative cells (arrowheads) within the thallus (UWC 93/171). Scale bar = 75 µm.

**Fig. 66.** Vertical section through an immature carpogonial conceptacle showing roof development from the periphery (arrowheads). Note the remains of the protective layer of epithallial and cortical cells (arrow) (UWC 94/16). Scale bar = 50 µm.

**Fig. 67.** Vertical section through a carposporangial conceptacle showing peripherally arranged gonimoblast filaments (g). The central region of the conceptacle chamber floor bears unfertilised carpogonial branches (arrowhead). The pore opening is occluded by a mucilage plug (arrow) (UWC 93/200). Scale bar = 100 µm.

**Fig. 68.** Vertical section through a carposporangial conceptacle showing short gonimoblast filaments (g) distributed across the chamber floor. The pore opening is occluded by a mucilage plug (arrow) (UWC 94/16). Scale bar = 50 µm.

**Fig. 69.** Magnified view of a carposporangial conceptacle floor showing a discontinuous fusion cell (arrowheads) bearing a peripherally arranged gonimoblast filament (1-4) terminating in a carpospore (C) (UWC 93/200). Scale bar = 20 µm.

**Figs 70-74.** Tetrasporangial anatomy of *P. repandum*.

**Fig. 70.** SEM of the thallus surface showing raised multiporate conceptacles (K) (UWC 93/201). Scale bar = 200 µm.

**Fig. 71.** Vertical section through a young developing conceptacle showing adventitious development from a group of tetrasporangial initials (between arrowheads) within the thallus. Note the protective layer of epithallial and cortical cells (E) (UWC 93/52). Scale bar = 50 µm.

**Fig. 72.** SEM of a conceptacle pore plate showing multiple pores (p) surrounded by rosette cells (*)(UWC 93/201). Scale bar = 5 µm.

**Fig. 73.** Vertical section through a conceptacle showing tetrasporangia (t) distributed across the chamber floor. Note the multiporate roof (arrow) bearing densely staining pore plugs and an infilled crescent-shaped scar (S) (UWC 93/171). Scale bar = 100 µm.

**Fig. 74.** Magnified view of the conceptacle pore plate showing apical pore plugs (p). The cells lining the pore canal (black arrowheads) are not different to those from the rest of the pore plate. Note the remains of the interspersed filaments (white arrowheads) that gave rise to the conceptacle roof (UWC 93/171). Scale = 10 µm.

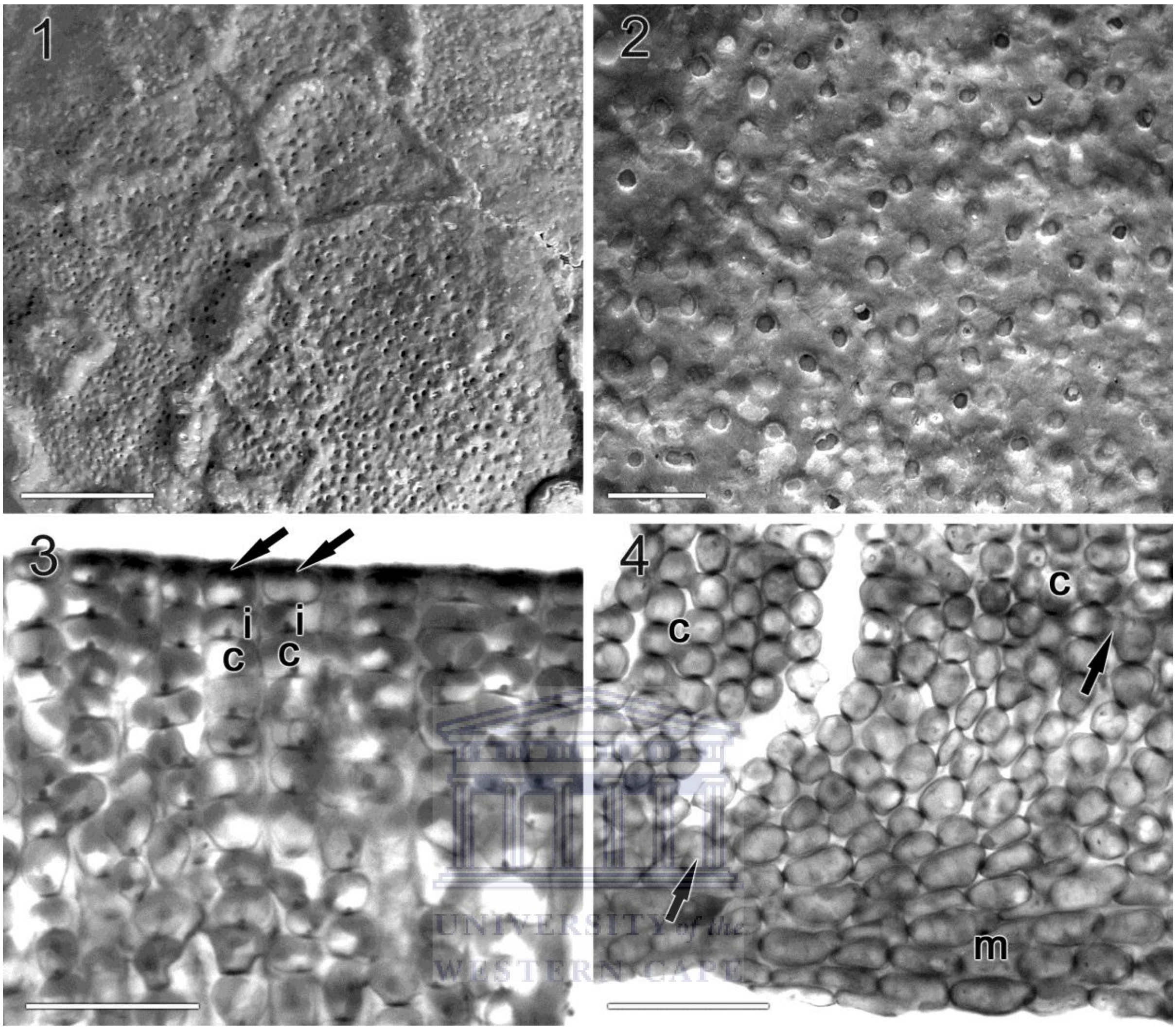
**Figs 75-78.** Habit photographs of the four species of *Phymatolithon*.

**Fig. 75.** Several individuals of *P. acervatum* encrusting a tide pool boulder.

**Fig. 76.** *Phymatolithon ferox* produces numerous marginal upgrowths that form back to back, mouth-like structures where they meet. The species is often found co-existing with *Spongites yendoi* (Sy) in the mid-intertidal zone.

**Fig. 77.** *Phymatolithon foveatum* produces numerous secondary margins (black arrowheads) across its surface giving the coralline an imbricate appearance. These secondary margins run more or less parallel to the primary margin (white arrowheads). The species is often found co-existing with *Spongites yendoi* (Sy) in the lower intertidal zone.

**Fig. 78.** Several individuals of *P. repandum* encrusting a subtidal boulder (UWC 93/52).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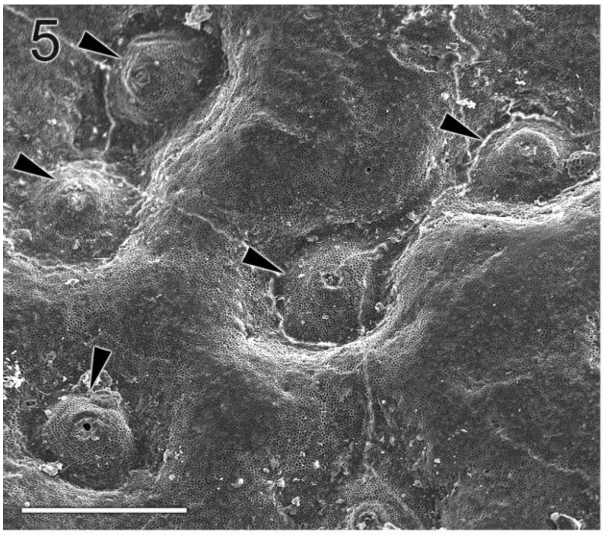
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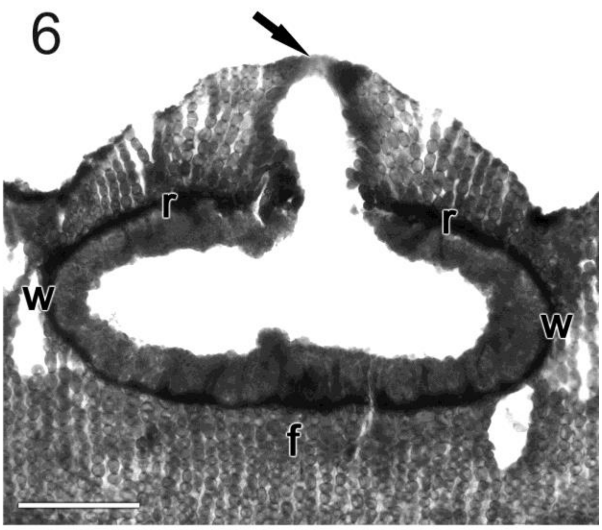
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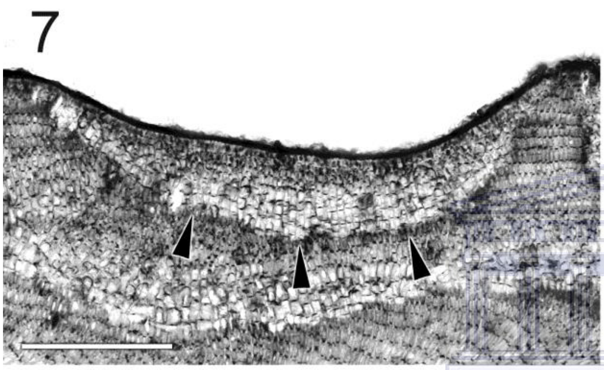
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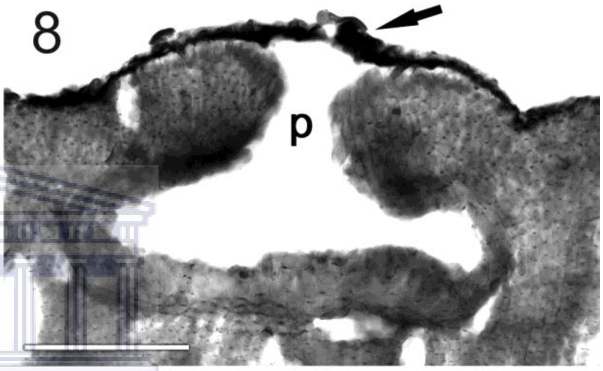
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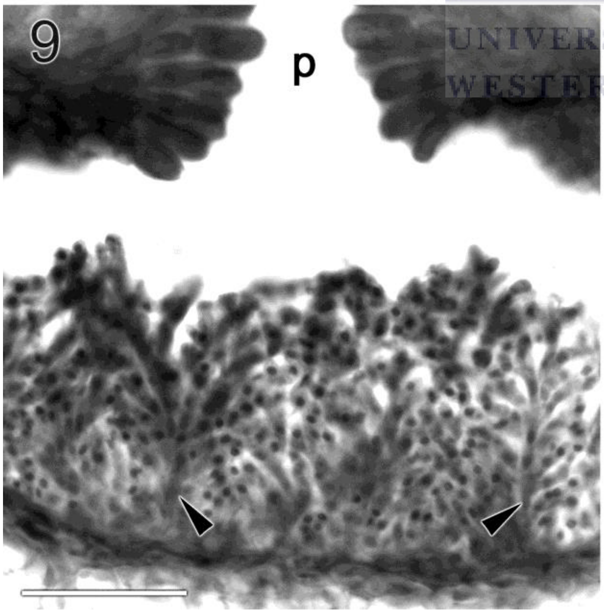
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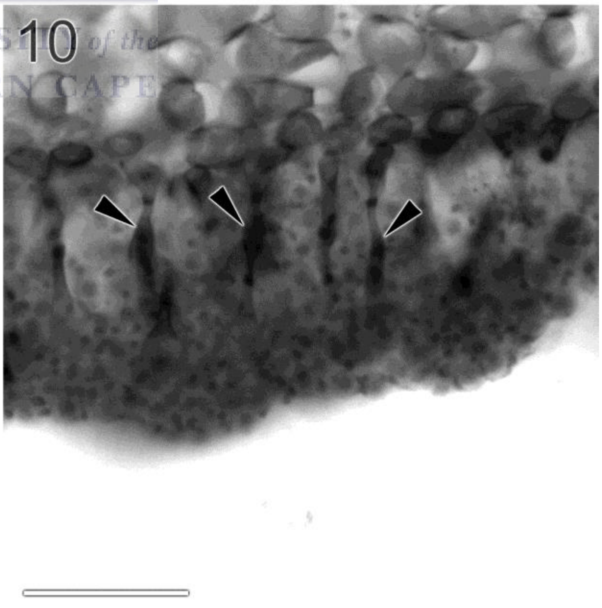
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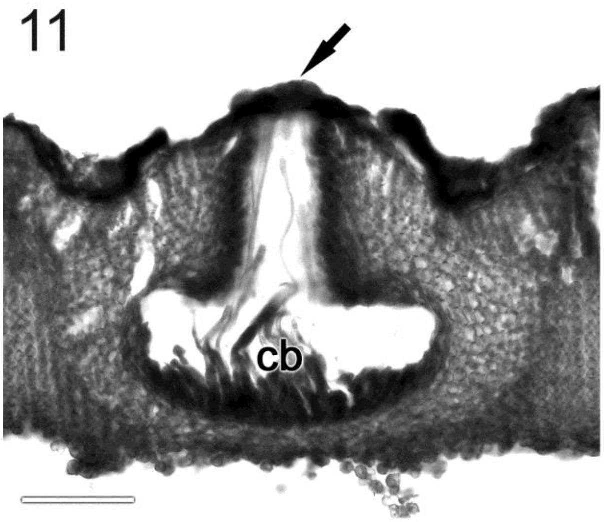
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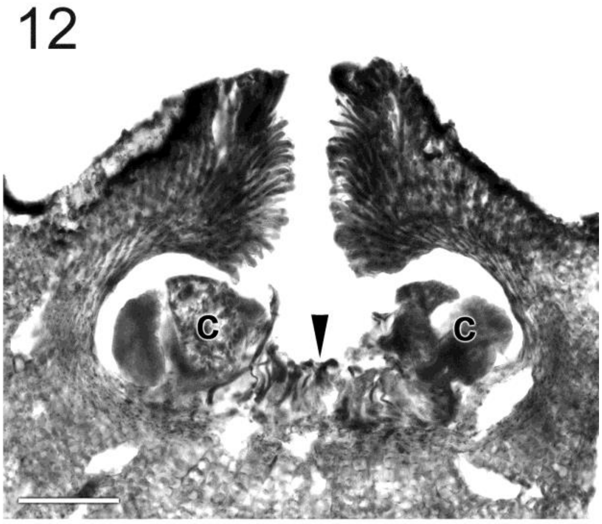
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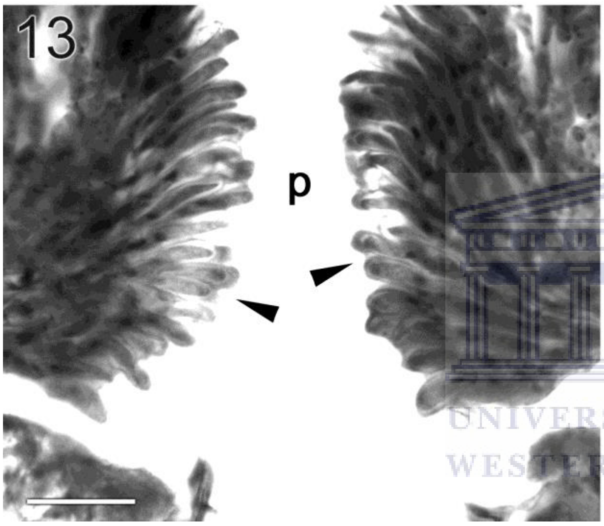
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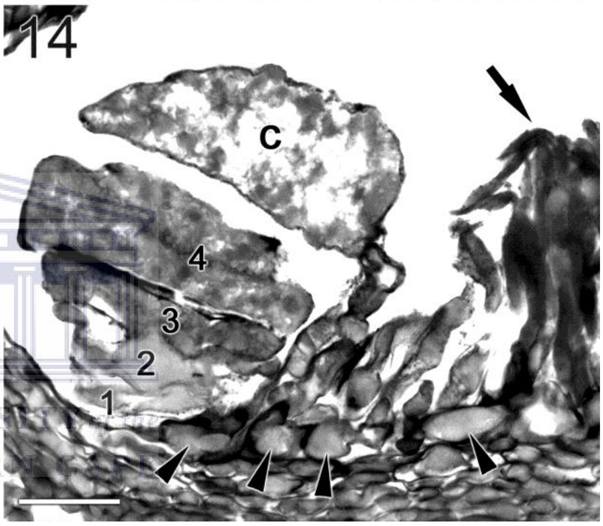
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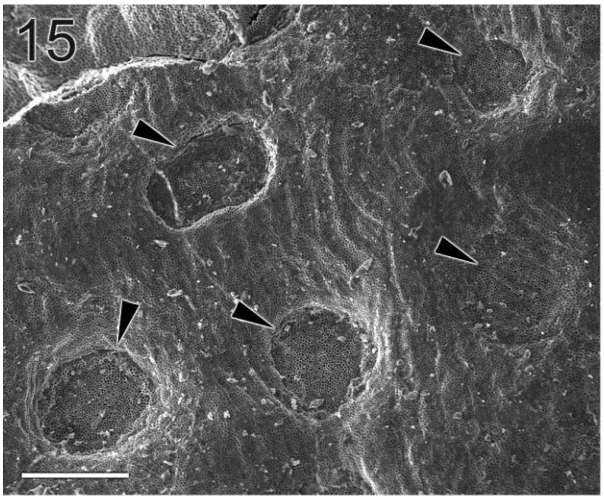
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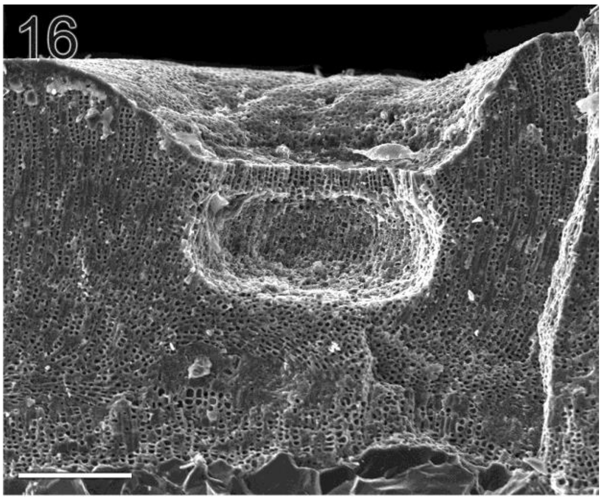
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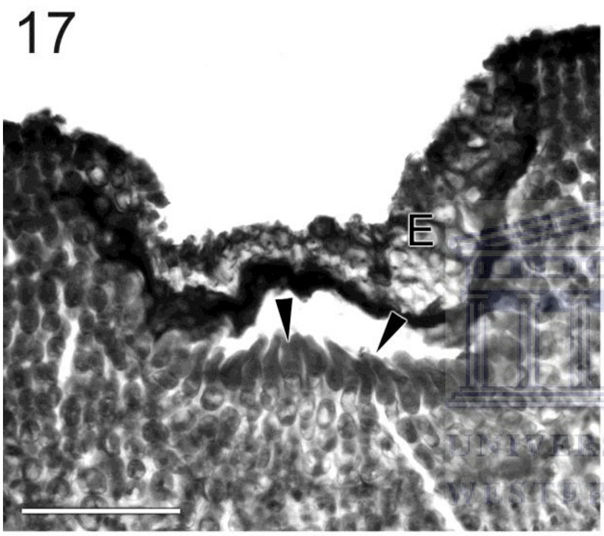
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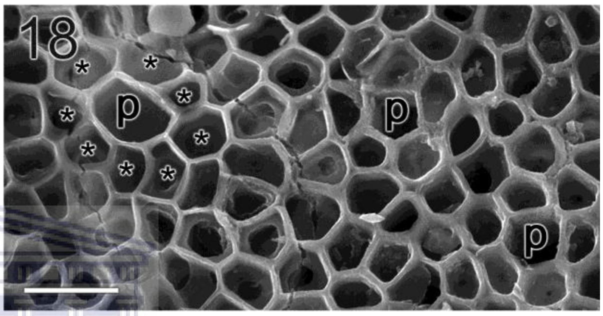
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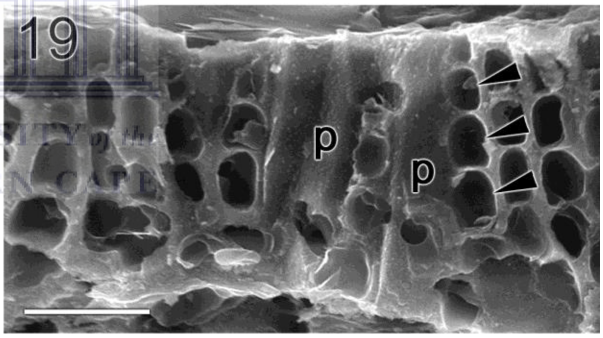
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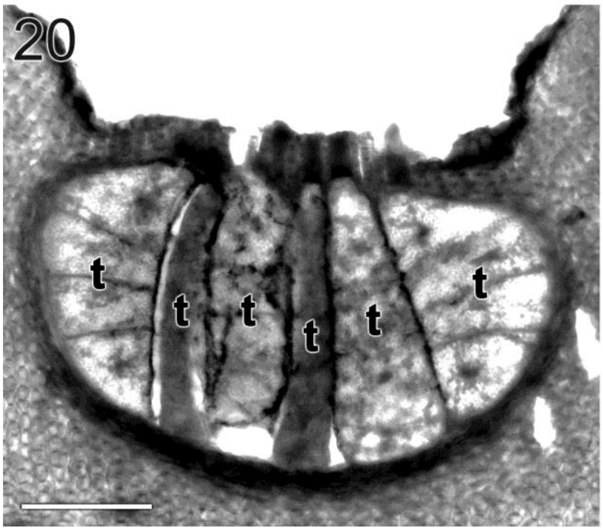
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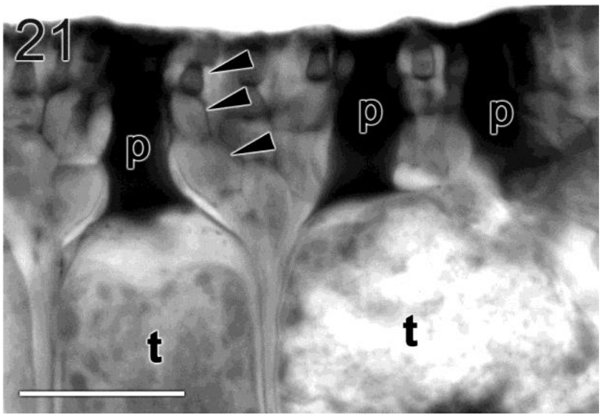
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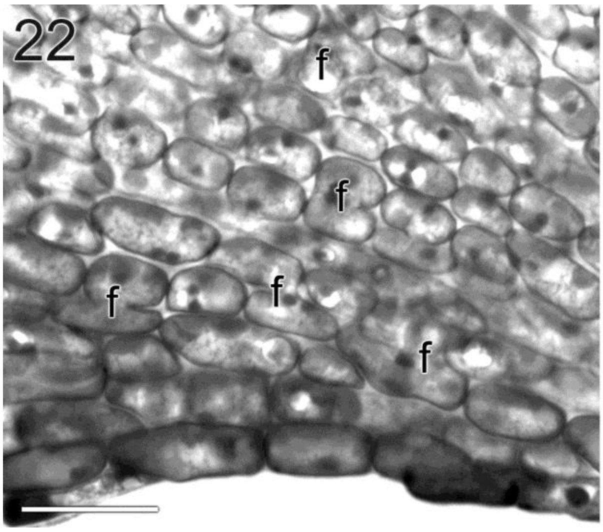
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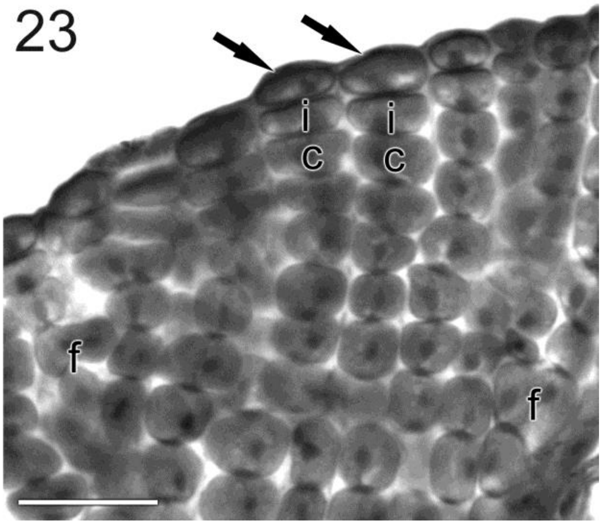
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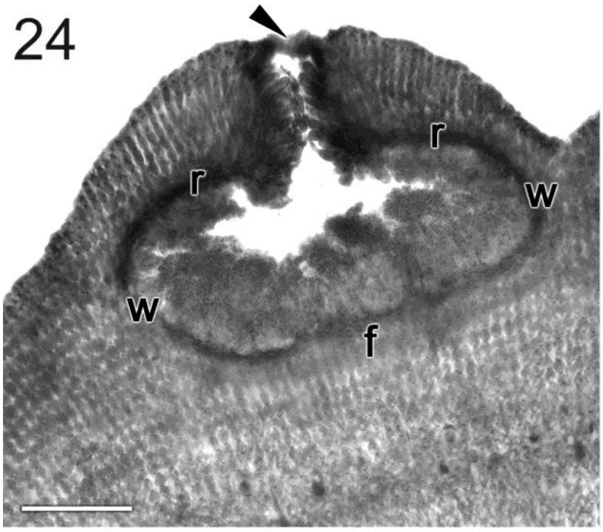
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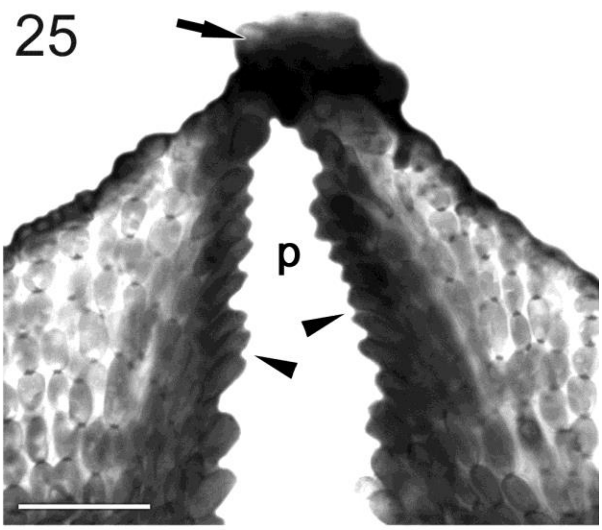
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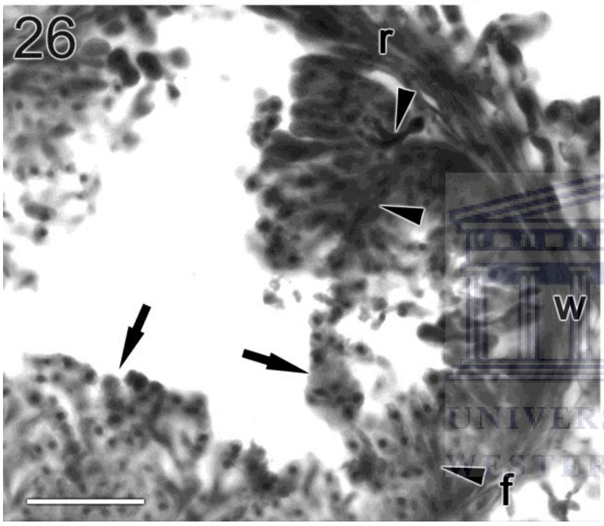
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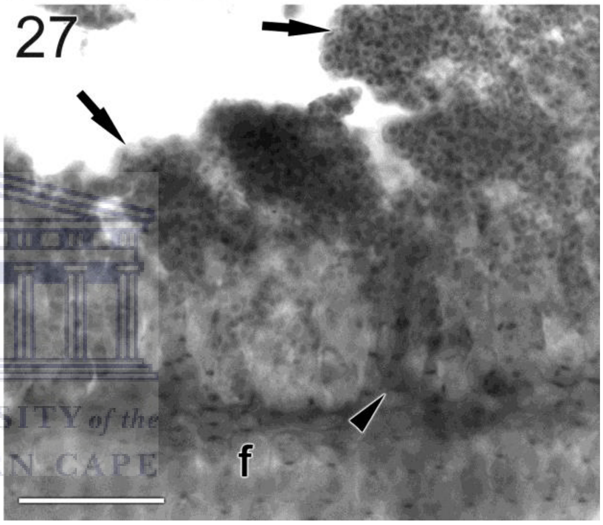
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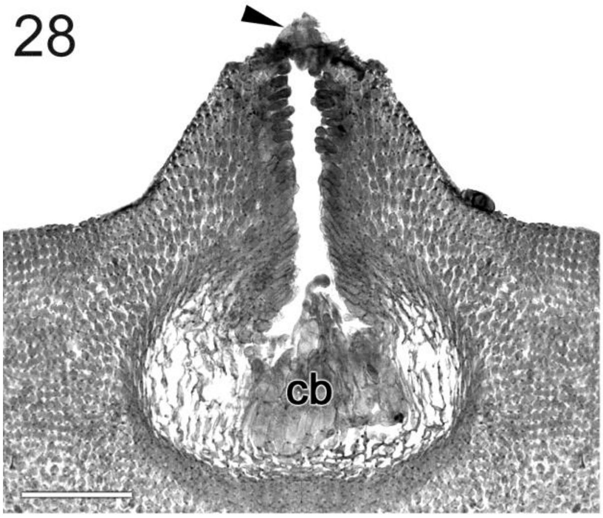
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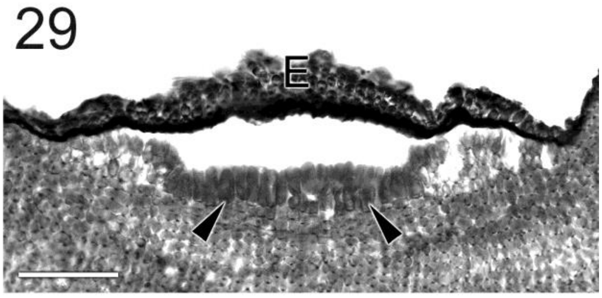
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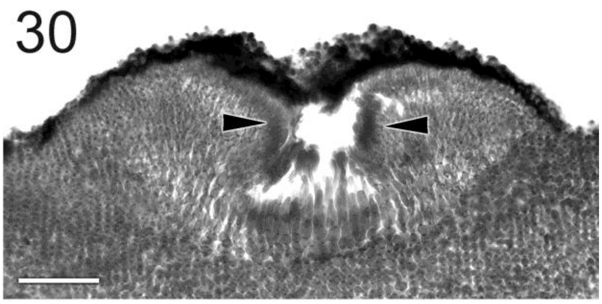
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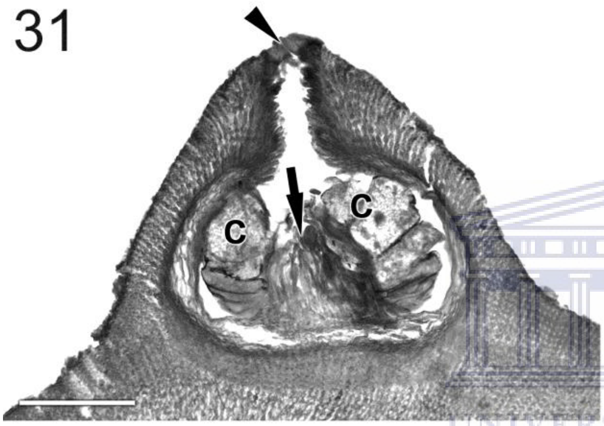
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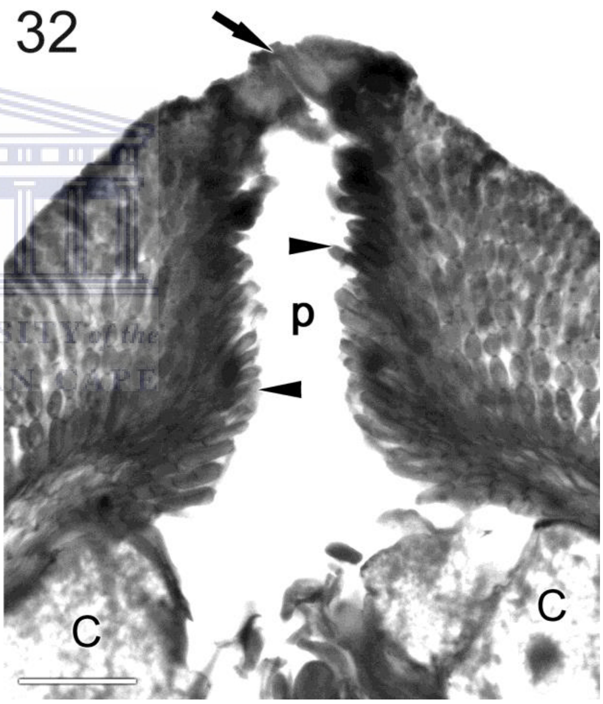
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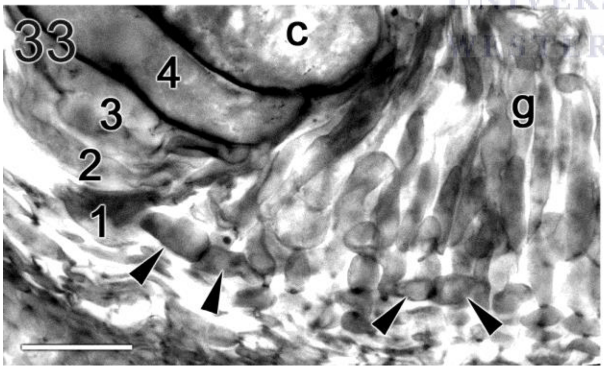
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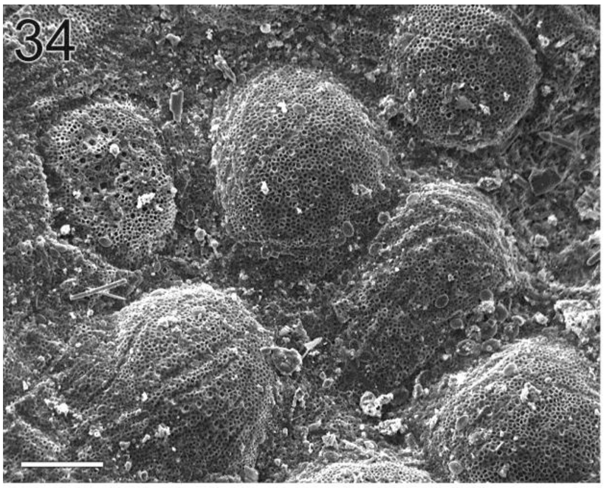
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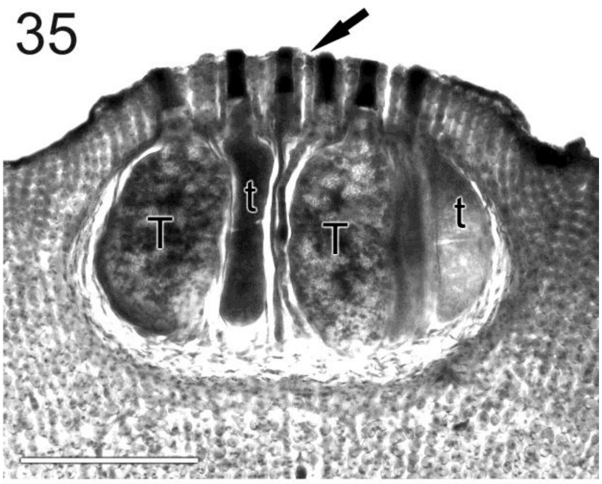
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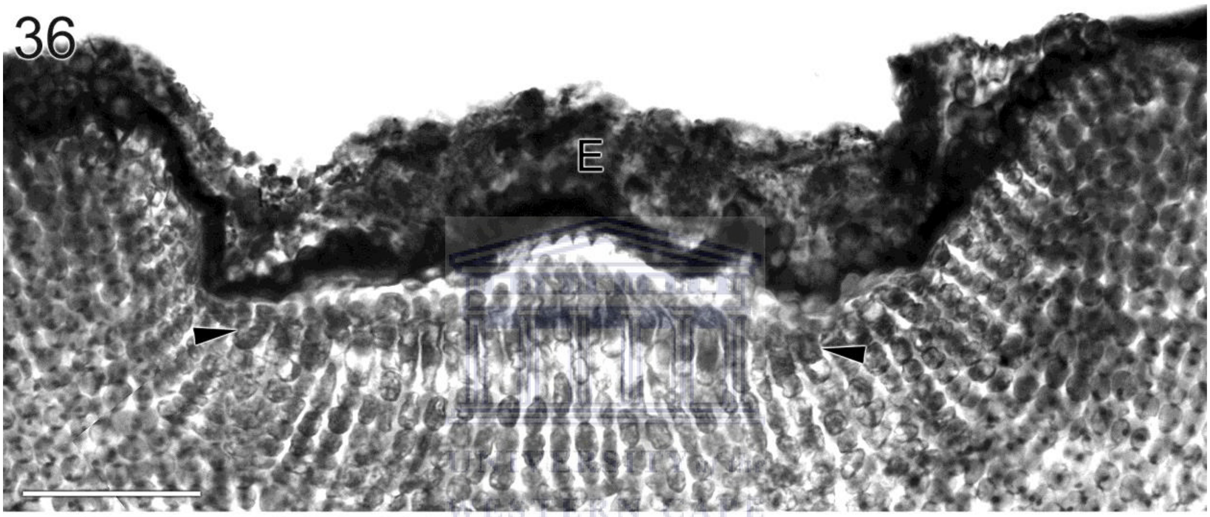
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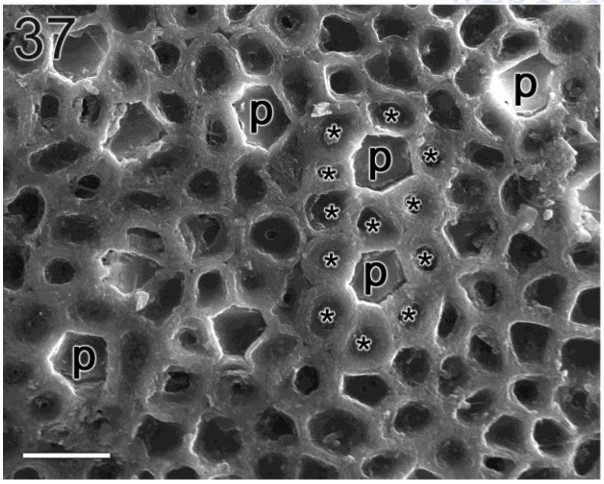
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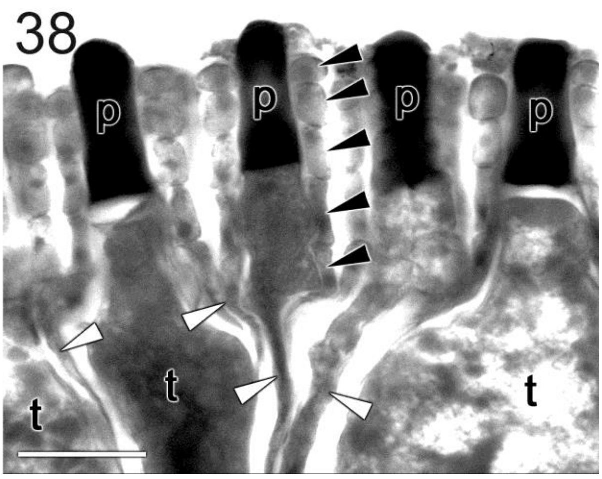
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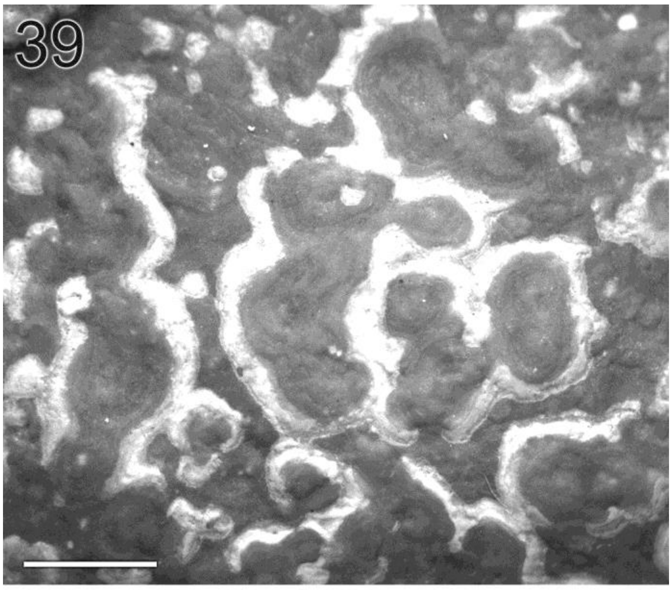
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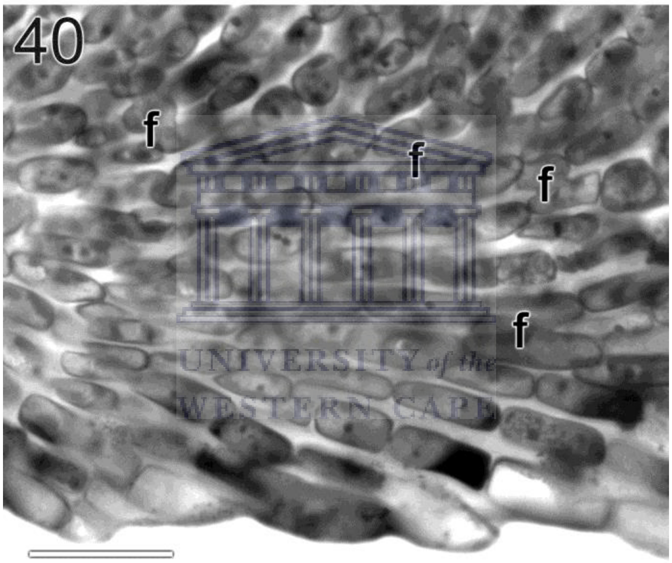
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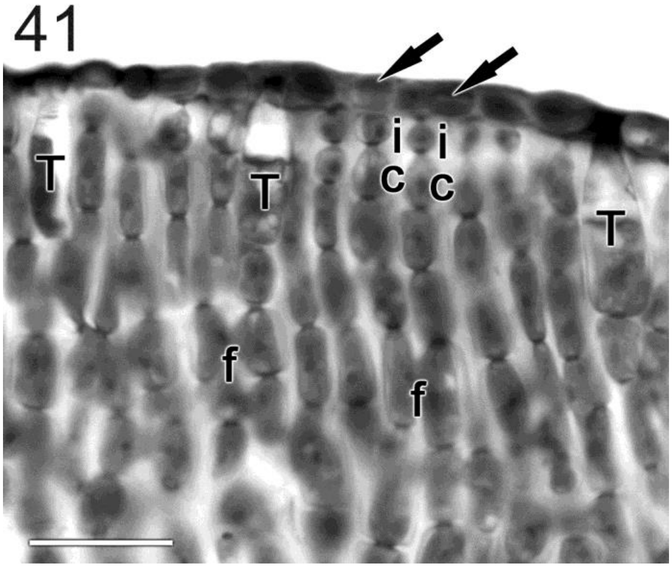
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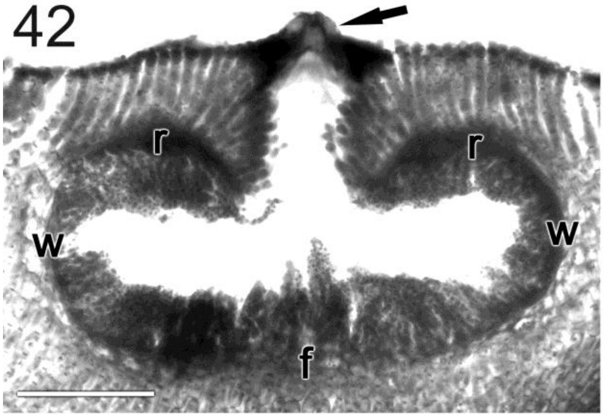
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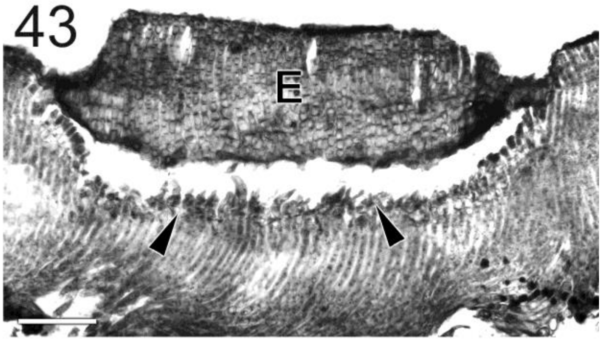
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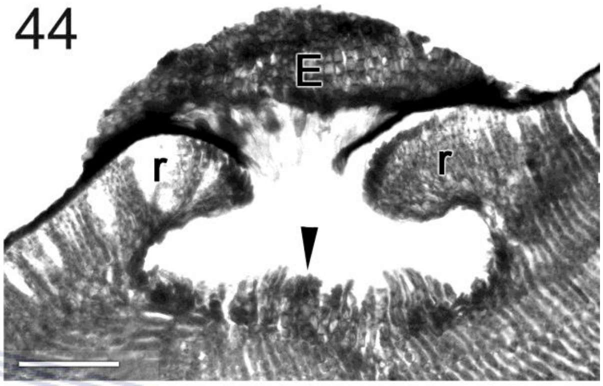
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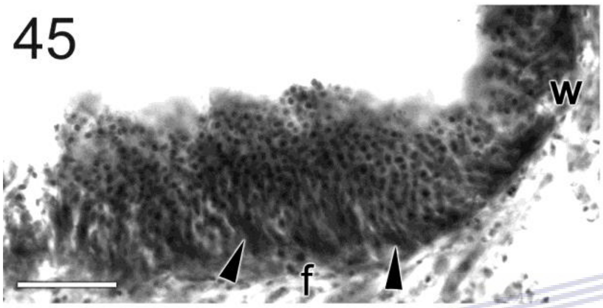
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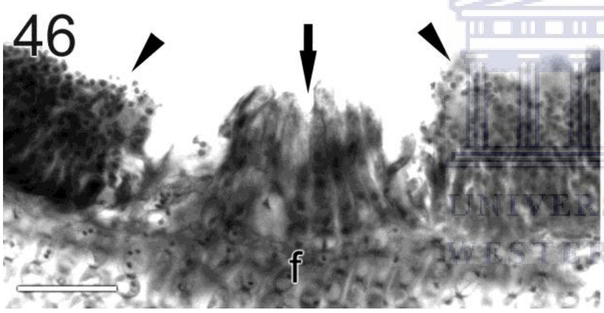
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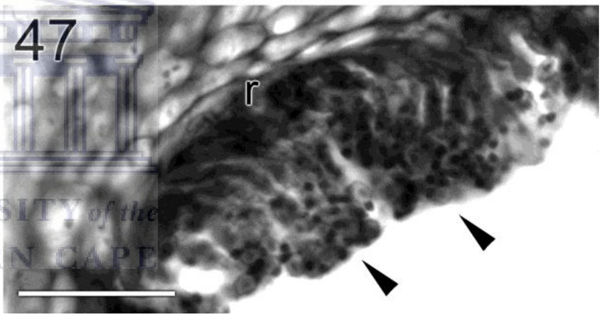
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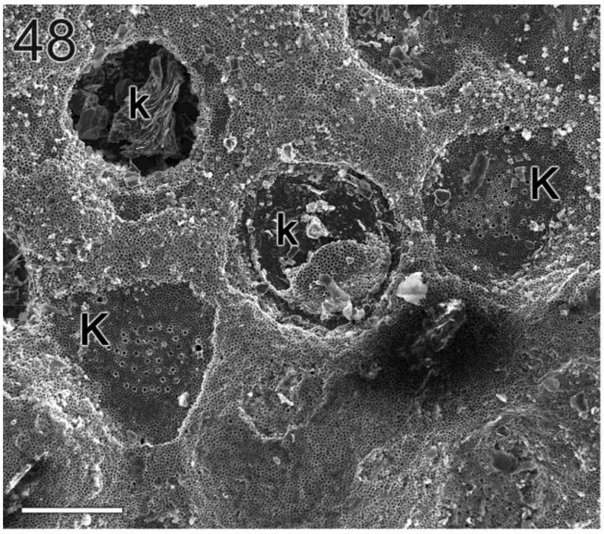
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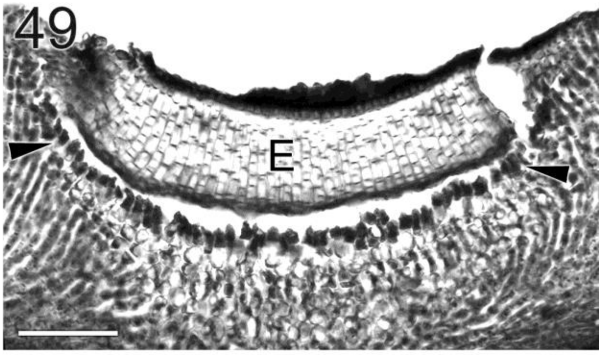
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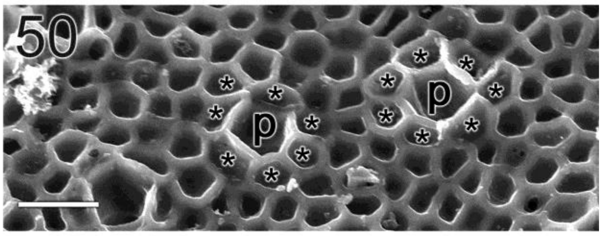
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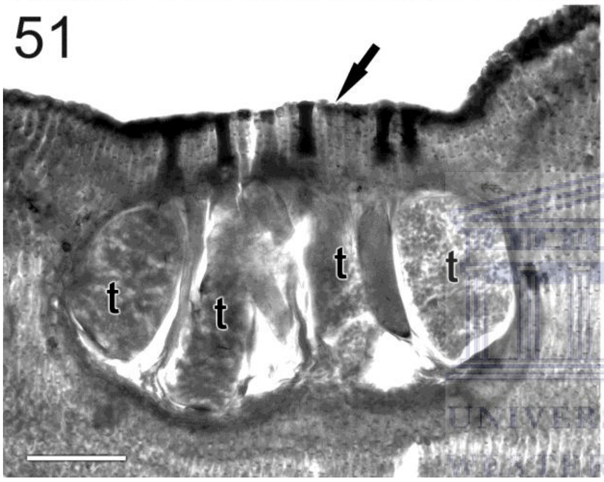
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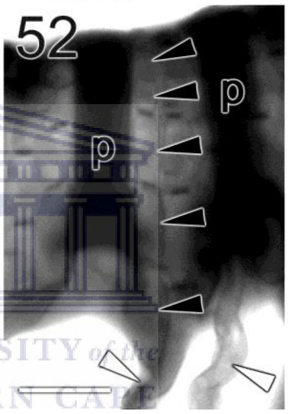
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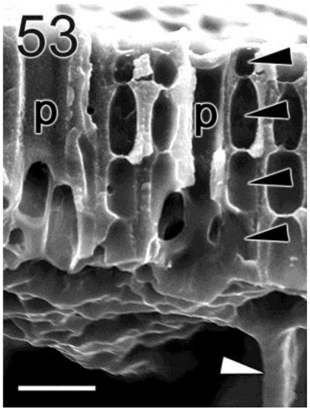
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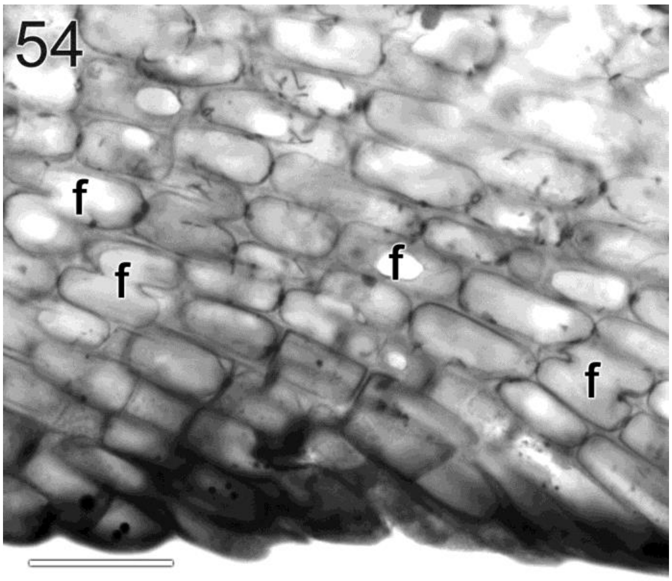
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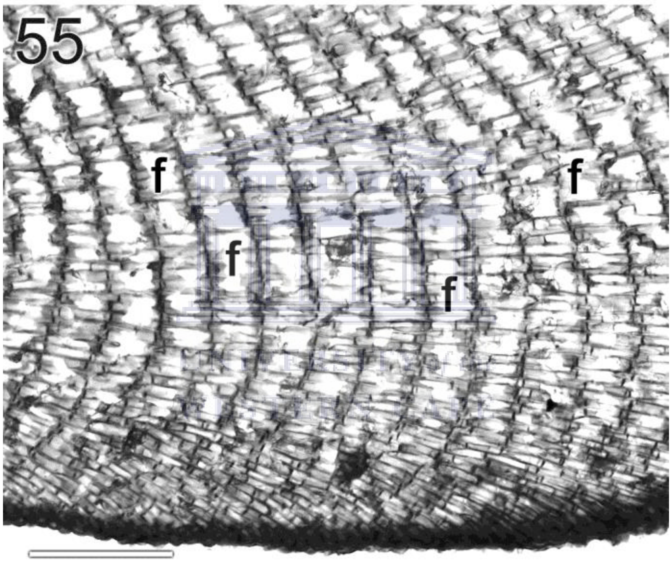
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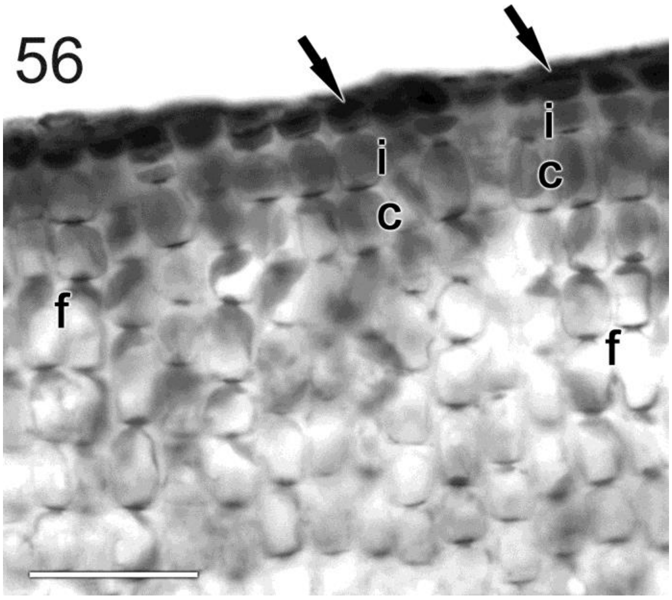
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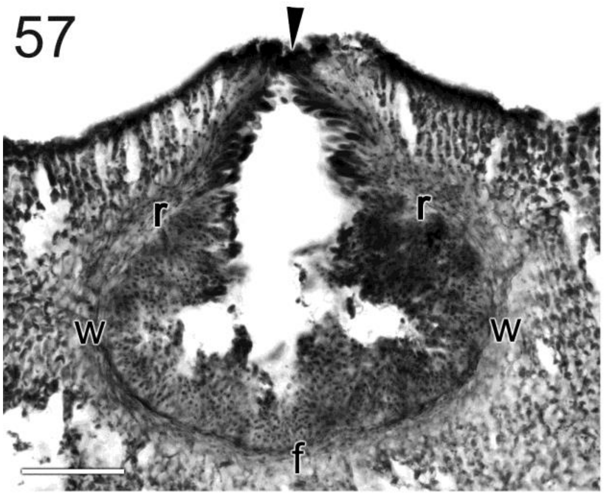
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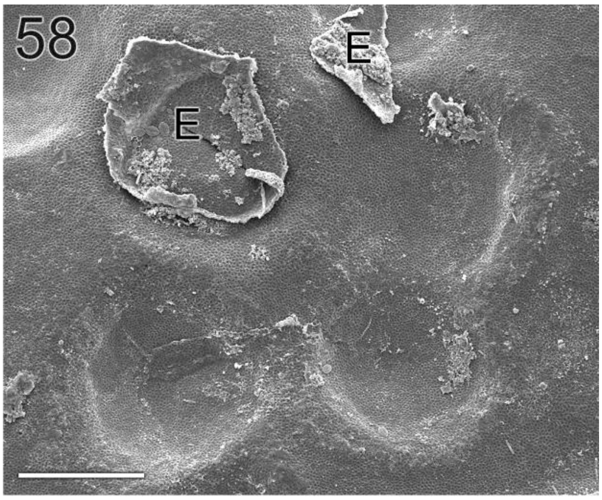
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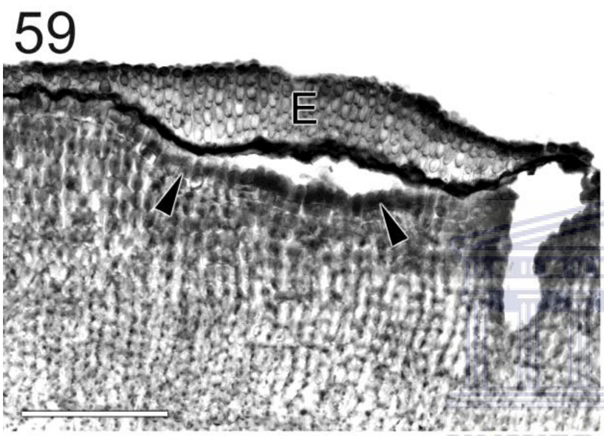
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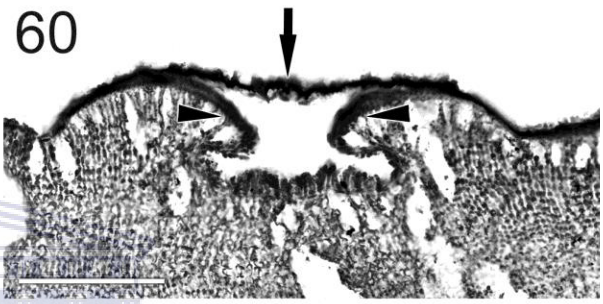
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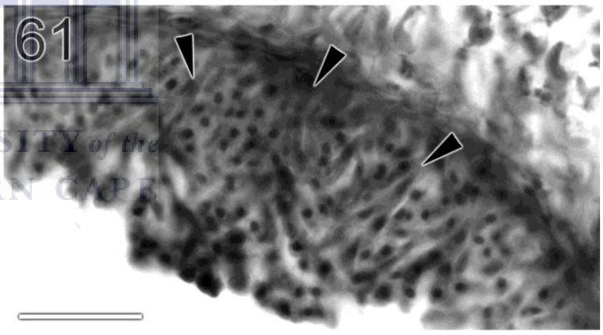
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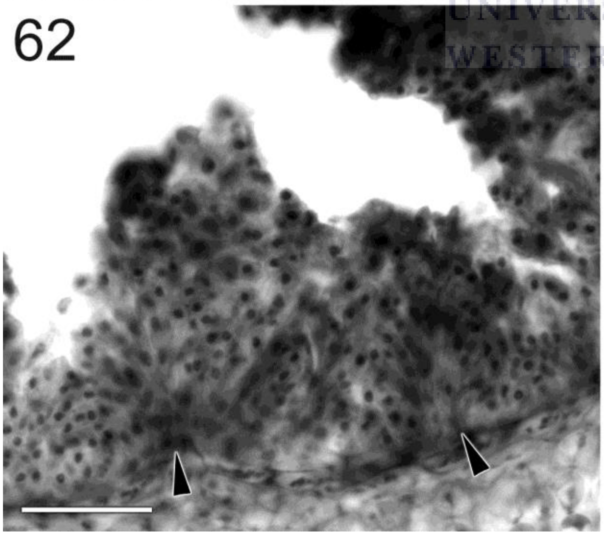
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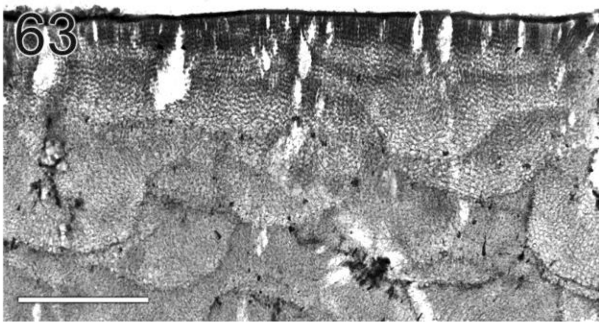
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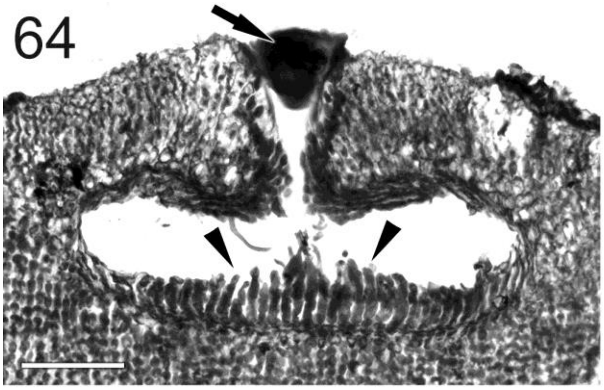

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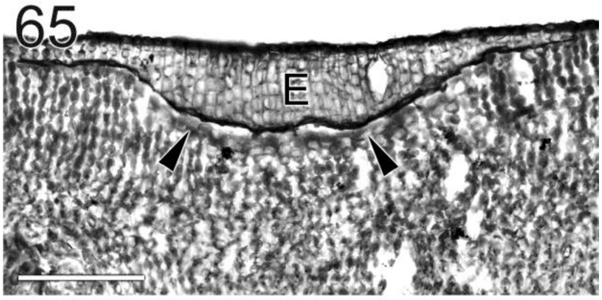

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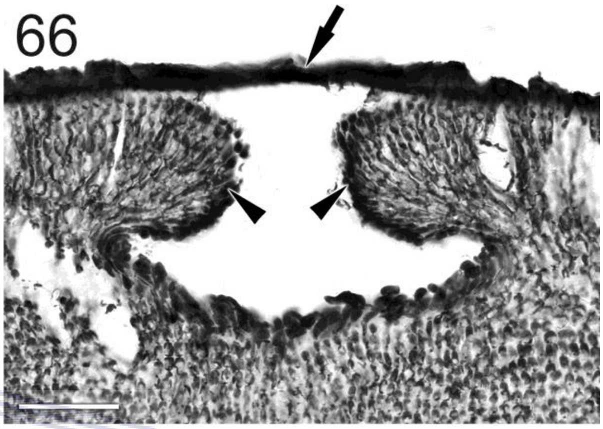

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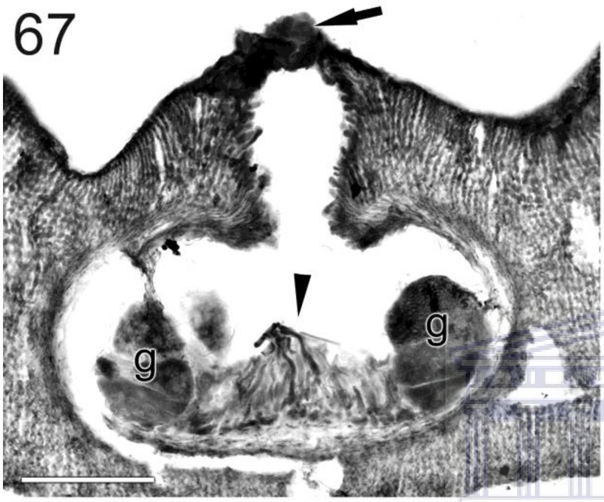

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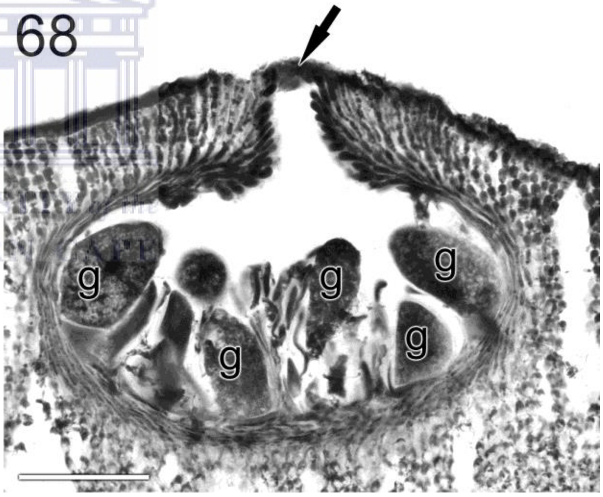

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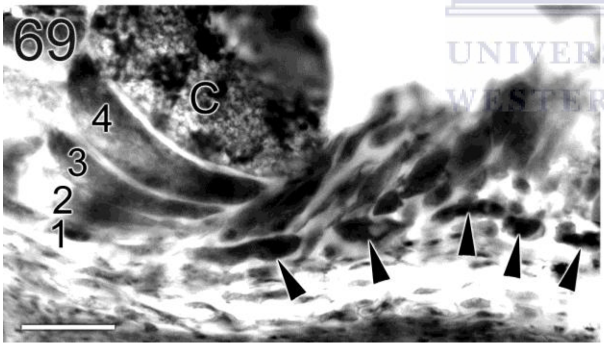

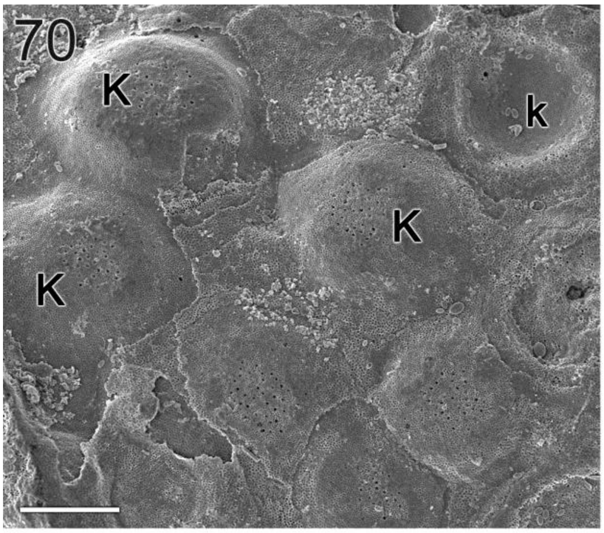
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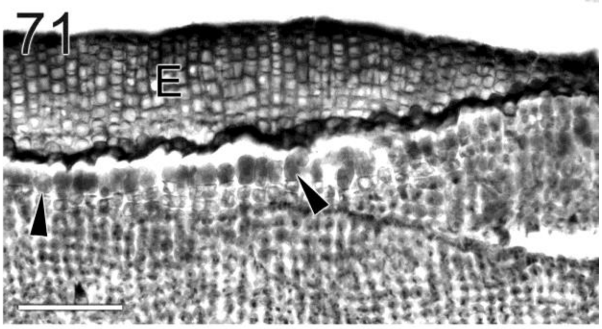
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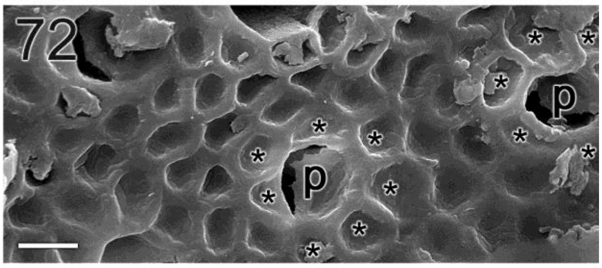
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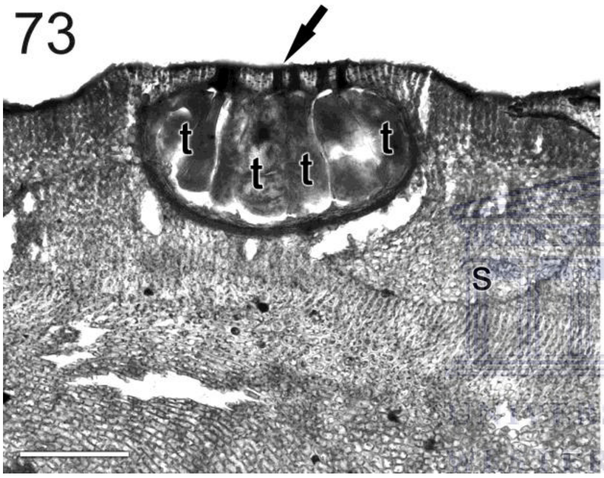
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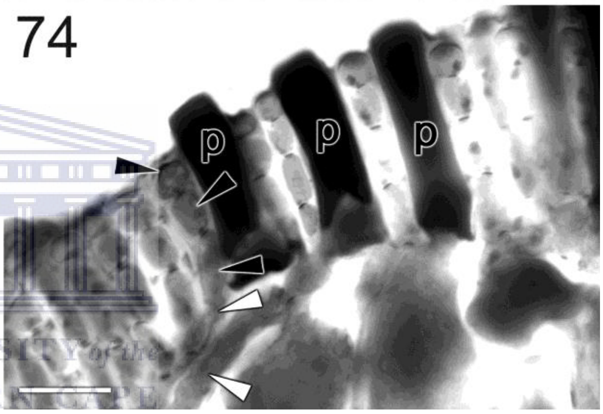
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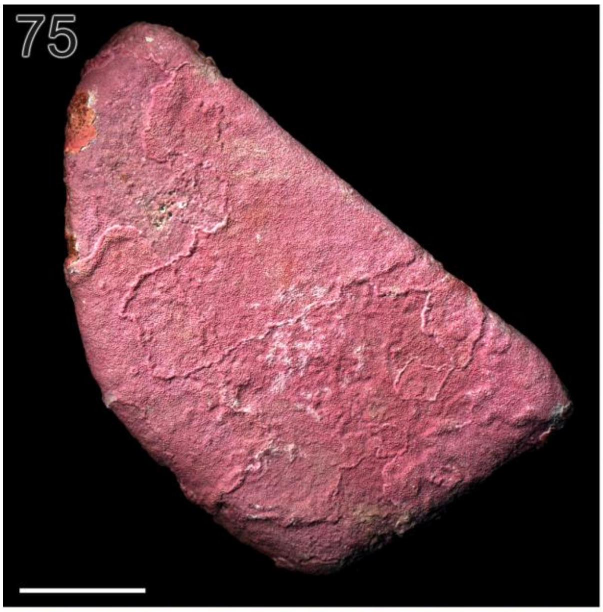
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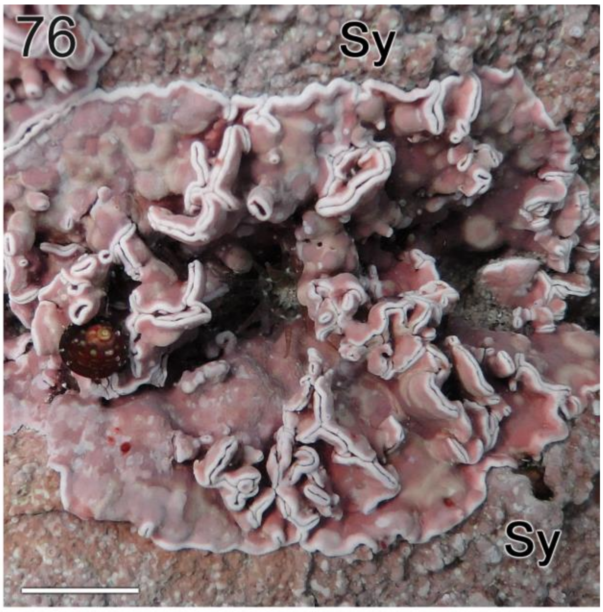
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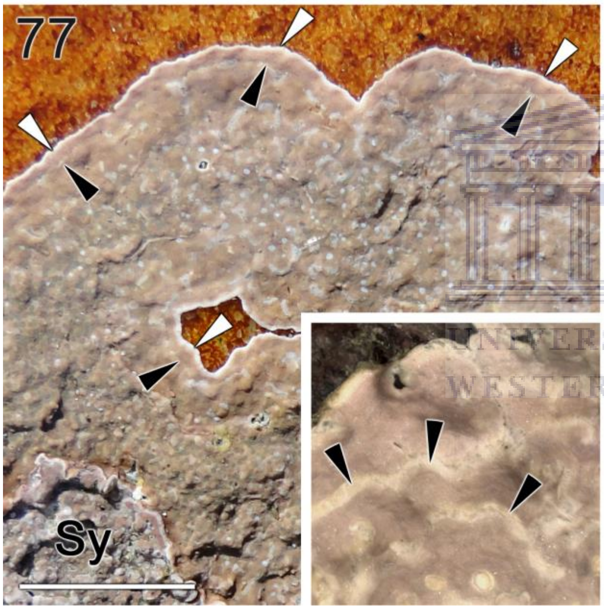
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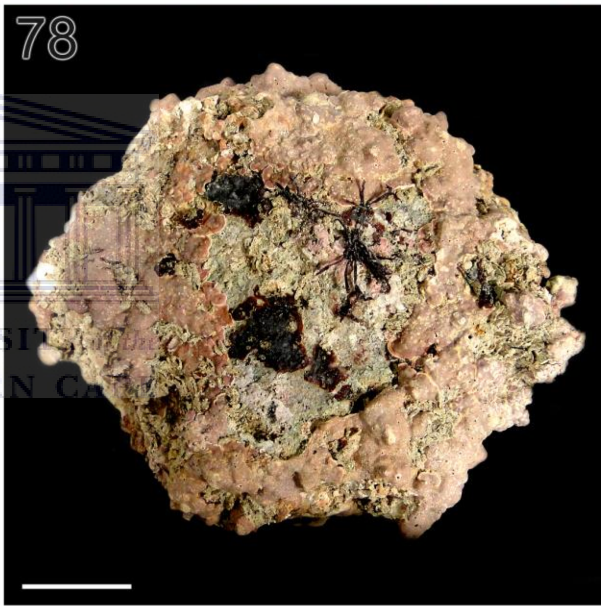
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# Chapter 4: Paper 3

## DNA sequencing resolves species of *Spongites* (Corallinales, Rhodophyta) in the Northeast Pacific and South Africa, including *S. agulhensis* sp. nov.

This chapter is currently in press:

Van der Merwe E., Miklasz K., Channing A., Maneveldt G.W. & Gabrielson P.W. 2015. DNA sequencing resolves species of *Spongites* (Corallinales, Rhodophyta) in the Northeast Pacific and South Africa, including *S. agulhensis* sp. nov. *Phycologia* 54(5), in press.

# DNA sequencing resolves species of *Spongites* (Corallinales, Rhodophyta) in the Northeast Pacific and South Africa, including *S. agulhensis* sp. nov.

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Running title: *Spongites* species NE Pacific and South Africa

KEY WORDS: *psb*A, *rbc*L, *Spongites decipiens*, *Spongites tumidum*, *Spongites yendoi*, sequencing type material

## ABSTRACT

DNA sequence data from a 296 base pair variable region of the plastid encoded *rbc*L gene was obtained from19th Century type material of *Spongites decipiens* and of *Lithophyllum tumidum* (=*Pseudolithophyllum neofarlowii*) and matched to field-collected material, confirming the application of these specific epithets in the NE Pacific. Phylogenetic analyses of separate and concatenated *rbc*L and *psb*A gene sequences show that both species belong in *Spongites*. Based on DNA sequences, the distribution of *S. decipiens* is confirmed from Haida Gwaii, British Columbia, Canada south to its type locality at San Pedro, Los Angeles Co., California (CA), USA, whereas *S. tumidum* is distributed from near Sitka, Alaska to Monterey Co., CA, USA. Sequence data from *S. decipiens* and South African specimens called *S. yendoi* confirm anatomical studies that these two species are distinct, but that a previously undescribed, cryptic species, *S. agulhensis*, also is present in South Africa. Anatomically and morphologically *S. agulhensis* is very similar to both Northeast Pacific *S. decipiens* and South African *S. yendoi*, differing from the former by a single anatomical character and from the latter by two anatomical characters. Anatomy, ecology and distributions are useful in separating the South African species of *Spongites*, as well as the NE Pacific species. Sequence divergence values align with biogeographic patterns and not with anatomical similarities for these *Spongites* species. We question the practice of placing into synonymy geographically widely separated non-geniculate coralline algal species based solely on anatomical features that likely have resulted from convergent evolution.

## INTRODUCTION

Molecular sequencing of coralline algae is revolutionizing our understanding of this important and ubiquitous group of benthic marine rhodophytes at all taxonomic ranks. Significant findings already have resulted in revisions at higher taxonomic ranks with the family Sporolithaceae elevated to ordinal rank (as Sporolithales, Le Gall *et al*. 2009) and, in the family Corallinaceae, support for a previously proposed subfamily (Lithophylloideae, Bailey & Chapman 1998) and recognition of several new subfamilies (Hydrolithoideae, Neogoniolithoideae and Porolithoideae, Kato *et al*. 2011). At the genus and species ranks progress has been slower, owing to the difficulty of obtaining generitypes with wide geographic distributions needed to molecularly confirm morphologically and anatomically defined genera, and of linking specific epithets, based on type specimens, with more recently collected field specimens (Adey *et al*. 2015).

In the Northeast Pacific, we have begun defining genera molecularly as well as anatomically/morphologically by sequencing generitypes and related species (Gabrielson *et al*. 2011; Martone *et al*. 2012) and confirming the application of specific epithets by comparing DNA sequences of type and recently collected specimens (Hind *et al*. 2014a, b). Species of *Spongites* Kützing present an ideal test of this latter methodology, as historically morpho-anatomically similar specimens from different localities worldwide, were identified as belonging to the same species. Thus, for example, *Spongites decipiens* (Foslie) Y.M. Chamberlain (type locality San Pedro, Los Angeles Co., CA, USA) was reported from southern South America (as *Lithophyllum decipiens* (Foslie) Foslie - Foslie 1900c); as *Hydrolithon decipiens* (Foslie) W.H. Adey - Mendoza & Cabioch 1986, Juan Fernandez Island (as *L. decipiens* - Levring 1943), Japan (as *L. decipiens* - Masaki 1968), India (as *L. decipiens* - Krishnamurthy & Jayagopal 1985), eastern Russia (Perestenko 1996), the Gulf of

California (as *L. decipiens* - Dawson 1944) and south of the type locality along the Pacific coast of both Mexico and Panama (as *L. decipiens* - Dawson 1960).

Similarly, *Spongites yendoi* (Foslie) Y.M. Chamberlain (type locality: Shimoda Harbor, Shizuoka Prefecture, Japan) was first reported from Japan and Monterey, CA, USA (as *Goniolithon yendoi* Foslie -1900a) and later from Indonesia (as *Lithophyllum yendoi* (Foslie) Foslie - Foslie 1900c), South Africa (Chamberlain 1993), Pacific Mexico (Chamberlain 1993), southern Australia (Penrose 1996), Korea (Lee & Kang 2001), New Zealand (Harvey *et al*. 2005) and Atlantic Mexico (Mendoza-Gonzalez 2007). Moreover, throughout their histories *S. decipiens* and *S. yendoi* were thought to possibly be conspecific (Foslie 1901a, 1904, 1906, 1907; Dawson 1960; Masaki 1968) until Chamberlain (1993), comparing type specimens, showed that *S. decipiens* has a dimerous thallus construction, whereas *S. yendoi* is monomerous. Herein we present DNA sequence data confirming that *S. decipiens* is a distinct species, that some specimens from South Africa morphologically similar to *S. yendoi* and morphologically and anatomically similar to NE Pacific *S. decipiens* are a new species, and that NE Pacific *Lithophyllum tumidum* Foslie (=*Pseudolithophyllum neofarlowii* (Setchell & L.R. Mason) W.H. Adey) also belongs in *Spongites*. Furthermore, sequence divergence values for species morphologically and anatomically distinct, but whose distribution ranges overlap are genetically more similar than morphologically and anatomically similar species from different parts of the world. The implications of these results are discussed for *Spongites* species reported to be widely geographically distributed and disjunct either within an ocean basin or across ocean basins based only on morpho-anatomical characters.

## MATERIAL AND METHODS

### Specimens

Freshly collected specimens were removed from the bedrock with a geology hammer and cold chisel; for specimens on pebbles, cobble or gastropod shells the substratum along with the coralline was removed. These specimens were air dried and/or placed in silica gel and/or were initially fixed in neutralised 10% commercial formalin seawater (4% formaldehyde) and stored in a 70% ethanol : 10% glycerol : 20% distilled water solution. Specimens were examined from the following herbaria: TRH, UC and UWC; voucher specimens were deposited in either L, NCU, UNB or UWC; herbarium acronyms follow Thiers (2015, continuously updated).

### Microscopy

Specimens for microscopy were prepared following Maneveldt & van der Merwe (2012). For scanning electron microscopy (SEM), air-dried material was fractured using forceps, diagonal cutters, or a small hammer and cold chisel. Fractured pieces were mounted on stubs, using adhesive tabs (Agar Scientific Ltd., M11 Business Link, Parsonage Lane, Stansted, Essex CM24 8GF, UK), stored in a desiccator for at least 24 h prior to examination, coated with carbon in a single cycle for 3 seconds in an Emitech K950X Carbon Evaporator (Quorum Technologies Ltd., Ashford, Kent, UK), and examined with a Hitachi X650 scanning electron microscope (Hitachi Ltd, Chiyoda, Tokyo, Japan) at an accelerating voltage of 25 kV.

For light microscopy, formalin preserved specimens were first decalcified in 10% nitric acid. Thereafter, specimens were immersed in 70%, 90% and 100% ethanol solutions respectively for a minimum of 60 min each in order to displace any water and acid in the specimens. Thereafter, each specimen was removed from the 100% ethanol solution and allowed to air dry for no more than a few seconds. Specimens were then immersed in Leica Historesin filtration medium (Leica Microsystems Ltd., Nussloch, Heidelberger, Germany) for several hours until completely infiltrated. A hardening solution was added to the infiltration medium and the specimens orientated in this final solution until set. Gelling of the hardener usually occurred within 30-45 min; for more rapid hardening, specimens were placed immediately in an oven at 60 °C for approximately 10-20 min.

Specimens were sectioned at 6 - 8 µm thickness using a Bright 5030 microtome. Sequential sections were removed from the microtome blade using a fine sable hair brush and transferred to a slide covered with distilled water. In this way, multiple sections were orientated on a single slide. Slides were then left to air dry for at least 24 h so that sections could stick. These slides were stained with toluidine blue (0.25 g borax 100 ml$^{-1}$ and 0.06 g toluidine blue 100 ml$^{-1}$), again left to air dry, and later covered with cover slips using DPX Mountant for microscopy (BDH Laboratory Supplies, The Birches, Willard Way, Imberhorne Industrial Estate, East Grinstead, West Sussex RH19 1XZ, UK).

In cell measurements, length is the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. Conceptacle measurements follow Adey & Adey (1973), thallus anatomical terminology follows Chamberlain (1990), and morphological (growth forms) terminology follows Woelkerling *et al*. (1993).

## Molecular analysis

Specimens that were sequenced are listed in Table S1. Specimen preparation, extraction amplification and sequencing for *rbc*L followed Gabrielson *et al.* (2011); for *psb*A followed

Adey et al. (2015). The forward *rbc*L primer used for amplifying DNA from type specimens is given in Sissini *et al*. (2014).

*rbc*L and *psb*A sequences of two species said to belong to *Spongites*, *S. decipiens* from the NE Pacific and *S. yendoi* from South Africa, were analysed along with sequences of South African specimens initially identified as *S. yendoi* as well as specimens of *Lithophyllum tumidum* (=*Pseudolithophyllum neofarlowii*) from the NE Pacific. Species of three genera belonging to subfamily Lithophylloideae were used as the outgroup (Fig. 1, Table S1) based on the sister taxon relationship of this subfamily to *Spongites* (Kato *et al*. 2011). The *rbc*L sequences for the phylogenetic analyses were 1387 bp long; *psb*A sequences were 851 bp long. The two loci were combined into a single concatenated dataset with two data partitions (*rbc*L and *psbA*). Maximum Likelihood (ML) analyses were performed using the default parameters of RaxML BlackBox (Stamatakis *et al*. 2008) with a mixed partition model until 1,000 bootstrap replications were amassed.

## RESULTS

In the absence of sequences from the generitype of *Spongites*, *S. fruticulosa* Kützing, specimens from the NE Pacific confirmed by sequencing type material to belong to *S. decipiens* and *Lithophyllum tumidum* (=*Pseudolithophyllum neofarlowii*) along with South African material identified as *S. yendoi*, all resolved as a single genus (Fig. 1) but as four distinct species with interspecific sequence divergence values ranging from 2.9 to 7.6% for *psb*A and from 5.0 to 9.8% for *rbc*L (Table 1). Each of these species is treated below. Of the three species of Lithophylloideae (the outgroup), two (*Lithothrix aspergillum* J.E.Gray and *Amphiroa zonata* Yendo) were represented by sequenced topotype material (Gabrielson *et al*. 2011) and one (*Lithophyllum incrustans* Phillipi) by sequenced type material (Hernandez-Kantun *et al*. in press).

### **Spongites decipiens** (Foslie) Y.M. Chamberlain, 1993: 113

(Figs 2-11)

BASIONYM: *Lithothamnion decipiens* Foslie, 1897: 20

LECTOTYPE: TRH (A2-97), W.A. Setchell #1482, *leg*. 5.xii.1895 (Fig. 2).

ISOLECTOTYPE: UC 736372; thallus on fragment of the same stone as the lectotype.

TYPE LOCALITY: San Pedro, Los Angeles, California, USA.

HOMOTYPIC SYNONYMS:

*Lithophyllum decipiens* (Foslie) Foslie, 1900b: 19 (see also Foslie 1900a: 21)

*Hydrolithon decipiens* (Foslie) W.H. Adey, 1970: 11

*Pseudolithophyllum decipiens* (Foslie) Steneck & R.T. Paine, 1986: 237

ETYMOLOGY: *decipiens* is Latin for deceiving (Stearn 1973). Foslie (1897) did not explain the origin of the epithet, but presumably it makes reference to this species closely resembling another.

DNA SEQUENCES: *rbc*L sequences varying in length from 296-1387 base pairs (bp) were obtained from six specimens, one (1387 bp) from Crescent City, Del Norte Co., CA, one (1387 bp) from Pacific Grove, Monterey Co., CA, three (702-1387 bp) from Shell Beach, San Luis Obispo Co., CA and one (296 bp) from the isolectotype specimen (UC 736372) from San Pedro, Los Angeles Co., CA, USA (Table S1). All sequences were identical over their comparable lengths except for the isolectotype that had one single nucleotide polymorphism (SNP). *psb*A sequences (851 bp) were obtained for four of the same specimens for which *rbc*L sequences were obtained, one from Crescent City, one from Pacific Grove, and two from Shell Beach, CA, and all of these sequences were identical to each other and to two sequences provided by Dr. Gary Saunders from northern British Columbia (BC), Canada (Table S1).

HABIT: Thalli were non-geniculate, encrusting with smooth surfaces and epilithic on primary bedrock or cobble, where they were firmly adherent and conformed to the substratum. Individual thalli were discernible from one another and did not appear to fuse together with abutting margins clearly visible under a dissecting microscope (Fig. 3).

VEGETATIVE ANATOMY: Thalli were dorsiventrally organised and dimerous, and haustoria were absent (Fig. 4). The single basal layer comprised cells that vary greatly in shape and size in radial view (along the filament) from squarish to rectangular to shoe-shaped (Figs. 4, 5), whereas in tangential view (across the filament) basal layer cells were rectangular to palisade-like (Fig. 6). Fusions between basal layer cells of contiguous filaments were abundant in tangential view and frequently occupied much of the adjoining cell wall (Fig. 6). Basal cells gave rise to erect filaments that made up the bulk of the thallus. The first one or two cells arising from basal cells were large and either, but not both, divided dichotomously to produce two rows of filaments that combined occupied more-or-less the same volume as the basal cells from which they were derived (Fig. 4). Where these cells were smaller, neither divided dichotomously (Fig. 5). Dichotomously dividing erect cells were irregularly square to rectangular with rounded corners (Fig. 4); non-dichotomously dividing erect cells were oval to square to rectangular with rounded corners, often forming bead-like filaments (Fig. 5). Fusions between cells of contiguous erect filaments were abundant and frequently occupied most of the adjoining cell wall. Secondary pit connections were not observed. Subepithallial initials were oval to square to rectangular with rounded corners and had cell lumens that stained no differently to cells of erect filaments (Fig. 7). Epithallial cells varied in shape from rounded to oval to domed, were dark-staining and occurred mostly in a single layer, but may be up to three cell layers when shedding (Fig. 7). Individual bottle-shaped trichocytes (Fig. 8) were occasionally observed at the thallus surface and did not become buried in the thallus.

REPRODUCTIVE ANATOMY: Thalli with neither carpogonial nor carposporangial conceptacles were observed; thus this species likely was dioecious. Spermatangial (male) conceptacles were domed, raised above, or occasionally flush with the surrounding thallus surface, and their chambers were rounded to transversely elliptical (Fig. 9). No conceptacle primordia were observed, but based on the orientation of the basal roof filaments (parallel to the roof), it appeared that the roof was formed from filaments that arose peripheral to the fertile area, the terminal initials of which were more elongated than their inward derivatives. These cells projected into the pore canal as papillae and were orientated more or less parallel to the conceptacle roof surface in fully developed conceptacles (Fig. 9). Unbranched (simple) spermatangial filaments developed only across the floor of the male conceptacle (Fig. 9). Senescent male conceptacles appeared to be shed as no buried conceptacles were observed.

Tetrasporangial thalli were morphologically similar to male thalli, but their conceptacles were larger. Their conceptacles were uniporate, domed, mostly raised above the surrounding thallus surface but occasionally were sunken with raised roofs (Figs 10, 11). Their chambers were transversely elliptical to rounded with a roof 3-6 (mostly 4) cells thick that was formed from filaments that arose peripheral to the fertile area, the terminal initials of which were more elongated than the surrounding cells (Fig. 10). These cells projected into the pore canal as papillae and were orientated more or less parallel or at a sharp angle to the conceptacle roof surface in fully developed conceptacles (Fig. 11). Throughout early development, a protective layer of epithallial cells surrounded the conceptacle primordium (Fig. 10); this protective layer was shed once the pore canal was fully developed. Mature conceptacles had floors that were sunken 12-16 cells (including the epithallial cell) below the surface. Zonately arranged tetrasporangia developed across the conceptacle floor; a central columella was absent (Fig. 11). Senescent tetrasporangial conceptacles appeared to be shed as no buried conceptacles were observed. See Tables 2 and 3 for a summary of the morphological and anatomical features.

REPRESENTATIVE SPECIMENS EXAMINED: NCU 591663; NCU 596899; NCU 596901; NCU 596902 (see Table S1 for specimen data).

DISTRIBUTION: By DNA sequence, confirmed from northernmost CA, Del Norte Co., south to San Pedro, Los Angeles Co., CA, USA with a disjunct population in Haida Gwaii, BC, Canada.

### ***Spongites yendoi*** (Foslie) Y.M. Chamberlain, 1993: 13

BASIONYM: *Goniolithon yendoi* Foslie, 1900a: 25-26

LECTOTYPE: TRH (A1-53), Yendo #66

TYPE LOCALITY: Shimoda Harbor (Shizuoka Prefecture), Japan

HOMOTYPIC SYNONYMS:

*Lithophyllum yendoi* (Foslie) Foslie, 1900b: 20

*Pseudolithophyllum yendoi* (Foslie) W.H. Adey, 1970: 14

ETYMOLOGY: *yendoi* named after its collector, K. Yendo.

DNA SEQUENCES: *rbc*L (1387 bp) and *psb*A (851 bp) sequences were obtained from two specimens (Table S1). The *rbc*L sequences were identical to each other as were the *psb*A sequences. These DNA sequences showed that *S. yendoi* from South Africa was a unique species compared to all other named *Spongites* specimens sequenced to date, including the Broom *et al*. (2008) specimen from New Zealand called *S. yendoi* (Table 1).

HABIT: Thalli were non-geniculate, encrusting and firmly adherent to substratum, epilithic on the primary bedrock and epizoic on live molluscs, smooth to lumpy to knobbly with pillar-like protuberances to 3 mm tall. Individual thalli with margins entire, thick and white-edged, but thalli frequently fusing and covering large expanses in the low intertidal, but also were present in the mid-intertidal and shallow subtidal (see also Chamberlain 1993, Maneveldt & Keats 2008).

VEGETATIVE & REPRODUCTIVE ANATOMY: Chamberlain’s (1993) observations are summarised in Table 3. Masaki’s (1968) observations on Japanese material are not included in Table 3 as we have sequenced only material from South Africa.

DISTRIBUTION: Reported to occur all along the coast of South Africa, but more common along the south and southwest coasts (Maneveldt *et al*. 2008). Confirmed by DNA sequence data from the Western Cape Province (Table S1), but possibly more widespread in South Africa.

### ***Spongites agulhensis*** Maneveldt, E. van der Merwe & P.W. Gabrielson *sp. nov.*

(Figs 12-24)

HOLOTYPE: L 0820786, 21.x.2011, *leg. G.W. Maneveldt*, epilithic on shale platform in the high intertidal zone, Fig. 12.

ISOTYPE: UWC 11/53.

TYPE LOCALITY: South Africa. Western Cape Province, Cape Agulhas: L'Agulhas, Stinkbaai (34° 49' 26.26"S; 20° 01' 0,69"E).

ETYMOLOGY: *agulhensis* making reference to the type locality at L'Agulhas, Cape Agulhas.

DIAGNOSIS: Uniformly encrusting (smooth) thalli that do not become secondarily thick and discoid with orbicular protrusions, nor warty, nor wrinkled; individuals usually easily discernible, not coalescing (fusing); colour of living thalli brownish pink; thallus construction dimerous, with cells of basal layer characteristically large and book-shaped; central columella present in tetrasporangial conceptacles; *rbc*L and *psb*A sequences unique.

DNA SEQUENCES: *rbc*L gene sequences (1387 bp) from two specimens, one topotype, the other paratype (Table 1) were identical to each other as were *psb*A sequences (851 bp) obtained from the same two specimens. These DNA sequences showed that *S. agulhensis* was different from all other named species of *Spongites* sequenced to date (Fig. 1, Table 1).

HABIT: Thalli were encrusting (smooth), firmly adherent, and brownish-pink when freshly collected (Figs 13, 14). Individual thalli were discernible, not fusing together, on average 10 mm in diameter, and rarely more than 20 mm with abutting margins clearly visible (Figs 12, 13). Thalli were epilithic on shale or quartzitic sandstone platforms in high and mid-intertidal zones (Figs 13, 14).

VEGETATIVE ANATOMY: Thalli were dorsiventrally organised and dimerous, and haustoria were absent (Fig. 15). The single basal layer comprised cells that were irregularly square and had the appearance of an upright book (Fig. 15). In radial section ('cover view' i.e. along the filament) cells were non-palisade (Fig. 16), whereas in tangential section ('spine view' i.e. across the filaments) they appeared palisade-like (Fig. 17). In tangential view fusions between cells of contiguous basal filaments were abundant and frequently occupied most of the adjoining cell wall. Basal cells gave rise to erect filaments that comprised the bulk of the thallus (Fig. 15). Erect filaments consisted of cells that were square to rectangular with rounded corners (Figs 15-17). Fusions between cells of contiguous erect filaments were abundant and frequently also occupied most of the adjoining cell wall (Fig. 17). Secondary pit connections were not observed in either basal or erect filaments. Subepithallial initials were square to rectangular with angular corners and cell lumens that stained differently to cells of erect filaments (Fig. 18). Epithallial cells occurred in 1-3 cell layers and were rounded to domed (Fig. 18).

REPRODUCTIVE ANATOMY: Gametangial thalli were dioecious. Spermatangial (male) conceptacles were low-domed, were raised above or only occasionally flush with the surrounding thallus surface (Fig. 19). Their chambers were transversely elliptical to flattened, with the roof nearly twice as thick along the pore canal (Fig. 20). The roof was formed from filaments that arose peripheral to the fertile area, the terminal initials of which were more elongate than the surrounding cells (Fig. 21). As they divided, the newly forming filaments curved inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate and very much enlarged. These cells projected into the pore canal and were orientated more or less parallel to the conceptacle roof surface in fully developed conceptacles (Fig. 20). Throughout the early development a protective layer of epithallial cells surrounded the conceptacle primordium; this protective layer was shed once the pore canal was near full development. Terminal initials near the pore opening were broader and more elongate and projected out of the pore to as much as 20 µm (Figs 19, 20). Until these extruding filaments were fully developed, the pore was somewhat occluded by a mucilage plug. These projecting filaments, however, did not persist in older conceptacles. Unbranched (simple) spermatangial structures developed only across the floor of the mature male conceptacle (Figs 20-21). Senescent male conceptacles appeared to be shed from the thallus surface as no buried conceptacles were observed.

Female thalli with carpogonia were not observed, but after presumed karyogamy, carposporophytes developed within female conceptacles and formed carposporangial conceptacles. Carposporangial conceptacles were larger than spermatangial conceptacles, low-domed and raised above the surrounding thallus surface (Fig. 22). Their chambers were transversely elliptical, with the roof nearly twice as thick along the pore canal (Fig. 22). Roof formation appeared similar to that of male conceptacles. A discontinuous central fusion cell was present that was free from, and raised above the chamber floor (Fig. 22). Arising peripherally from the fusion cell were gonimoblast filaments that were 4-7 cells long, each including a terminal carposporangium (Fig. 22). The remains of unfertilised carpogonia persisted across the dorsal surface of the fusion cell (Fig. 22). Senescent female conceptacles appeared to be shed from the thallus surface as no buried conceptacles were observed.

Tetrasporangial thalli were morphologically similar to gametangial thalli. Tetrasporangial conceptacles were uniporate, low-domed, and raised above the surrounding thallus surface (Fig. 23). Their chambers were transversely elliptical to rounded to dumbbell-shaped, with the roof 4-8 cells thick. Similar to spermatangial conceptacles, the roof was formed from filaments that arose peripheral to the fertile area, the terminal initials of which were more elongate than the surrounding cells (Fig. 24). As they divided, the newly forming filaments curved inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate (Fig. 24). These cells projected into the pore canal and were orientated more or less parallel or at a sharp angle to the conceptacle roof surface in fully developed conceptacles. Throughout the early development a protective layer of epithallial cells surrounded the conceptacle primordium; this protective layer was shed once the pore canal was near fully developed. Mature conceptacles had floors that were sunken 10-15 cells (incl. the epithallial cell) below the surrounding thallus surface. Zonately arranged tetrasporangia at maturity were peripherally arranged around an extensive central columella (Fig. 23). Only the lower cells of the central columella appeared to be calcified often giving the conceptacle chamber a dumbbell-shaped appearance. Senescent tetrasporangial conceptacles appeared to be shed from the thallus surface as no buried conceptacles were observed. See Tables 3 and S2 for a summary of the morphological and anatomical features.

REPRESENTATIVE SPECIMENS EXAMINED: Six samples represented our entire collection for this taxon: South Africa. Western Cape Province: Cape Agulhas, L'Agulhas, Stinkbaai, L 0820786 (holotype); UWC 11/53 (isotype); UWC 10/142, 34° 49' 26.44"S; 20° 01' 1.61"E, 16.vi.2010, *G. W. Maneveldt & E. van der Merwe*, epilithic on shale platform, high intertidal; UWC 11/23, 34° 49' 26.24"S; 20° 01' 0.74"E (Table S1); Struisbaai, UWC 11/24, 34° 48' 49.91"S; 20° 03' 2.74"E (Table S1); UWC 11/55, 34° 48' 36.85"S; 20° 03' 26.49"E, 21.x.2011, *G. W. Maneveldt*, epilithic on quartzitic sandstone platforms in the high to upper mid intertidal.

DISTRIBUTION: Known only from South Africa; Western Cape Province, Struisbaai westward to L'Agulhas (Cape Agulhas). The species has a remarkably limited distribution of only about 10 km, despite extensive collections either side of the recorded distribution.

### ***Spongites tumidum*** (Foslie) K.A. Miller, P.W. Gabrielson, Miklasz, E. van der Merwe & Maneveldt *comb. nov.*

(Figs 25-38)

BASIONYM: *Lithophyllum tumidum* Foslie, 1900 (9) [1901b]: 18

LECTOTYPE: TRH (A3-138), unnumbered, May 1885, W. G. Farlow

ISOLECTOTYPE: UC 341301

TYPE LOCALITY: Monterey, Monterey Co., CA, USA

HOMOTYPIC SYNONYM:

*Lithophyllum farlowii* Foslie 1900 (6) [1901a]: 12 *nom. illeg.*, later homonym of *L. farlowii* Heydrich

*Lithophyllum neofarlowii* Setchell & L.R. Mason, 1943: 95

*Pseudolithophyllum neofarlowii* (Setchell & L.R. Mason) W.H. Adey, 1970: 13

ETYMOLOGY: *tumidum* Latin meaning swollen.

DNA SEQUENCES: *rbc*L sequences from seven specimens were obtained: one (1387 bp) from Tatoosh Island, Washington (WA), USA; one (702 bp) from San Juan Island, WA, USA; one (702 bp) from Lone Ranch Beach, Curry Co., Oregon (OR), USA; and four (296, 702 and 1387 bp) from Monterey Co., CA, USA, including the lectotype (TRH A3-138) and isolectotype (UC 341301). Specimens from Del Norte Co., CA and northward had two or three (Tatoosh I., WA specimen) SNP compared to Monterey Co., CA, USA material (all identical), representing an intraspecific species sequence divergence of 0.14-0.22%. *psb*A sequences were obtained from the same four field-collected specimens from which *rbc*L sequences were obtained, as well as from one specimen from Three Entrance Bay (near Sitka), Alaska and nine provided by Dr. Gary Saunders from northern and southern BC, Canada (Table S1). All were identical.

HABIT: Thalli were encrusting to warty (Figs 25, 26), typically adherent to the substratum (but high intertidal specimens were friable and easily removed) and 1-2 mm thick with complex, irregular and variable protuberances to 1-2 mm tall and 1-4 mm diameter. Living thalli were blue-purple to pink in damp habitats, becoming chalky-white when desiccated, and this varied seasonally, with white, desiccated thalli becoming pigmented. Individual thalli were indistinguishable from one another and fused together with abutting margins not clearly visible even under a dissecting microscope. Mostly epilithic, rarely epizoic on live chitons; common in upper intertidal shaded habitats, uncommon in tidepools and in mid-low intertidal habitats. This species was intensively grazed by herbivores such as limpets and snails, and radular teeth marks were often observed on thalli surfaces.

VEGETATIVE ANATOMY: Thalli were dorsiventrally organized and dimerous, and haustoria were absent (Figs 27, 28). The single basal layer comprised cells that varied greatly in shape and size in radial view (along the filament) from oval to squarish (Fig. 27), whereas in tangential view (across the filament) cells of the basal layer were rectangular to palisade-like (Fig. 28). Fusions between cells of contiguous basal filaments were abundant in tangential view and frequently occupied much of the adjoining cell wall (Fig. 28). The first one or two cells of erect filaments arising from basal cells were comparatively large (Fig. 27), and either one of these, but not both, divided dichotomously to produce two rows of filaments that combined occupied more-or-less the same volume as the basal cells from which they are derived. This dichotomous branching did not occur when cells arising from the basal layer were comparatively small. Dichotomously dividing erect cells were irregularly squarish to rectangular with rounded corners as were cells of erect filaments that often formed bead-like filaments (Figs 27-30). Fusions between cells of contiguous erect filaments were abundant and frequently also occupied most of the adjoining cell wall. Secondary pit connections were not observed between cells of basal and erect filaments. Subepithallial initials were oval to square to rectangular with rounded corners and had cell lumens that stained no differently to cells of erect filaments (Figs 29, 30). Epithallial cells occurred in mostly 1-2 layers and varied in shape from oval to domed to flattened to triangular (Figs 29, 30). When undergoing shedding or when subepithalial initials were actively dividing, up to 4 layers of epithallial cells were present (Fig. 30) or they were absent, presumably due to shedding or grazing by herbivores.

REPRODUCTIVE ANATOMY: Gametangial thalli presumably were dioecious, although female conceptacles were not found. Spermatangial (male) conceptacles were flush with the surrounding thallus surface (Figs 31, 33). Their chambers were transversely elliptical to flattened, with the roof nearly twice as thick along the pore canal (Fig. 35). The roof was formed from filaments that arose peripheral to the fertile area, the terminal initials of which are more elongated than their inward derivatives (Figs 33, 35). In fully developed conceptacles, these cells projected into the pore canal as papillae and were oriented more or less parallel to the conceptacle roof surface (Fig. 35). Throughout early development a protective layer of epithallial cells surrounded the conceptacle primordium (Figs 31, 33); this protective layer was shed once the pore canal was fully developed (Fig. 35). Unbranched (simple) spermatangial filaments developed only across the floor of the male conceptacle (Fig. 33, 35). Senescent male conceptacles appeared to be shed from the thallus surface as no buried conceptacles were observed.

Tetrasporangial thalli were morphologically similar to male thalli, but their conceptacles were substantially larger. Their conceptacles were uniporate, domed and raised above the thallus surface (Fig. 36). Their chambers were transversely elliptical, with the roof 3-6 cell layers thick. Similar to spermatangial conceptacles, the roof was formed from filaments that arose peripheral to the fertile area (Figs 32, 34), the terminal initials of which were more elongate than the surrounding cells (Fig. 36, 38). In fully developed conceptacles, these cells projected into the pore canal as papillae and were orientated more or less parallel or at a sharp angle to the conceptacle roof surface (Fig. 38). Throughout early development a protective layer of epithallial cells surrounded the conceptacle primordium (Figs 32, 34, 36); this protective layer was shed once the pore canal and tetrasporangia were fully developed. Throughout development of the immature tetrasporangial conceptacle, a prominent columella of sterile filaments formed at the centre of the conceptacle chamber (Figs 34, 36). This central columella appeared to be weakly calcified as with maturity it disintegrated to form a low mound with zonately divided tetrasporangia arranged around its periphery (Figs 37, 38). Mature conceptacles have floors that were sunken 13-21 cells (incl. the epithallial cell) below the surrounding thallus surface (Fig. 38). Senescent tetrasporangial conceptacles appeared to be shed from the thallus surface as no buried conceptacles were observed. Confluent thalli bearing tetrasporangial and spermatangial (male) conceptacles were occasionally observed (Fig. 37). See Tables 2, 3 and S2 for a summary of the morphological and anatomical features.

REPRESENTATIVE SPECIMENS EXAMINED: NCU 588179; NCU 591459; NCU 601317; NCU 600394; NCU 591648; TRH; UC (see Table S1 for specimen data).

DISTRIBUTION: Confirmed by DNA sequences from near Sitka, (southeast) Alaska to Monterey Co., CA, USA. Records from further south in the NE Pacific (Mason 1953, Dawson 1960), and from Japan (Yoshida *et al*. 1985, Baba 2000) have not been confirmed by DNA sequences.

## DISCUSSION

### Placement in *Spongites*

It is the generitype species that defines a genus, and to that species all others placed in the genus need to be related. In the absence of some diagnostic anatomical characters and lacking any molecular data about *S. fruticulosa* (type species) based on type or topotype material, it is uncertain, but likely, that *S. decipiens*, *S. agulhensis*, *S. tumidum* and South African *S. yendoi* belong in this genus. We kindly were sent field-collected material identified as *S. fruticulosa* by Dr. Daniella Basso, but were unable to obtain any useful DNA sequences that potentially could be compared to sequences from type material. Kato *et al*. (2011), using a combination of SSU and *psb*A sequences split from the Mastophoroideae the following clades: Neogoniolithoideae, Porolithoideae, Hydrolithoideae, *Spongites* and *Pneophyllum*. The last two taxa, however, were not represented by their generitype species, and therefore Kato *et al*. (2011) did not recognise these clades as subfamilies. Kato *et al*. (2011) characterized *Spongites* by the following combination of characters, some of which first had been proposed by Penrose & Woelkerling (1992): 1) absence of genicula; 2) presence of cell fusions and absence of secondary pit connections between cells of adjacent (contiguous) filaments; 3) absence of a ventral (basal) layer of palisade cells; 4) absence of trichocytes in tightly packed horizontal fields without vegetative cells between individual trichocytes; 5) uniporate, Type 1 (in which the roof development occurs only from filaments peripheral to the fertile area) (tetra)sporangial conceptacles; and 6) spermatangia found only on the floor of male conceptacles. All of these features are confirmed in either type (Woelkerling 1985) or topotype (Basso & Rodondi 2006) material of *S. fruticulosa* except whether tetrasporangial conceptacles have Type 1 or Type 2 (in which the roof development occurs from filaments peripheral to, and interspersed amongst the developing sporangia) development, the one feature that according to Kato *et al*. (2011) segregates *Pneophyllum* from *Spongites*. We await both additional anatomical/morphological and molecular characterization of the generitypes of these genera based on type or topotype material to confirm placement of the species treated herein in *Spongites*.

## Assignment of species names

The most unequivocal way to link a name of historical or recently collected specimens to type material is to compare informative DNA sequences obtained from both (Hughey *et al*. 2001). The first application of this methodology to coralline algae was by Gabrielson *et al*. (2011) for species of the geniculate coralline genus *Calliarthron* and more recently for species of the non-geniculate coralline genera *Clathromorphum, Callilithophytum, Neopolyporolithon* (Adey *et al.* 2015), *Mesophyllum* (Sissini *et al.* 2014) and *Lithophyllum* (Hernandez-Kantun *et al*. 2015). Using this method, we are confident that the names *S. agulhensis*, *S. decipiens* and *S. tumidum* are correctly applied to field collected material as partial *rbc*L sequences from type specimens are identical over comparable lengths to field-collected specimens and differ from all other sequenced species. Moreover, field-collected specimens that we have sequenced are from localities not far removed from the type locality for each species, except for *S. yendoi.*

## *Spongites decipiens*

Compared to other *Spongites* species, interspecific sequence divergence values for *S. decipiens* of both *rbc*L and *psb*A (Table 1) indicate a clearly distinct species. The partial *rbc*L sequence from the isotype collected in 1896, which is part of the same stone that bears the holotype (Chamberlain 1993), as well as sequenced field-collected material, shows that *S. decipiens* is not restricted to the type locality as suggested by Chamberlain (1993), nor is it a warm water species only found south of Point Conception, CA, USA as proposed by Steneck & Paine (1986). It is widely distributed in CA from the northernmost county (Del Norte) to Los Angeles Co., USA, covering some 1200 km of coastline and has a disjunct population in Haida Gwaii, British Columbia (BC), Canada (Table S1), about 1350 km to the north. In its morphological and anatomical features, *S. decipiens* closely resembles *S. agulhensis* from the southern coast of South Africa, differing by only a single feature, the absence of a central columella in tetrasporangial conceptacles in the former (Table 3). All other measurable anatomical features overlap between the two species (Table S2).

Recently, Saunders (2014) proposed the kelp conveyor hypothesis to explain the distribution of species widespread in CA (mostly north of Point Conception), but known only as disjunct populations in Haida Gwaii, BC, Canada, minimally some 1350 km to the north and not reported from any intervening localities despite intensive, recent collecting, particularly in southern BC. *Spongites decipiens* fits this distribution pattern, reported from Los Angeles Co. to the northernmost county, Del Norte, CA and then only from two localities in Haida Gwaii (Table S1). Moreover, due to its presence on small cobble and particularly on gastropod shells (Table S1), this non-geniculate coralline species could readily be transported in kelp rafts. Genetic population markers are needed to test this hypothesis for many of the taxa in Saunders (2014) list, and *S. decipiens* should be included.

Due to the morphological and anatomical similarity among genetically distinct and biogeographically isolated *Spongites* species, all occurrences of *S. decipiens* and its reported synonyms, e.g., *Lithothamnion mangini* Me. Lemoine & Rosenvinge (type locality: Petermann Island, Antarctica) outside of the range confirmed by DNA sequencing need to be confirmed also by DNA sequencing. This includes material reported from: the Northeast Pacific south of CA to Panama and the Gulf of California by Dawson (1944, 1960); southern South America by Mendoza & Cabioch (1986); Juan Fernandez Island by Levring (1943);

India by Krishnamurthy & Jayagopal (1985) and eastern Russia by Perestenko (1996). It is doubtful that any report outside the Northeast Pacific will be confirmed.

### *Spongites yendoi*

DNA sequences confirm Chamberlain's (1993) hypothesis that *Spongites decipiens* and South African *S. yendoi* are distinct species. However, we have DNA sequences only from South African specimens called *S. yendoi* and not from type or topotype material from Japan. Moreover, *psb*A sequences deposited in GenBank from 28 specimens called *S. yendoi* from New Zealand are not the same species as South African material called *S. yendoi*. We did not include the New Zealand sequences in our phylogenetic analyses, as they clearly represent a mix of species. Consequently, we find that we must question whether any of the sequenced material from either South Africa or New Zealand called *S. yendoi* is conspecific with type material. We refrain from changing the name of South African specimens called *S. yendoi*, until sequence data is available from type material of *S. yendoi*. Specimens called *S. yendoi* in South Africa are one of the most commonly reported non-geniculate coralline algae in the mid- to low-intertidal zones (Maneveldt & Keats 2008, Maneveldt *et al*. 2008). From other currently recognized *Spongites* species whose type localities are in South Africa, they can be distinguished by their monomerous thallus construction (Table 3) and *rbc*L and *psb*A gene sequences.

### *Spongites agulhensis*

The *rbc*L and *psb*A gene sequences (Fig. 1, Table 1) along with a dimerous thallus construction in which cells of the basal filament are book-shaped and a central columella is present in tetrasporangial conceptacles clearly distinguish *S. agulhensis* from all other *Spongites* species worldwide. This is despite its morphological similarity to both South

African *S. yendoi* and NE Pacific *S. decipiens* (Tables 3 and S2), and despite its very narrow distribution range. In the field, *S. agulhensis* previously was confused with South African *S. yendoi*, but can be distinguished by its characteristically brownish-pink colour compared to *S. yendoi*'s more grey colouration (Fig. 14), by distinct individual thalli (Figs 13, 14), whereas those of *S. yendoi* typically fuse with adjacent conspecifics, and by growing in the high intertidal zone (Table 3). Anatomically it is distinguished from *S. yendoi* by only two characters. The first and most distinctive character is *S. agulhensis*' dimerous thallus construction in which basal cells are book-shaped. Secondly, in *S. agulhensis* conceptacles are never buried. From NE Pacific *S. decipiens, S. agulhensis* anatomically is distinguished by only a single character, the presence of a central columella in its tetrasporangial conceptacles (Table 3).

***Spongites tumidum***

Foslie (1901a) described *Lithophyllum farlowii* based on material sent to him by W. G. Farlow from Monterey, CA, USA noting that the species differed morphologically from *L. yendoi*, but was anatomically very similar. Foslie's (1901a) cell and conceptacle measurements are in Table 2. Setchell and Mason (1943) pointed out that *L. farlowii* Foslie was a later homonym (by a month) of *L. farlowii* Heydrich, and they proposed the substitute name *L. neofarlowii* for the former, not realizing that Foslie (1901b) already had proposed the substitute name *L. tumidum*. Smith (1944: 228) added the first habitat information, and expanded the distribution of *L. tumidum* (as *L. neofarlowii*) north to Fort Bragg and south to Carmel Bay, USA. Mason (1953) elaborated on Foslie's (1901a) description (Table 2), further expanded the distribution of the species south to Cambria, CA and north to Puget Sound, WA, USA. She noted that the species grew higher in the intertidal zone than all other encrusting corallines, where it occurs in large patches, is dull purple to lavender, and varies from somewhat irregular to very bumpy, appearing to be composed of numerous small spheres cemented together. Mason (1953) designated the material in TRH (as Herb. Mus. Nidaros) as the lectotype (TRH A3-138) and UC 341301 as an isotype (isolectotype). Dawson (1960) repeated Mason's (1953) description and expanded the distribution south to Bahia Asunción, Baja California, Norte, Mexico based on a single collection in a tidepool. Adey (1970) later transferred *L. neofarlowii* to *Pseudolithophyllum*. Steneck & Paine (1986) mostly confirmed the observations of previous authors; these are summarized in Table 2. The only report of this species from outside the NE Pacific was by Yoshida *et al*. (1985) from Japan, and only much later were its habit and conceptacles illustrated based on Japanese material (Baba 2000).

*Lithophyllum tumidum* clearly belongs in *Spongites* based on *rbc*L and *psb*A gene sequences (Fig. 1) as well as a suite of morpho-anatomical features. Thalli are non-geniculate, lack a ventral (i.e. basal) layer of palisade cells (in radial view), and cells of contiguous vegetative filaments are joined only by cell fusions. Tetrasporangial conceptacle pore canals are lined by cells that arise from peripheral roof filaments, and these cells protrude into the canal as papillae orientated more or less parallel or at a sharp angle to the conceptacle roof surface. Spermatangial conceptacles bear unbranched spermatangial systems restricted to the conceptacle floor (see Kato *et al*. 2011). This species has long been recognized as distinct in the NE Pacific based on its habit and habitat. The findings from earlier reports are confirmed by the species' unique *rbc*L and *psbA* gene sequences. New observations include its dimerous thallus construction, and its occurrence in tidepools and on the plates of live chitons (Table 3). Its presence in Japan (Baba 2000) needs to be confirmed by DNA sequences.

## Coralline Species Determinations, Distributions and Convergent Evolution

As shown here, two widely geographically separated *Spongites* species, *S. agulhensis* from South Africa and *S. decipiens* from the NE Pacific, required detailed anatomical and morphological observations to find even a single character to segregate them (presence vs. absence of a central columella in tetrasporangial conceptacles respectively, Tables 3 and S2). However, *rbc*L and *psb*A sequence divergence values (Table 1) clearly indicate that they are distinct species. Moreover, in South Africa, *S. agulhensis* historically was confused with specimens called *S. yendoi* as these species appear similar morphologically and their habitats somewhat overlap. Only two anatomical characters segregate these species, dimerous vs. monomerous thallus construction and the absence of old, buried conceptacles in *S. agulhensis* (Tables 3 and S2). As these examples show, it requires detailed morpho-anatomical observations, frequently of material from a particular life history stage, to find even one or two characters that distinguish these species, and these characters may not be present in any given specimen.

This is the first report for non-geniculate coralline algae where names have been unequivocally assigned that demonstrates geographically overlapping species are genetically more similar than morpho-anatomical nearly indistinguishable species whose distributions are widely disjunct. Even the novice collector would not confuse the morphologically and habitat distinct NE Pacific species *S. decipiens* and *S. tumidum*, and yet they are most similar genetically in both plastid markers (Table 1). In contrast, the morpho-anatomical nearly indistinguishable, but geographically widely separated *S. agulhensis* and *S. decipiens* also are among the most distinct species genetically based on these same markers (Table 1). That *S. agulhensis* from South Africa and *S. decipiens* from the NE Pacific are anatomically nearly identical, yet genetically very distinct, argues for convergent evolution of many anatomical features in non-geniculate coralline algae. Moreover, many of these same features have been used both historically and recently to place into synonymy coralline species from different biogeographic provinces. Based on these observations, we find ourselves having to question all reports, based only on morpho-anatomy of the widespread and disjunct distributions of *Spongites* species, particularly of *S. decipiens*, *S. tumidum* and *S. yendoi*, but also of *S. fruticulosa* [Mediterranean Sea and southern Australia (Penrose 1996)] and *S. discoidea* [Tierra del Fuego, Argentina and South Africa (Chamberlain 1994)]. If this observation holds true more generally, then all reports of geographically widespread and disjunct non-geniculate coralline species distributions will need to be reinvestigated.

## ACKNOWLEDGEMENTS

We thank the Department of Biodiversity and Conservation Biology at the University of the Western Cape for providing funding and research equipment, and the South African National Research Foundation (NRF) for research grants to GWM and AC. Adrian Josephs provided valuable assistance with the operation of the SEM. Dr. Gary Saunders generously provided unpublished DNA sequences. Dr. S. C. Lindstrom, Mr. W. Wood and students and teacher, Mr. Larry Madrigal, of the Saint Joseph High School Science Research Institute in Santa Maria, CA we thank for providing specimens. Dr. Kathy Ann Miller (UC) kindly shared with us her knowledge of an earlier specific epithet that was found by and is documented in INA (Index Nominum Algarum, http://ucjeps.berkeley.edu/INA.html). Dr. Wilson Freshwater, DNA Analysis Core Facility, University of North Carolina, Wilmington provided sequencing support, and Dr. Todd Vision provided research space and equipment to PWG who also acknowledges a private family trust for research support. A portion of this research was completed while PWG was a visiting professor at the Friday Harbor Labs, University of Washington.

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## TABLES

**Table 1**. Sequence divergence values (in %) among species of *Spongites* for *psb*A (first number) and *rbc*L (second number). *Spongites yendoi* (NZ = New Zealand) is the sequence from Broom *et al*. (2008). nr = no *rbc*L sequence reported. SA = South Africa.

| | *S. agulhensis* | *S. decipiens* | *S. tumidum* | *S. yendoi* (NZ) |
|---|---|---|---|---|
| *S. decipiens* | 7.6%, 9.2% | | | |
| *S. tumidum* | 7.4%, 9.8% | 2.9%, 5.0% | | |
| *S. yendoi* (NZ) | 5.8%, nr | 6.8%, nr | 7.0%, nr | |
| *S. yendoi* (SA) | 6.0%, 8.1% | 7.5%, 9.5% | 7.3%, 9.9% | 5.9%, nr |

**Table 2.** Comparison of historical data for *S. decipiens* and *S. tumidum*. Mason's (1953) data on *S. decipiens* is not included as her concept of this species included at least two other species. ND = no data.

| Character | Foslie (1897, 1909, as *Lithophyllum decipiens*) | Steneck & Paine (1986, as *Pseudolithophyllum decipiens*) | Chamberlain (1993, as *Spongites decipiens*) | Foslie (1901, as *Lithophyllum neofarlowii*) | Mason (1953, as *Lithophyllum neofarlowii*) | Steneck & Paine (1986, as *Pseudolithophyllum neofarlowii*) |
|---|---|---|---|---|---|---|
| Substratum | epilithic | epilithic | epilithic | epilithic | epilithic | epilithic |
| Growth form | encrusting with smooth surfaces | encrusting with smooth surfaces | encrusting with smooth surfaces | encrusting to warty | encrusting to warty | encrusting to warty |
| Thallus thickness | 200 µm | 178 ± 61 µm | to 250 µm | 1 mm | to 300 (500) µm | to 2 mm |
| Thallus construction | dimerous | monomerous[1] | dimerous[2] | ND | monomerous[3] | monomerous[1] and dimerous |
| Epithallial cell layers | ND | 1-2 | 1-2 | ND | 2-3 | 1-3 |
| Perithallial cell length x width | 4-11 x 4-8 µm | ND | 4-13 x 4-10 µm | 5-10-(12) x 4-7- (9) µm | 5-15 x 5-12 µm | 6.4 x 3.9 µm |

| | | | | | | |
|---|---|---|---|---|---|---|
| Gametangial conceptacle elevation | ND | flush to slightly raised | flush to slightly raised to slightly sunken | ND | ND | raised |
| Spermatangial conceptacles (external diameter) | 100 µm | 156 ± 23 | ND | ND | 90-100 µm | ND |
| Carposporangial conceptacles (external diameter) | 100 µm | 156 ± 23 µm | to 300 µm | ND | 190-215 µm | ND |
| Tetrasporangial conceptacle elevation | raised (mostly) to slightly sunken | flush to slightly raised | flush to slightly raised to slightly sunken | raised | sunken[4] | raised |
| Tetrasporangial conceptacle (external diameter) | 200 µm | 156 ± 23 µm | to 300 µm | 220 µm | 180-225 µm | 220 ± 40 µm |
| Tetrasporangia length | ND | ND | 55-75 x 30-50 µm | 90-100 x 50-60 µm | 90-100 x 50-60 µm | ND |

| | | | | | | |
|---|---|---|---|---|---|---|
| x width | | | | | | |
| Old conceptacles buried/shed | ND | buried | shed | ND | shed (see Plate 40, Figure b) | ND |

[1] Earlier researchers such as Foslie (1897, 1901a), Mason (1953) and Steneck & Paine (1986) did not recognise monomerous vs. dimerous constructions.  We have applied these terms based on their anatomical descriptions.

[2] The holotype and isotype of *S. decipiens* also show a dimerous construction with large basal cells (Chamberlain (1993).

[3] Mason (1953) states that hypothallial cells are multilayered (monomerous), but her Plate 40, Fig. C clearly shows dimerous construction.

[4] Mason (1953) reports immersed (sunken) sporangial conceptacles probably in reference to conceptacle chambers because Plate 40 Fig. C shows flush to slightly raised conceptacle roofs.

**Table 3.** Characters found to be informative among of Australian (AUS), Northeast Pacific (USA) and South African (SA) species of *Spongites*. *Spongites* species reported from Australia and South Africa, but whose type localities are not on those continents were not included, except South African *S. yendoi*. NA = not applicable. ND = no data.

| Character | *S. agulhensis* (This study, SA) | *S. decipiens* (This study, USA) | *S. hyperellus* (Penrose 1996, AUS) | *S. impar* (Chamberlain 1994, SA) | *S. tumidum* (This study, USA) | *S. tunicatus* (Penrose 1996, AUS) | *S. yendoi* (Chamberlain 1993, SA) |
|---|---|---|---|---|---|---|---|
| Substrate | epilithic | epilithic, epizoic | epilithic | epilithic, epizoic | epilithic, epizoic | epilithic, epizoic | epilithic, epizoic |
| Habitat | high intertidal | mid-low intertidal | low intertidal | intertidal | mid- to high, rarely low intertidal, | intertidal | mid- to low intertidal, and tidepools |
| Growth form | encrusting, smooth | encrusting, smooth | encrusting to fruticose | encrusting, becoming crested and convoluted | encrusting to warty | encrusting to warty | encrusting, smooth to lumpy to knobbly |
| Habit | no fusion of individual thalli | no fusion of individual thalli | ND | ND | thalli fuse to form large expanses | ND | thalli fuse to form large expanses |
| Thallus construction | dimerous | dimerous | monomerous | monomerous | dimerous | dimerous | monomerous |
| Trichocyte | none observed | solitary | solitary or in | none observed | none observed | NA | solitary to paired |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| arrangement | | | horizontal fields | | | | |
| No. of epithallial cell layers | 1-3 | 1 (mostly) -3 | 1-7 | 6 | 1-4 (mostly 1-2) | 1 | 1 |
| Shape of the fusion cell | narrow, thick and discontinuous | ND | wide, thin | NA | ND | NA | narrow, thick and continuous |
| Columella (present/absent) | present | absent | present | present | present | absent | present |
| Distribution of tetra/bisporangia | peripheral | across the conceptacle floor | peripheral and across[1] the conceptacle floor | peripheral | peripheral | across the conceptacle floor | peripheral |

[1] Womersley (1996: 274, Fig. 125C shows peripherally arranged tetrasporangia. However, in the description Womersley (1996: 275) reports tetrasporangia to be distributed across the conceptacle floor.

## FIGURE CAPTIONS

Fig. 1. Consensus maximum likelihood tree inferred from concatenated *rbc*L and *psb*A sequences. Numbers above nodes are bootstrap values.

**Figs 2-8. Habit and vegetative anatomy of *S. decipiens*.**

Figs 2. Isolectotype and label (UC 736372) showing thin crust covering fractured cobble; rest of cobble with crust comprises holotype in TRH (A2-97). Scale bar = 20 mm.

Fig. 3. Magnified view showing several discrete individuals of *S. decipiens* whose margins (arrowheads) have not fused. Scale bar = 2 mm.

Fig. 4. Vertical section of thallus in radial view showing large, squarish to shoe-shaped, non-palisade basal cells (b) linked by primary pit connections and giving rise to erect filaments (e) dorsally. Large cells (asterisk) of erect filaments near base often divide dichotomously to produce two rows of filaments (NCU 596901). Scale bar = 20 µm.

Fig. 5. Vertical section of inner thallus in radial view showing small, squarish to rectangular basal cells (b) that are no different in size to cells of erect filaments (e) that arise from them (NCU 596899). Scale bar = 20 µm.

Fig. 6. Vertical section of inner thallus in tangential view showing rectangular to palisade-like cells (b) of basal layer. Note cell fusions (f) between cells of adjoining basal filaments (NCU 596901). Scale bar = 20 µm.

Fig. 7. Vertical section of outer thallus showing epithallial cells (e) subtended by layer of subepithalial initials (i). Epithallial cells occur in mostly one cell layer, but can occur in up to three (middle right) (NCU 596899). Scale bar = 20 µm.

Fig. 8. Vertical section of outer thallus showing individual, bottle-shaped, trichocytes (T) (NCU 596902). Scale bar = 20 µm.

**Figs 9-11. Reproductive anatomy of *S. decipiens*.**

Fig. 9. Vertical section through mature, raised spermatangial conceptacle showing simple spermatangial systems confined to conceptacle floor (NCU 596901). Scale bar = 20 µm.

Fig. 10. Early stage tetrasporangial conceptacle primordium showing peripheral (arrow) roof development and inner tetrasporangial initials (arrowheads). Note protective layer of epithallial cells (E) (NCU 596899). Scale bar = 50 µm.

Fig. 11. Mature, raised tetrasporangial conceptacle showing tetrasporangia (t) distributed across chamber floor; central columella is absent. Note pore canal filaments projecting into pore as papillae (arrowheads) (NCU 596899). Scale bar = 50 µm.

**Figs 12-14. Habits of *S. agulhensis*.**

Fig. 12. Holotype specimen (L 0820786) showing several individuals (tetrasporangial and gametangial). Scale bar = 20 mm.

Fig. 13. Individual, epilithic, thalli in their common high intertidal habitat from L'Agulhas, Cape Agulhas, Western Cape Province. Scale bar = 20 mm.

Fig. 14. *Spongites agulhensis* (arrowheads) growing side by side with *S. yendoi* (Sy) in upper reaches of mid-intertidal zone. Scale bar = 30 mm.

**Figs 15-18. Vegetative anatomy of *S. agulhensis*.**

Fig. 15. Dimerous thallus construction evident in side by side radial view, with large, irregularly square, non-palisade cells (arrow), and tangential view, with palisade-like cells (arrowhead), due to change in direction of growing margin (UWC 11/24). Scale bar = 140 µm.

Fig. 16. Vertical section of leading edge in radial view showing terminal marginal initial (m) and single basal cell (b) layer. Large, irregularly square, non-palisade basal (b) cells linked

by primary pit connections (white arrowheads) and giving rise to erect filaments dorsally (black arrowheads). Cells (asterisk) of erect filaments distal to basal cells each divide dichotomously to produce two rows of filaments. Note a cell fusion (f) between cells of two adjoining erect filaments (UWC 11/23). Scale bar = 20 µm.

Fig. 17. Vertical section of inner thallus in tangential view showing basal cell (b) layer. Seen in 'spine view' cells of basal layer appear palisade-like. Note primary pit connections (black arrowheads) between adjoining basal and erect cells of same corresponding filaments and cell fusions (f) between cells of adjoining erect filaments (UWC 11/23). Scale bar = 20 µm.

Fig. 18. Vertical section of outer thallus showing several layers of epithallial cells (arrowheads) subtended by a layer of subepithalial initials (arrow) whose cell lumens stain differently from cell lumens of more proximal cells (UWC 11/24). Scale bar = 20 µm.

**Figs 19-24. Reproductive anatomy of *S. agulhensis*.**

Fig. 19. SEM view of male thallus showing raised, domed conceptacles. Note extruded pore canal filaments (arrow) present in one conceptacle. Older, more mature conceptacles do not show this extrusion (UWC 10/142). Scale bar = 200 µm.

Fig. 20. Vertical section through spermatangial conceptacle showing enlarged, ballooned papillate cells (arrowheads) lining pore canal and elongate initials extruded above pore canal (arrow). Simple, unbranched spermatangial structures distributed only across chamber floor (UWC 10/142). Scale bar = 30 µm.

Fig. 21. Spermatangial conceptacle primordium showing roof development only from periphery (black arrowhead) and advanced formation of simple, unbranched and elongated spermatangial mother cells (white arrowhead). Note persisting layer of protective epithallial cells (arrow) (UWC 11/24). Scale bar = 25 µm.

Fig. 22. Vertical section through carposporangial conceptacle showing centrally raised pore canal structure (p) and gonimoblast filaments (arrowheads) borne along margins (peripherally) of conceptacle chamber (UWC 10/142). Scale bar = 50 µm.

Fig. 23. Vertical section of tetrasporangial conceptacle showing tetrasporangia (t) peripherally arranged around an extensive central columella (C) (UWC 10/142). Scale bar = 75 µm.

Fig. 24. Tetrasporangial conceptacle primordium showing roof development only from periphery (arrow), peripheral tetrasporangial initials (t) and sterile filaments (between black arrowheads) that form extensive central columella. Note layer of protective epithallial cells (white arrowheads) (UWC 11/24). Scale bar = 30 µm.

**Figs 25-30. Habit and vegetative anatomy of *S. tumidum*.**

Fig. 25. Lectotype (TRH A3-138) comprising four individual fragments. Scale bar = 20 mm.

Fig. 26. Magnified view showing confluent warty thalli of *S. tumidum* that are indistinguishable from one another. Scale bar = 2 mm.

Fig. 27. Vertical section of inner thallus in radial view showing oval to squarish to rectangular, non-palisade basal cells (b) giving rise to erect filaments (e) dorsally. Larger cells (asterisk) of erect filaments adjacent to cells of basal layer often divide dichotomously to produce two rows of filaments. Cell fusions (f) are common between cells of adjoining basal and erect filaments (NCU587541). Scale bar = 20 µm.

Fig. 28. Vertical section of inner thallus in tangential view showing rectangular to palisade-like cells (b) of basal layer. Note cell fusions (f) between cells of adjoining basal and erect filaments (NCU587541). Scale bar = 20 µm.

Fig. 29. Vertical section of outer thallus showing two layers of epithallial cells (e) subtended by layer of subepithalial initials (i) (NCU587541). Scale bar = 20 µm.

Fig. 30. Vertical section of outer thallus showing four layers of epithallial cells (e) subtended by layer of subepithalial initials (i) (NCU587541). Scale bar = 20 µm.

**Figs 31-38. Developmental and mature spermatangial and tetrasporangial anatomy of *S. tumidum* (NCU 588179).**

Fig. 31. Early stage spermatangial conceptacle primordium showing spermatangial initials (between black arrows), and protective layer of epithallial and outer cortical cells (E). Scale bar = 50 µm.

Fig. 32. Early stage tetrasporangial conceptacle primordium showing tetrasporangial initials (between black arrows) and protective layer of epithallial cells (E). Scale bar = 50 µm.

Fig. 33. Later stage spermatangial conceptacle primordium showing peripheral roof development (arrows) and advanced formation of unbranched (simple), elongated sperm mother cells (arrowheads). Note persisting layer of protective epithallial and outer cortical cells (E). Scale bar = 50 µm.

Fig. 34. Later stage tetrasporangial conceptacle primordium showing peripheral roof development (arrowheads) and tetrasporangial initials (t) arranged peripherally around central columella (C) of sterile cells. Note persisting layer of protective epithallial cells (E). Scale bar = 50 µm.

Fig. 35. Mature spermatangial conceptacle showing open, unoccluded pore canal (P); pore lined with terminal initials (arrows) more elongate than their inward derivatives and these cells project into pore canal as papillae. Unbranched (simple) spermatangial systems (S) distributed only across floor of conceptacle chamber. Scale bar = 30 µm.

Fig. 36. Maturing tetrasporangial conceptacle showing peripheral roof development (arrowheads) and tetrasporangial initials (t) arranged peripherally around central

columella (C) of sterile cells. Note persisting layer of protective epithallial cells (E). Scale bar = 50 µm.

Fig. 37. Confluent thalli bearing tetrasporangial (T) and spermatangial (S) conceptacles. Scale bar = 250 µm.

Fig. 38. Mature, raised tetrasporangial conceptacle showing tetrasporangia (t) peripherally arranged around low mounded remnant of central columella (C). Note pore canal filaments projecting into pore as papillae (arrows). Scale bar = 50 µm.

## SUPPLEMENTARY DATA AND INFORMATION

**Table S1.** List of specimens sequenced, herbarium number, with notes about type material, if relevant, collection data and GenBank Accession number. Taxa are listed in alphabetical order. ND = not determined.

| Species | Herbarium # | Collection Data | GenBank Accession # | |
|---|---|---|---|---|
| | | | *rbc*L | *psb*A |
| *Amphiroa zonata* | NCU 590262 topotype | Japan, Chiba Prefecture, Katsuura, Beach fronting Coastal Branch of Natural History Museum & Institute, 5.viii.2009, *leg*. S. C. Lindstrom | JN701462 | KT184811 |
| *Lithophyllum incrustans* | GALW15746 | France (Atlantic), Brittany, Bay of Brest, 20.vii.2010, 4.8 m depth, *leg*. J. Hernandez & J. Grall | KR708543 | JQ896238 |
| *Lithothrix aspergillum* | UBC A68043 topotype | Canada, British Columbia, Strait of Georgia, Bath Island, 19.iv.1973, *leg*. S. C. Lindstrom | HQ322336 | JQ917417 |
| *Spongites agulhensis* | UWC 11/23 topotype | South Africa, Western Cape Province, Cape Agulhas, L'Agulhas 20.iii.2011, epilithic on shale platform, high intertidal, *leg*. G. W. Maneveldt | KT184833 | JQ917419 |
| *Spongites* | UWC 11/24 | South Africa, Western Cape | KT184834 | KT184812 |

| | | | | |
|---|---|---|---|---|
| *agulhensis* | paratype | Province, Struisbaai, 20.iii.2011, epilithic on quartzitic platform, high intertidal, *leg*. G. W. Maneveldt | | |
| *Spongites decipiens* | UNB GWS013481 | Canada, British Columbia, Burnaby (Dolomite) Narrows, Gwaii Haanas, 23.vi.2009, on cobble low intertidal, *leg*. G.W. Saunders & D. McDevit | ND | KT184813 |
| *Spongites decipiens* | UNB GWS020634 | Canada, British Columbia, North Beach (near Naval Station), Haida Gwaii, 17.vi.2010, on bedrock, low intertidal pool, *leg*. G.W. Saunders & K. Dixon | ND | KT184814 |
| *Spongites decipiens* | NCU 622324 | USA, CA, Del Norte Co., Crescent City, on cobble mid-intertidal, 2.viii.2008, *leg*. W. Wood | KT184835 | JQ917420 |
| *Spongites decipiens* | NCU 597504 | USA, CA, Monterey Co., Pacific Grove, Mussel Point, 9.ii.2009, epilithic mid-intertidal tidepool, *leg*. K. Miklasz 51 | KT184836 | KT184816 |
| *Spongites decipiens* | NCU 596901 | USA, CA, San Luis Obispo Co., Shell Beach, 9.vi.2009, epizoic *Tegula funebralis*, low intertidal, | KT184837 | JQ917420 |

| | | | | |
|---|---|---|---|---|
| | | *leg*. C. Anton, P.W. Gabrielson & U. Kim | | |
| *Spongites decipiens* | NCU 596902 | USA, CA, San Luis Obispo Co., Shell Beach, 9.vi.2009, bedrock, low intertidal, *leg*. C. Anton, P.W. Gabrielson & U. Kim | KT184838 | KT184817 |
| *Spongites decipiens* | NCU 596899 | USA, CA, San Luis Obispo Co., Shell Beach, 8.vi.2009, epizoic shelled gastropod, low intertidal pool, *leg*. C. Anton, P.W. Gabrielson & U. Kim | KT184839 | ND |
| *Spongites decipiens* | UC 736372 isotype | USA, CA, Los Angeles Co., San Pedro, 5.xii.1896, epilithic on small cobble, *leg*. W. A. Setchell #1482 | KT184840 | ND |
| *Spongites tumidum* | NCU 635733 | Alaska, Three Entrance Bay, unnamed islet, 22.iv.2011, on bedrock, mid-intertidal, *leg*. S. C. Lindstrom 14655 | ND | KT184818 |
| *Spongites tumidum* | UNB GWS020653 | Canada, British Columbia, North Beach (near Naval Station), Haida Gwaii, 17.vi.2010, on bedrock under overhang, upper intertidal, *leg*. G.W. Saunders & K. Dixon | ND | KT184819 |

| | | | | |
|---|---|---|---|---|
| *Spongites tumidum* | UNB GWS019717 | Canada, British Columbia, Alder Island, Gwaii Haanas, 11.vi.2010, on bedrock, mid- intertidal, *leg.* G.W. Saunders & K. Dixon | ND | KT184820 |
| *Spongites tumidum* | UNB GWS019800 | Canada, British Columbia, Alder Island, Gwaii Haanas, 11.vi.2010, on rock wall, low intertidal, *leg.* G.W. Saunders & K. Dixon | ND | KT184821 |
| *Spongites tumidum* | UNB GWS019934 | Canada, British Columbia, Koga Islet, Gwaii Haanas, 12.vi.2010, on bedrock, mid-intertidal, *leg.* G.W. Saunders & K. Dixon | ND | KT184822 |
| *Spongites tumidum* | UNB GWS019956 | Canada, British Columbia, Koga Islet, Gwaii Haanas, 12.vi.2010, on bedrock, low intertidal, *leg.* G.W. Saunders & K. Dixon | ND | KT184823 |
| *Spongites tumidum* | UNB GWS020307 | Canada, British Columbia, East Copper Island (easternmost point), Gwaii Haanas, 14.vi.2010, on bedrock, upper intertidal, *leg.* G.W. Saunders & K. Dixon | ND | KT184824 |
| *Spongites tumidum* | UNB GWS019215 | Canada, British Columbia, Seppings Island, Bamfield, 27.v.2010, on bedrock, mid- | ND | KT184825 |

| | | | | |
|---|---|---|---|---|
| | | intertidal, *leg.* G.W. Saunders | | |
| *Spongites tumidum* | UNB GWS010889 | Canada, British Columbia, Brady's Beach, Bamfield, 06.vi.2008, on rock wall, cave entrance, mid-intertidal, *leg.* G.W. Saunders & B. Clarkston | ND | KT184826 |
| *Spongites tumidum* | NCU 588179 | USA, WA, east side of Tatoosh Island, 15.vi.2007, boulder, high intertidal, *leg*. P. W. Gabrielson | KT184841 | KT184827 |
| *Spongites tumidum* | NCU 591459 | USA, WA, San Juan Island, Cattle Point, 12.vii.2007, epilithic, high intertidal pool, *leg*. P. W. Gabrielson & K. Britton-Simmons | KT184842 | KT184828 |
| *Spongites tumidum* | NCU 601317 | USA, OR, Curry Co., south end Lone Ranch Beach, 3.viii.2008, mid- low intertidal pool, *leg*. W. Wood | KT184843 | KT184829 |
| *Spongites tumidum* | NCU 600394 | USA, CA, Monterey Co., Pacific Grove, foot of 15th St., 31.xii.2007, epilithic, high intertidal, *leg*. P. W. Gabrielson & P. T. Martone | KT184844 | KT184830 |
| *Spongites tumidum* | NCU 591648 | USA, CA, Monterey Co., Pacific Grove, Mussel Point, 3.v.2010, | KT184845 | KT184831 |

| | | | |
|---|---|---|---|
| | | epizoic on chiton, *leg*. K. Miklasz 91 | |
| *Spongites tumidum* | TRH A3-138 lectotype | USA, CA, Monterey Co., Monterey, v.1885, no habitat data, *leg*. W. G. Farlow | KT184846 ND |
| *Spongites tumidum* | UC 341301 isolectotype | USA, CA, Monterey Co., Monterey, v.1885, no habitat data, *leg*. W. G. Farlow | KT184847 ND |
| *Spongites yendoi* | UWC 09/157 | South Africa, Western Cape Province, Kalk Bay, 21.ix.2009, epilithic on primary bedrock, mid-intertidal, *leg*. G. W. Maneveldt & E. van der Merwe | KT184848 KT184832 |
| *Spongites yendoi* | UWC 11/38 | South Africa, Western Cape Province, Kalk Bay, 20.iv.2011, epilithic on primary bedrock, low intertidal, *leg*. G. W. Maneveldt | KT184849 JQ917422 |

**Table S2.** Uninformative morpho-anatomical characters among Australian (AUS), Northeast Pacific (USA) and South African (SA) species of *Spongites*, and *Spongites* species reported from Australia, but whose type localities are not in the southern hemisphere were not included. NA = not applicable. ND = no data.

| Character | *S. agulhensis* (This study, SA) | *S. decipiens* (This study, USA) | *S. hyperellus* (Penrose1996. AUS) | *S. impar* (Chamberlain 1994, SA) | *S. tumidum* (This study, USA) | *S. tunicatus* (Penrose 1996, AUS) | *S. yendoi* (Chamberlain 1993, SA) |
|---|---|---|---|---|---|---|---|
| Thallus thickness/height | to 650 µm | to 650 µm | ND | to 750 µm | to 860 µm | ND | to 1 mm (thicker in protuberances) |
| Basal cell shape (in radial view) | large and irregularly square, book-shaped | vary greatly in shape and size from squarish to rectangular to shoe-shaped | NA | NA | vary greatly in shape and size from oval to squarish to rectangular | non-palisade | NA |
| Basal cell length (radial view) | 10-29 µm | 10-28 µm | NA | NA | 6-20 µm | ND | NA |
| Basal cell width (radial view) | 10-22 µm | 7-25 µm | NA | NA | 9-27 µm | ND | NA |
| Basal cell shape | rectangular to | rectangular to | NA | NA | rectangular to | ND | NA |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| (tangential view) | palisade-like | palisade-like | | | palisade-like | | |
| Basal cell length (tangential view) | 10-22 µm | 7-25 µm | NA | NA | 10-42 µm | ND | NA |
| Basal cell diameter (tangential view) | 5-10 µm | 4-12 µm | NA | NA | 3-12 µm | ND | NA |
| Gametangial conceptacles | flush to slightly raised | flush to slightly raised | ND | flush | raised | NA | flush to raised |
| Spermatangial external diameter | 150-260(340) µm | 147-220 µm | ND | ND | 98-245 µm | NA | to 250 µm |
| Spermatangial chamber diameter | 98-160 µm | 78-123 µm | 109 µm | 150-200 µm | 123-169 µm | NA | 117-169 µm |
| Spermatangial chamber height | 25-40 µm | 25-60 µm | 55 µm | 35-40 µm | 27-51 µm | NA | 52-60 µm |
| Carpogonial conceptacle external diameter | 200-460 µm | ND | ND | NA | ND | NA | to 430 µm |
| Carpogonial conceptacle | 118-220 µm | ND | ND | NA | ND | NA | 138-234 (450) µm |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| chamber diameter | | | | | | | |
| Carpogonial conceptacle chamber height | 56-64 µm | ND | ND | NA | ND | NA | 52-109 µm |
| No. of cells in gonimoblast filament | 4-7 | ND | ND | NA | ND | NA | to 7 |
| Arrangement of gonimoblast filaments | peripheral | ND | ND | NA | ND | NA | peripheral |
| Tetrasporangial conceptacle | raised | raised (mostly) to slightly sunken | raised | flush | raised | flush | flush to raised |
| External diameter | 220-450 µm | 210-500 µm | ND | ND | 310-510 µm | ND | to 430 µm |
| Chamber diameter | 137-196 µm | 162-225 µm | 141-186 µm | 180-247 µm | 176-260 µm | 136-142 µm | 147-207 µm |
| Chamber height | 66-108 µm | 59-115 µm | 136-163 µm | 70-104 µm | 64-147 µm | 109-158 µm | 62-117 µm |
| Roof thickness (µm) | 29-47 µm | 20-37 µm | ND | 39-50 µm | 37-59 µm | ND | 26-65 µm |
| Old conceptacles buried/shed | shed | shed | ND | shed | shed | ND | buried and shed |

**Supplemental History**

*Spongites decipiens*

This species has a complicated history due to its incomplete original description and later descriptions that included more than one species, frequently from localities far distant from its type locality. Foslie (1897) originally described the species as *Lithothamnion decipiens* based on several small confluent crusts up to 200 µm thick and firmly adherent to a stone. Convex sporangial (presumably tetra/bisporangial) conceptacles were clearly described as multiporate, and conical gametangial conceptacles were present. Foslie (1900b) later transferred the species to *Lithophyllum* and subsequently (Foslie 1900c) also reported it from Fuegia (mouth of the Rio Grande, Argentina). Foslie (1900c) compared the color of the specimens from both California and Fuegia, so clearly he was describing material from both localities. Moreover, in a footnote Foslie (1900c) noted that the (multiporate) sporangial conceptacles that he described originally (Foslie 1897) do not belong to this species. Foslie (1906) later referred the Fuegia specimens to *L. decipiens* f. *subantarctica* and material from the West Indies to *L. decipiens* f. *caribaea* and noted that these two forms were weakly different from the California material. Foslie (1907) subsequently raised the two varieties to species, making the combinations *L. subantarcticum* (Foslie) Foslie (type locality: mouth of the Rio Grande, Argentina) and *L. caribaeum*[3] (Foslie) Foslie (type locality: St. Thomas Harbor, US Virgin Islands).

Referring likely to type material, Foslie (1909) described the anatomy of *L. decipiens*. Only Foslie’s 1897 (not including the sporangia, see above) and 1909 observations, however, are summarised in Table 2 as they alone undoubtedly appear to be based solely on type

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[3] *Lithophyllum caribaeum* is currently regarded as a taxonomic synonym of *Hydrolithon samoënse* (Maneveldt *et al.* 2015). For *L. subantarcticum*, Maneveldt (2005) argued that Mendoza & Cabioch’s (1986) descriptions of thalli (as *Hydrolithon subantarcticum*) collected from subantarctic and Antarctic zone Argentina matched the present-day characterisation of the genus *Pneophyllum*, but that the type material (particularly tetrasporangial) of *L. subantarcticum* was insufficient to come to any conclusion about the identity of the specimen.

material. Subsequent to Foslie, Levring (1943) reported the species from Juan Fernandez Island.

Dawson (1944) collected and sectioned tetrasporangial material from the northern Gulf of California that he identified as *L. decipiens*. Mason (1953) described the anatomy of *L. decipiens*, but her description included material based on two heterotypic synonyms, *L. impressum* Foslie (type locality: "Botany Beach", south of Port Renfrew, Vancouver Island, British Columbia, Canada) and *L. incrustans* f. *orbiculare* Foslie in Setchell & Gardner (1903: 358) non *Lithophyllum orbiculatum* (Foslie) Foslie (type locality: Kristiansund, Norway). Mason (1953) designated the W. A. Setchell #1482 material in TRH (as Herb. Mus. Nidaros) as type (lectotype) and cited UC 736372 (Fig. 2) as an isotype (isolectotype) of *L. decipiens*, and she gave the distribution as British Columbia, Canada to La Jolla, California, USA. Dawson (1960) noted that this species was one of the most common intertidal crustose corallines along the Pacific coast of Baja California, Mexico, and he expanded the distribution south to Panama and the depth profile to 14 meters. Masaki (1968) reported *L. decipiens* from two prefectures (Kochi and Wakayama) in Japan.

In a revision of the Foslie crustose coralline herbarium, Adey (1970) transferred *L. decipiens* to *Hydrolithon* (Foslie) W.H. Adey, commenting that the perithallial (cortical) cells were not as regular as other species in that genus. Mendoza & Cabioch (1986), in their treatment of *Hydrolithon* from the Antarctic and subantarctic regions adjacent to Argentina, recognised both *H. decipiens* and *H. subantarcticum* (Foslie) Mendoza & Cabioch, the latter based on *Lithophyllum decipiens* f. *subantarctica*. They distinguished these species based on thallus color, the clustering of conceptacles, size of perithallial (cortical) cells and abundance of trichocytes. Steneck & Paine (1986) subsequently transferred *H. decipiens* to *Pseudolithophyllum* Me. Lemoine due to the absence of trichocytes and the variable nature of the hypothallial (medullary) cells in the latter, both of these characters, they believed to be present in *P. decipiens* (Table 2). Steneck and Paine (1986) regarded *P. decipiens* as a warm water species, not present north of Point Conception, California, USA.

Throughout his writings, Foslie (1901a, 1904, 1906, 1907) repeatedly questioned whether *L. decipiens* and *L. yendoi* (Foslie) Foslie, first described *as Goniolithon yendoi* Foslie (1900a, type locality: Shimoda Harbor, Shimoda Prefecture, Japan), were distinct species, as did Dawson (1960) and Masaki (1968). This led Chamberlain (1993) to undertake a study of the type material of both species as well as field-collected material in South Africa identified by her as *S. yendoi*. Chamberlain (1993) concluded that all of the type material belonged to *Spongites*, but that *S. decipiens* type material with dimerous thallus construction was distinct from *S. yendoi* type material with monomerous thallus construction (Table 1). Chamberlain (1993) further noted that *S. decipiens* was now known only from San Pedro, CA, USA (type locality) and collections from Argentina and the Falkland Islands (described by Mendoza & Cabioch 1986), whereas *S. yendoi* occurred in Japan, South Africa and Pacific Mexico.

### *Spongites yendoi*

Beginning with its original description as *Goniolithon yendoi*, this species has been reported from very distant localities, namely Shimoda Harbor and Otaru, Japan and Monterey, California, USA (Foslie 1900a). Material from the two aforementioned localities in Japan was sent to Foslie by K. Yendo, whereas the Monterey material was collected by W. G. Farlow and is now located in Bornet's herbarium in Paris (PC). We do not know, however, which material formed the basis of Foslie's description. Clearly Foslie (1900a) had the Japanese material in hand, but may also have included observations on the California material. Foslie (1900a) described *G. yendoi* as suborbicular to irregular, thin, smooth and purplish when young, but becoming increasingly uneven and warty when older. Conceptacles were described as subhemisperic-conical and here and there crowded on the surface. Foslie (1900b) subsequently transferred *G. yendoi* to *Lithophyllum*, and then (Foslie 1904) reported *L. yendoi* from seven additional localities in the Malay Archipelago, wherein he also presented type material from Japan (Pl. XI, fig. 1). Foslie (1904) noted that the Malay Archipelago material was fully in agreement with Japanese material, but that some cells were a little larger. Much later, Masaki (1968) provided a detailed description of *L. yendoi* based on material from Kochi Prefecture, Japan, but there is no indication that he examined type material. Chamberlain (1993), based on her morpho-anatomical observations of type material from Japan in TRH and on field-collected material from South Africa, as well as on comparative measurements reported by Masaki (1968) from Japan that he called *L. decipiens* and *L. yendoi*, and Dawson (1960) from Pacific Mexico that he called *L. decipiens*, concluded that both *L. decipiens* and *L. yendoi* belonged in *Spongites*, but that both species were distinct.

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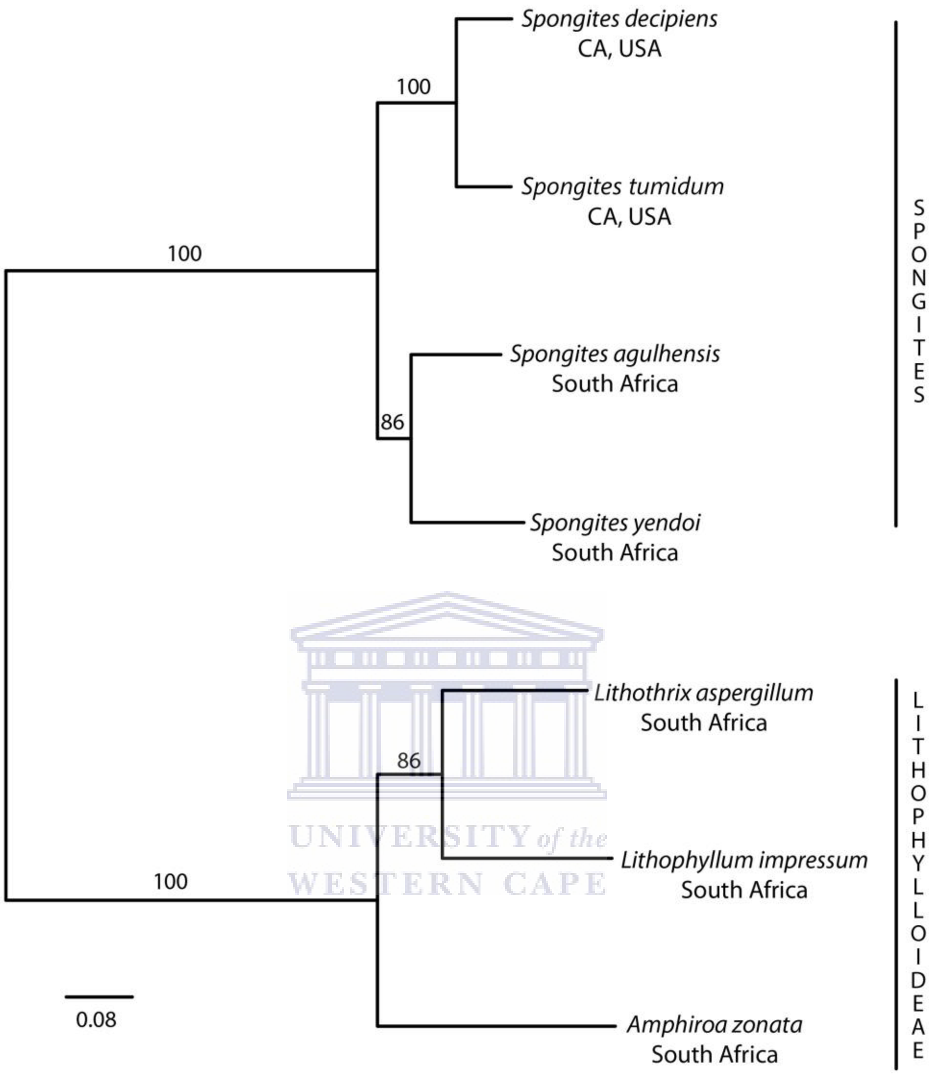
*Spongites decipiens*
CA, USA
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*Lithothrix aspergillum*
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*Lithophyllum impressum*
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*Amphiroa zonata*
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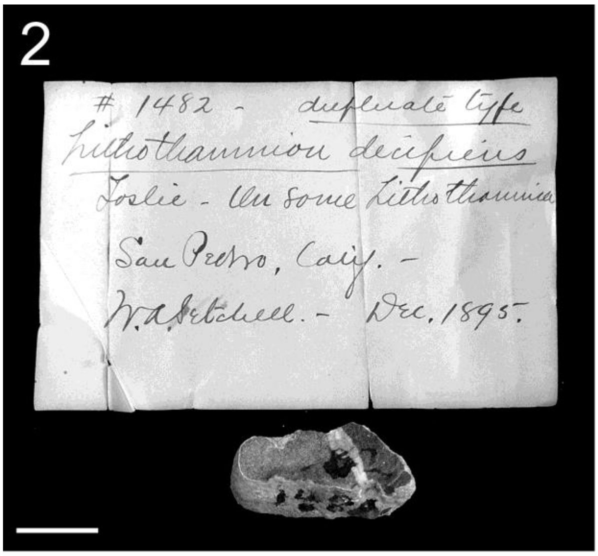
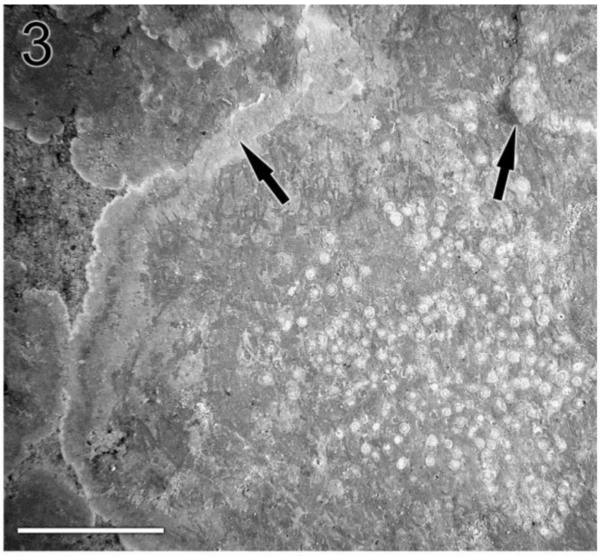
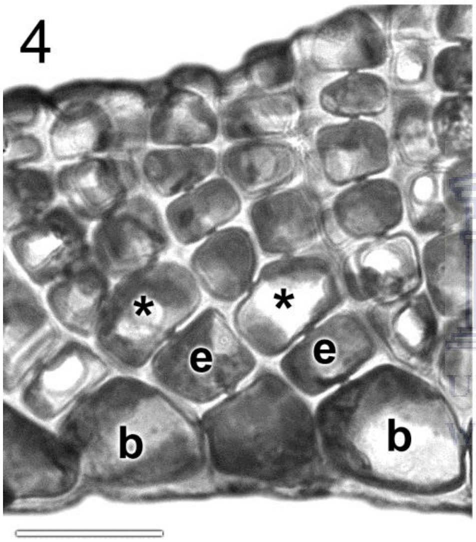
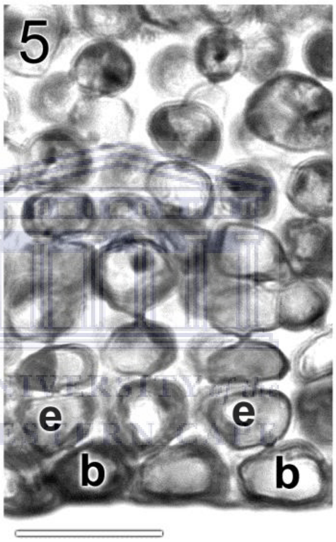
SPONGITES
LITHOPHYLLOIDEAE

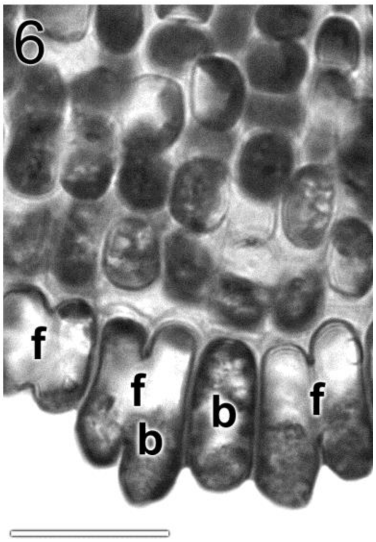


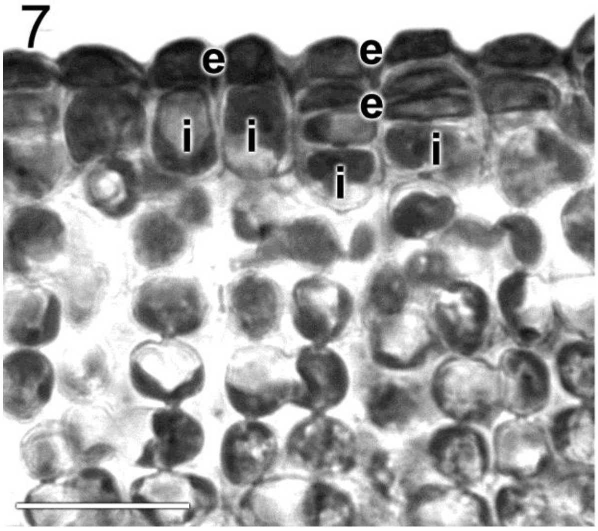
\# 1482 - duplicate type
Lithothamnion decipiens
Foslie - On some Lithothamnia
San Pedro, Calif. -
W.A. Setchell. - Dec. 1895.

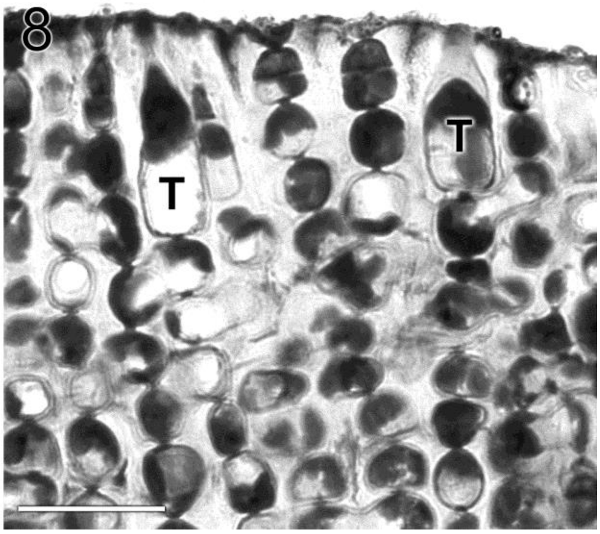












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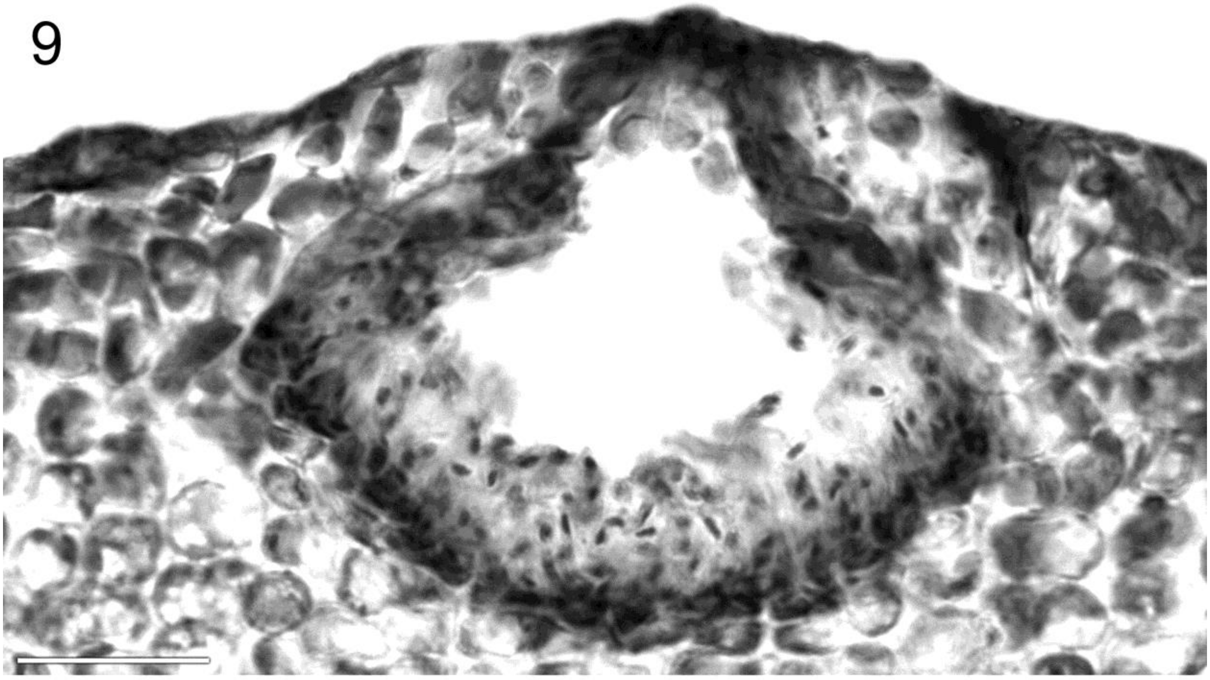

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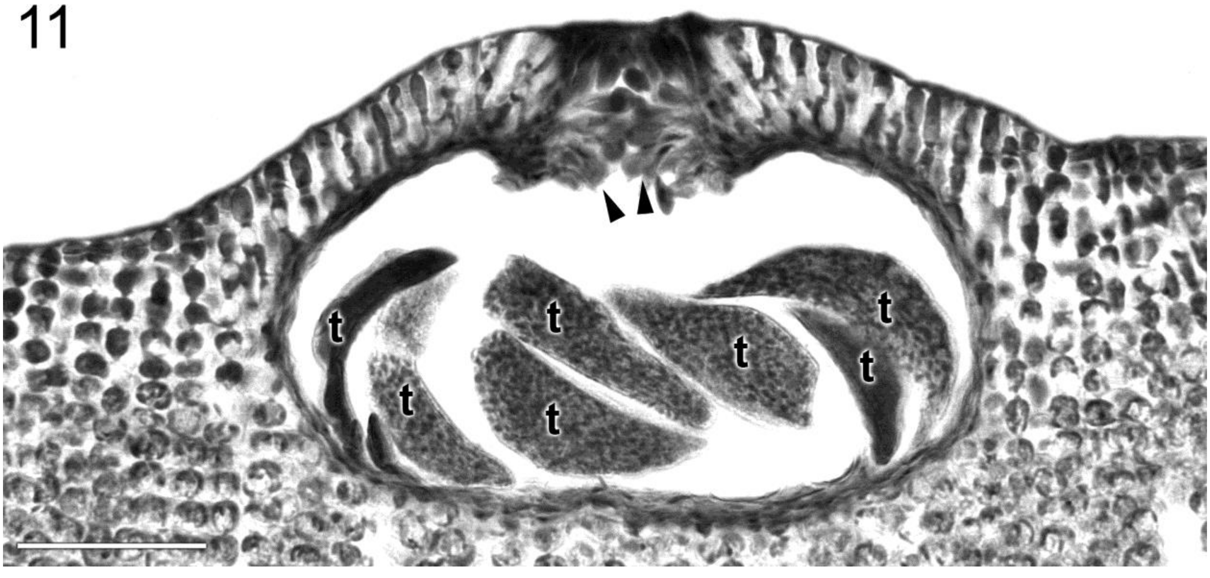

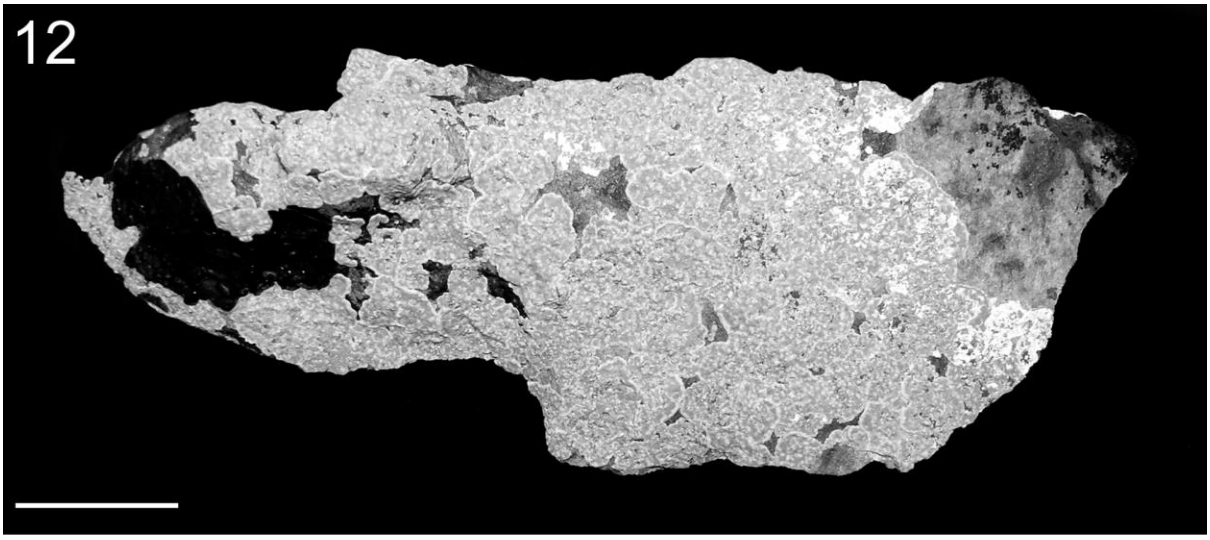
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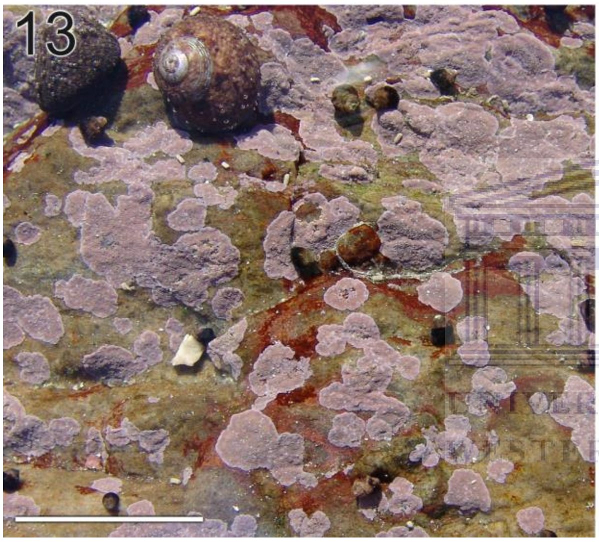
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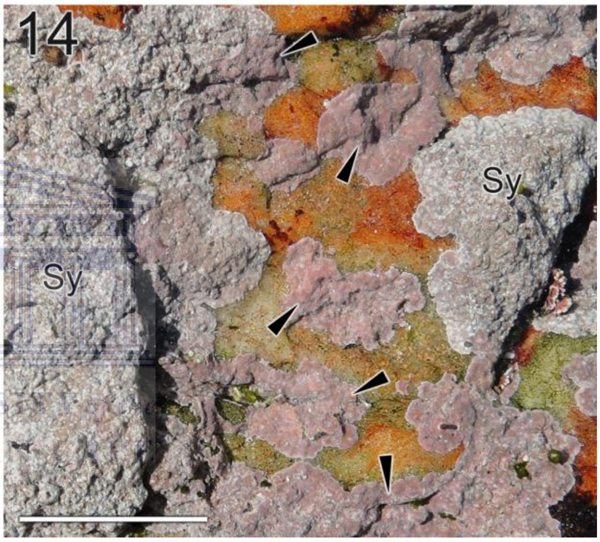
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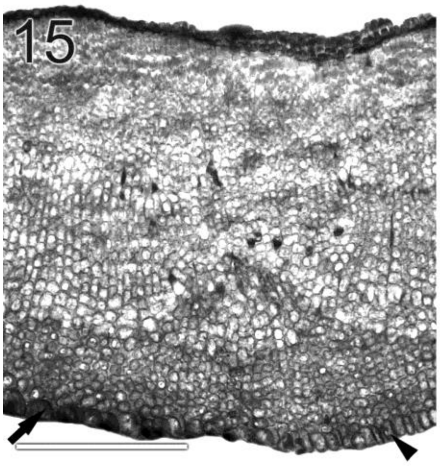
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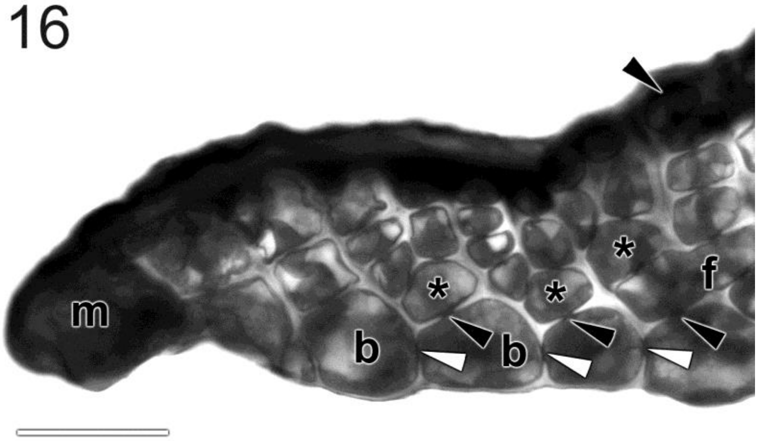
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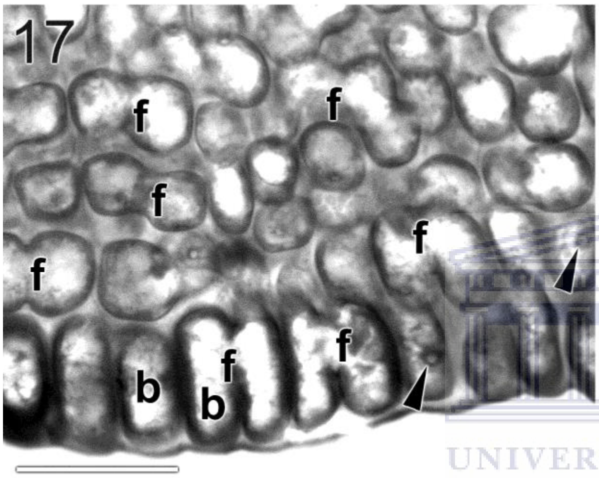
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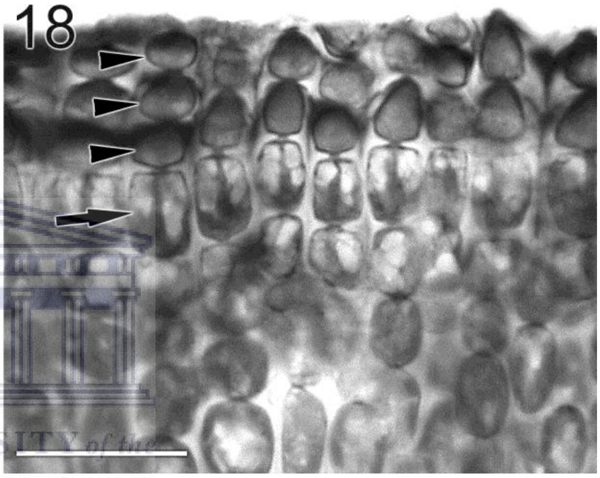
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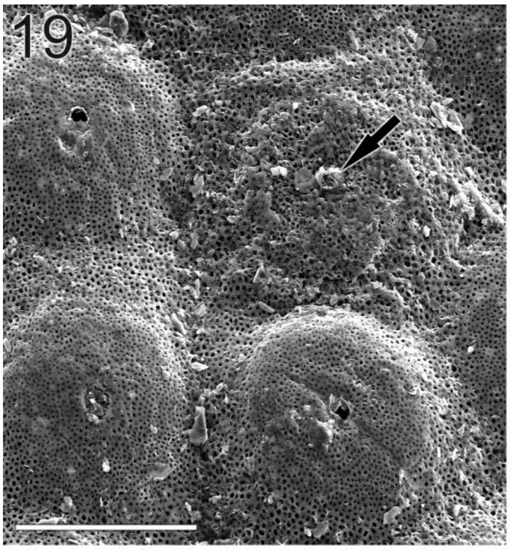
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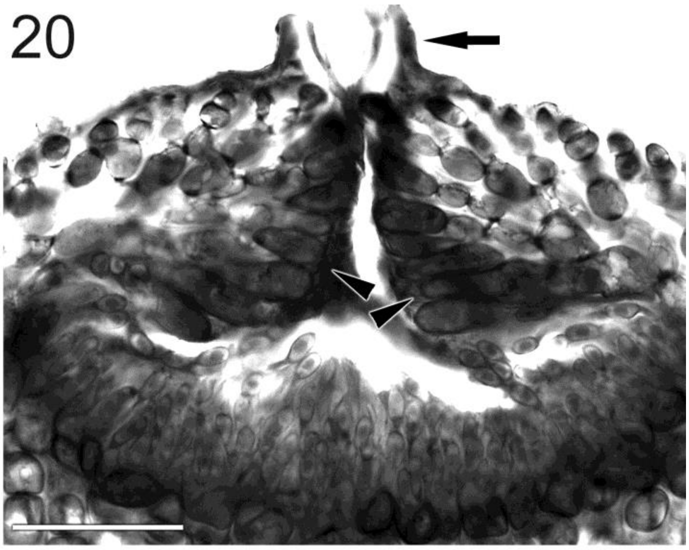
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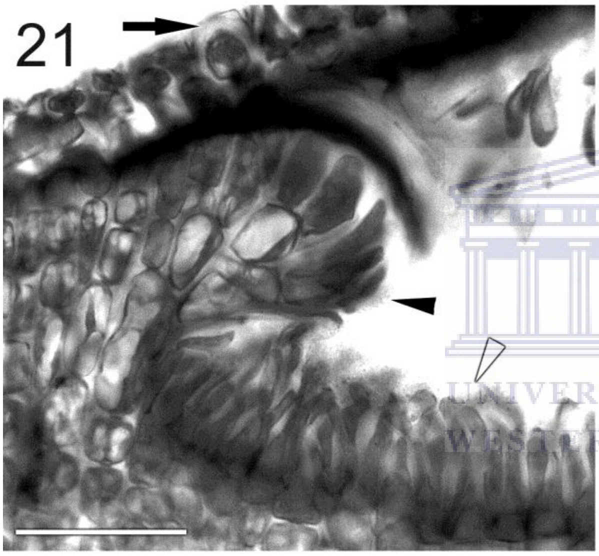
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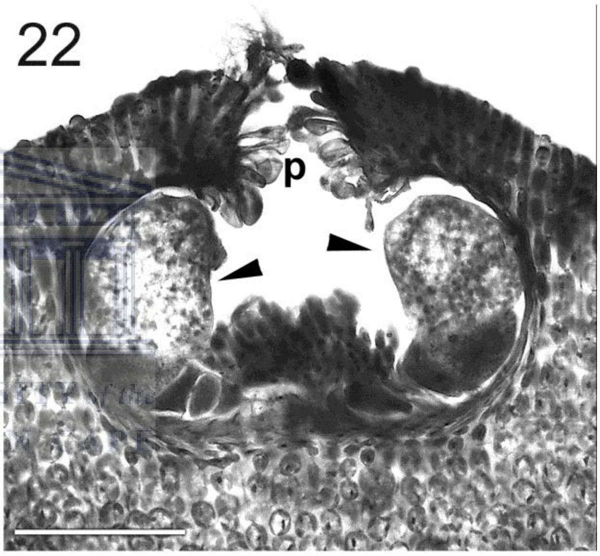
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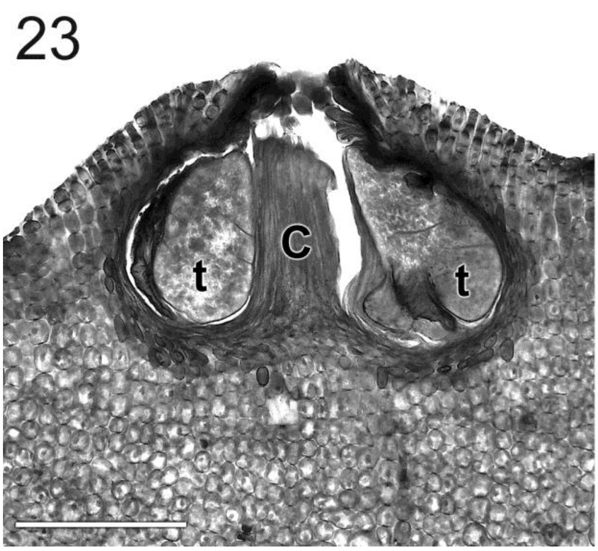
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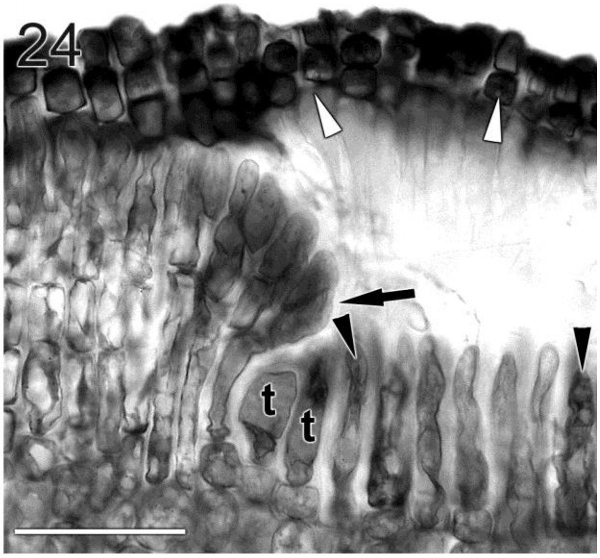
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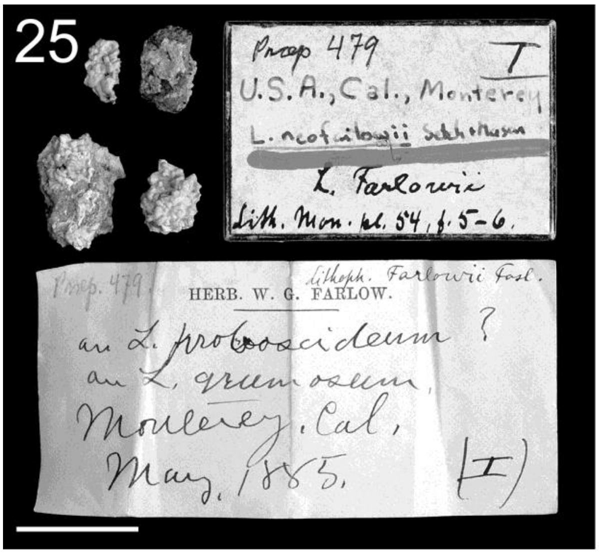
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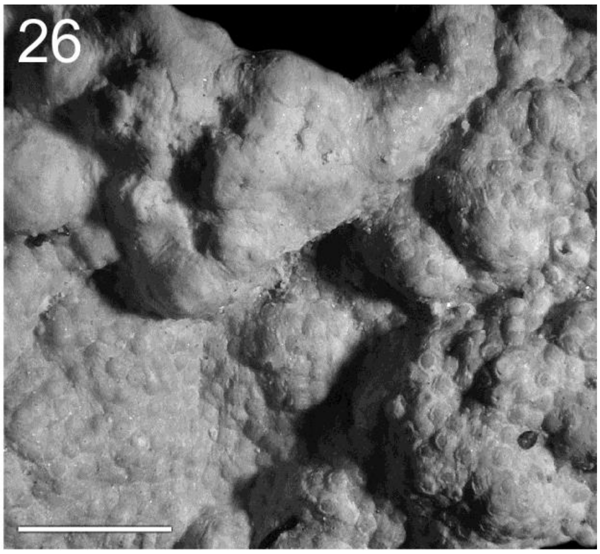
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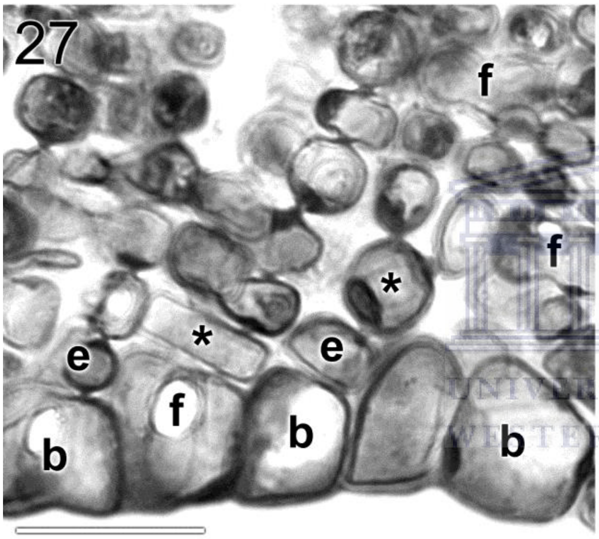
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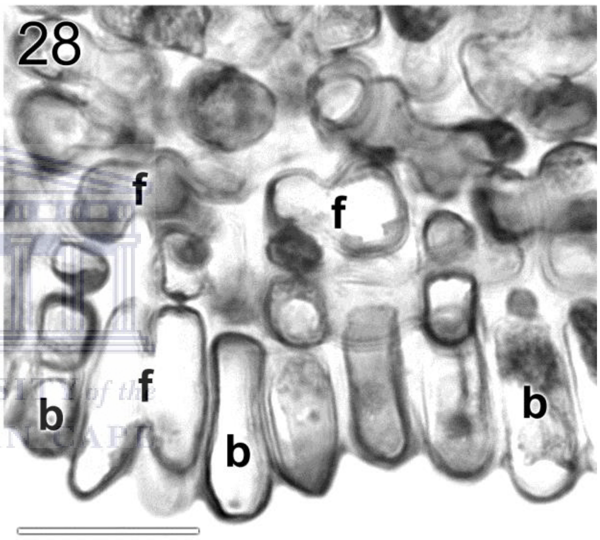
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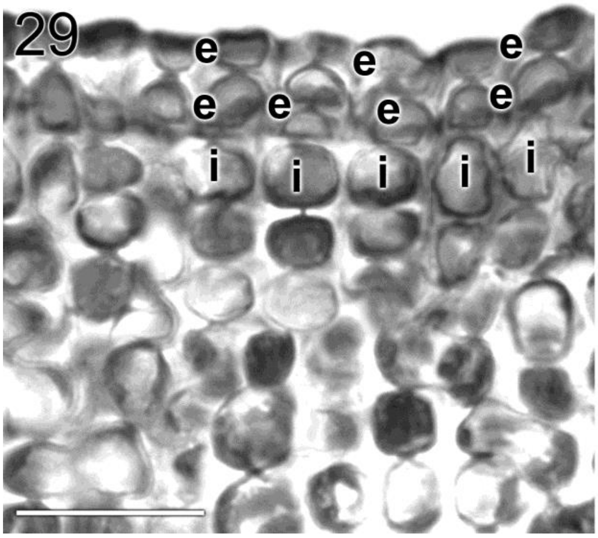
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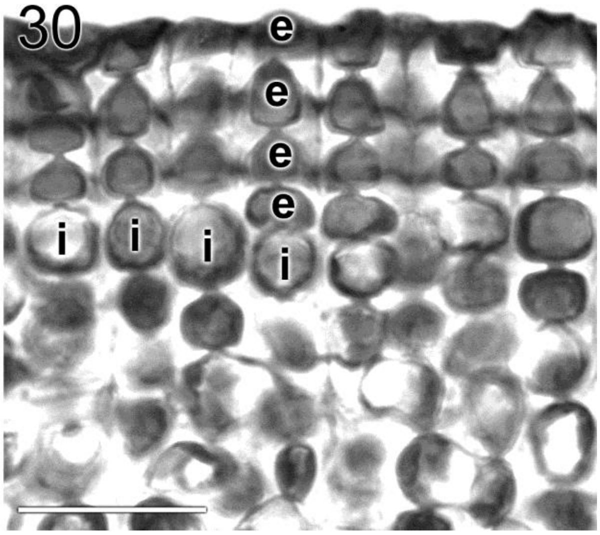
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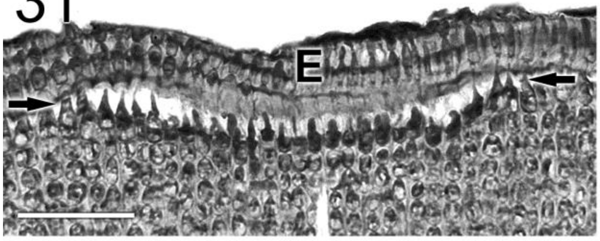
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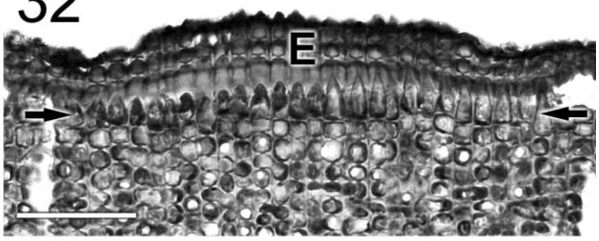
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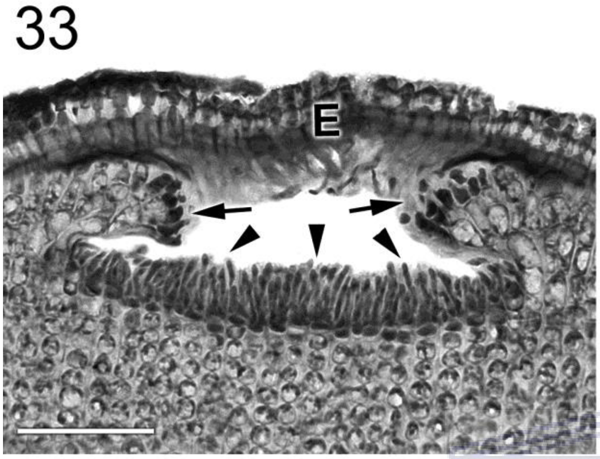
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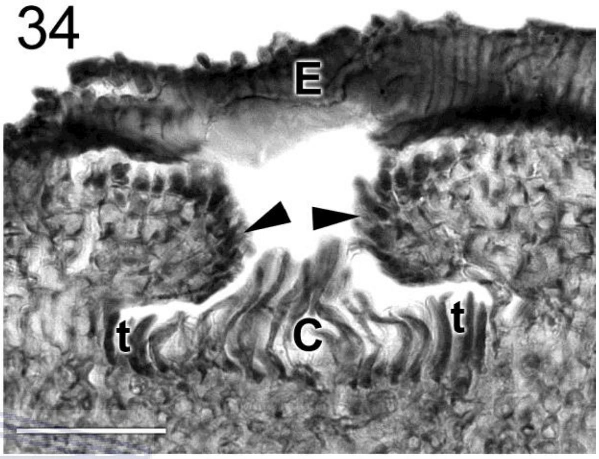
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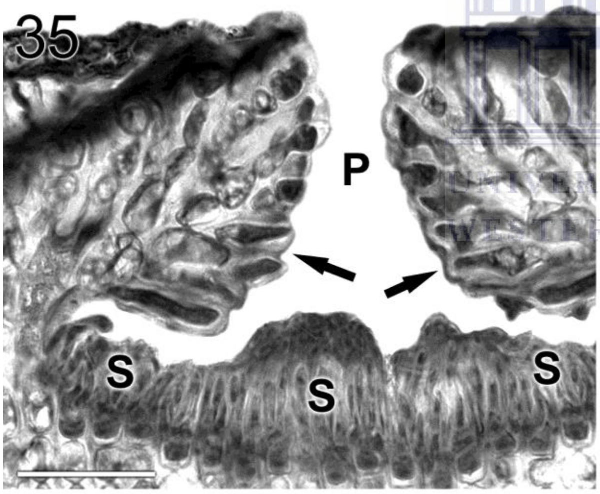
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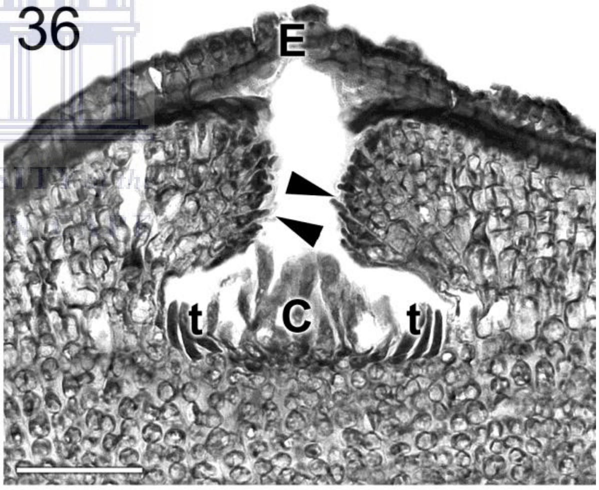
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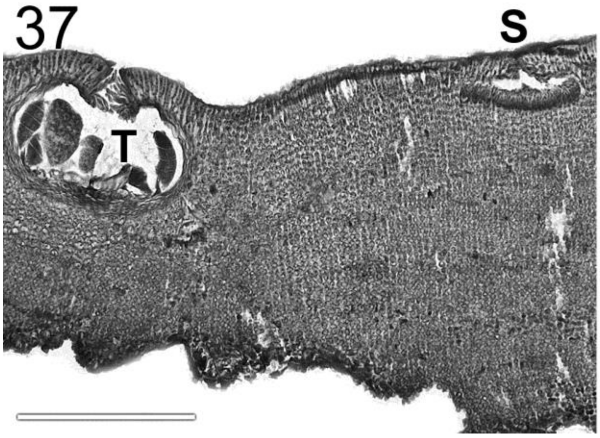
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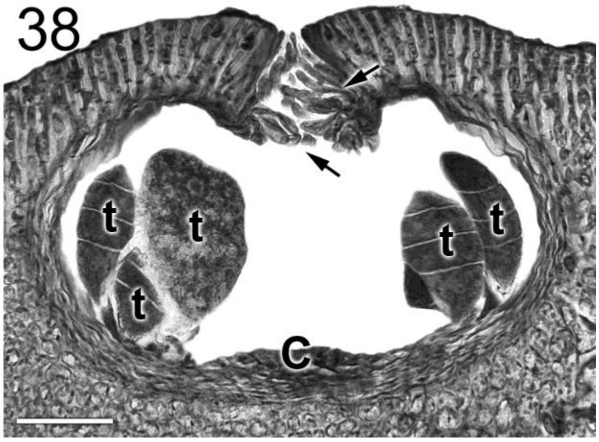
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## Chapter 5: Paper 4

# A modern account of the South African non-geniculate Lithophylloideae (Corallinales, Corallinophycidae, Rhodophyta)

This chapter is currently in press:

Van der Merwe, E. & Maneveldt, G.W. 2015. A modern account of the South African non-geniculate Lithophylloideae (Corallinales, Corallinophycidae, Rhodophyta). *South African Journal of Botany*: in press.

## Chapter 5: Paper 4

# A modern account of the South African non-geniculate Lithophylloideae (Corallinales, Corallinophycidae, Rhodophyta)

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Running Head: The South African non-geniculate Lithophylloideae

## Abstract

Of the genera within the coralline algal subfamily Lithophylloideae, the genera *Lithophyllum* and *Titanoderma* have probably been the most contentious in recent years. Two opposing taxonomic views currently exist. One view considers *Titanoderma* to be a heterotypic synonym of *Lithophyllum*, arguing that the morphological criteria proposed to separate the two genera do not stand up to rigorous testing. The other view, which is increasingly being supported by molecular data, considers *Titanoderma* and *Lithophyllum* to be distinct genera. Based on our study of numerous recently collected specimens and of detailed published accounts on the genera, we support the separation of *Titanoderma* from *Lithophyllum* as we found no difficulty in assigning species to either genus on the basis of the characters proposed to separate them. Three species of *Lithophyllum* (*L. acrocamptum*, *L. incrustans*, *L. neoatalayense*) and three species of *Titanoderma* (*T. corallinae*, *T. polycephalum*, *T. pustulatum*) are currently reported to occur in South Africa. Here we present detailed illustrated accounts of the species, including: first time detailed descriptions for South African *T. corallinae* and *T. pustulatum*; new data on female and carposporangial conceptacles; and comparisons from other geographical locations where the same species have been described in detail. A key for identifying South African specimens is included. Our data support the characterisation of the genus *Titanoderma* separate from *Lithophyllum*.

**Keywords:** *Lithophyllum*; *Lithophyllum acrocamptum*; *Lithophyllum incrustans;* *Lithophyllum neoatalayense*; taxonomy; *Titanoderma*; *Titanoderma corallinae*; *Titanoderma polycephalum*; *Titanoderma pustulatum*.

## 1. Introduction

Within the family Corallinaceae (Corallinales, Corallinophycidae, Rhodophyta) the subfamily Lithophylloideae Setchell is characterised by thalli in which contiguous vegetative filaments are joined primarily by secondary pit connections; cell fusions are absent or comparatively rare (Harvey et al., 2003). The Lithophylloideae is the only subfamily that comprises both geniculate and non-geniculate genera. In geniculate forms, genicula are composed of one to several tiers of cells and cortication may be present or absent (Harvey et al., 2003).

The Lithophylloideae are quite specious and, depending on which classification system is followed, currently comprises five (*Amphiroa* J.V.Lamouroux, *Ezo* W.H.Adey, T.Masaki & Akioka, *Lithophyllum* Philippi, *Lithothrix* J.E.Gray, *Paulsilvella* Woelkerling, Sartoni & Boddi) to six (including *Titanoderma* Nägeli) extant genera. Of the genera within the Lithophylloideae, the non-geniculate genera *Lithophyllum* and *Titanoderma* have probably been the most contentious in recent years. Campbell and Woelkerling (1990) and Woelkerling and Campbell (1992) consider *Titanoderma* to be a heterotypic synonym of *Lithophyllum*, arguing that the morphological criteria proposed to separate the two genera do not stand up to rigorous testing. However, Chamberlain and Irvine (1994) and Chamberlain (1996) consider *Titanoderma* to be a distinct genus from *Lithophyllum*. Chamberlain (1996) argued that "although it is difficult to assign the southern Australian species *L. johansenii* Woelkerling et Campbell to either genus, nevertheless two distinct lines of development are considered to be present, and maintaining both genera pending more conclusive, probably genetic, data to determine their relationship is preferable." The molecular evidence currently available (see Bailey, 1999; Bittner et al., 2011) supports Chamberlain's (1996) findings and favours placing the type species of *Lithophyllum* and *Titanoderma* in separate genera. We support this latter view and use the following criteria (after Woelkerling, 1988; Chamberlain, 1991, 1996; Chamberlain and Irvine, 1994) to distinguish between the genera *Lithophyllum* and *Titanoderma*:

1) the possession of a basal layer consisting predominately of non-palisade cells (*Lithophyllum*) as opposed to a basal layer of predominantly palisade cells throughout, except sometimes near the margin (*Titanoderma*); and

2) no areas of bistratose thallus present, as the thallus begins to thicken immediately behind the primary meristematic cell (*Lithophyllum*) as opposed to a thallus partly to entirely bistratose (consisting of a basal cell and an epithallial cell) (*Titanoderma*).

Although the majority of the South African non-geniculate Lithophylloideae have previous been described in detail, two (*T. corallinae* and *T. pustulatum*) have not, these latter two species having only been listed to occur along the South African coastline (see Maneveldt et al., 2008). Furthermore, *L. incrustans* previously reported has not been encountered during this research despite extensive collections. This paper presents a modern, detailed account with new information of the non-geniculate coralline algal species ascribed to the genera *Lithophyllum* and *Titanoderma* for South Africa.

## 2. Materials & Methods

Field collections (sampled during 1990-1995 and 2008-2011) were made throughout the intertidal and shallow subtidal zones of the Western, Eastern and KwaZulu-Natal Provinces of South Africa. Thalli were examined as far as possible when fresh; otherwise they were air-dried or fixed in neutralized 10 % commercial formalin seawater (4 % formaldehyde) and stored in a 70 % ethanol: 10 % glycerol: 20 % distilled water solution.

Specimens for microscopy were prepared following Maneveldt and van der Merwe (2012). For light microscopy, formalin preserved specimens were first decalcified in 10 % nitric acid. Thereafter, specimens were immersed in 70 %, 90 % and 100 % ethanol solutions respectively for a minimum of 60 mins each in order to displace any water and acid in the specimens. Thereafter, each specimen was removed from the 100 % ethanol and allowed to air dry for no more than a few seconds. Specimens were then immersed in Leica Historesin filtration medium for several hours (3-6 h) until completely infiltrated. A hardening solution was then added to the infiltration medium and the specimens orientated in this final solution until set. Gelling of the hardener usually occurred within 30-45 mins; for more rapid hardening, specimens were placed immediately in an oven at 60 °C for approximately 10-20 mins.

Specimens were then sectioned at 8-10 µm thickness using a Bright 5030 microtome. Individual cut sections were removed from the microtome blade using a fine sable hair brush and transferred to a slide covered with distilled water. In this way, multiple sections were orientated on a single slide. Slides were then left to air dry for at least 24 hrs. Once dried, slides bearing sections were stained with toluidine blue (0.25 g borax/100 ml and 0.06 g toluidine blue/100 ml) that was previously filtered to prevent dye crystal formation, again left to air dry, and later covered with cover slips using DPX Mountant for microscopy (BDH Laboratory Supplies, England).

In cell measurements, length denotes the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this.  Conceptacle measurements follow Adey and Adey (1973).  Thallus anatomical terminology follows Chamberlain and Irvine (1994).  Morphological (growth forms) terminology follows Woelkerling et al. (1993).  Typification data follow Woelkerling (1993).  Herbarium abbreviations follow Thiers (2015, continuously updated).

Collection data are presented firstly according to geographic location from west to east, followed by date of collection within a region (earliest first), and finally by collection number on a particular day.

## 3. Generic Concept and Species Accounts

### 3.1. *Lithophyllum* Philippi, 1837 and *Titanoderma* Nägeli, 1858

*Lithophyllum*, as characterised by Chamberlain and Irvine (1994: 59), collectively comprise specimens that are non-geniculate and of variable growth form. Thalli are pseudoparenchymatous, dorsiventral, primarily dimerous (but may be secondarily monomerous), and composed of a single basal layer of predominantly non-palisade cells; are not bistratose; and the outermost walls of terminal epithallial cells are rounded or flattened, but not flared. Gametangial conceptacles with simple (unbranched) spermatangial systems that are confined to the conceptacle floor; and carposporangial conceptacles with a central fusion cell bearing peripherally arranged gonimoblast filaments.

*Titanoderma*, as characterised by Chamberlain and Irvine (1994: 88), collectively comprise specimens that are non-geniculate and of variable growth form. Thalli are pseudoparenchymatous, dorsiventral, primarily dimerous (but may be secondarily monomerous), and composed of a single basal layer of predominantly sinuous palisade cells; margins are bistratose (composed of a single layer of sinuous palisade basal cells plus a single layer of epithallial cells only); and the outermost walls of terminal epithallial cells are rounded or flattened, but not flared. Gametangial conceptacles with simple (unbranched) spermatangial systems that are confined to the conceptacle floor; and carposporangial conceptacles with a central fusion cell bearing peripherally arranged gonimoblast filaments. Based on Chamberlain and Irvine's (1994) characterisation, *Lithophyllum* and *Titanoderma* are distinguished from each other by the nature of the basal layer (predominantly palisade vs. predominantly non-palisade) and the presence/absence of a bistratose margin.

The five other genera of the Lithophylloideae differ from *Lithophyllum* and *Titanoderma* in the following ways. *Amphiroa* and *Lithothrix* comprise only geniculate species. *Ezo* is the only genus whose species are known to produce haustoria. Species of *Paulsilvella* are characterised by possessing protuberant branches that resemble a series of fused beads that are entirely monomerous, and with a core region composed of single arching tiers of elongate, columnar cells alternating with two tiers of short, non-columnar cells. *Tenarea*, currently regarded as a taxonomic synonym of *Lithophyllum* by Schneider and Wynne (2007), have species bearing a unique isobilateral organisation composed of a stratified core of palisade cells. Based on the Chamberlain and Irvine (1994) characterisation, *Tenarea* is probably more closely allied to *Titanoderma* than to *Lithophyllum*.

Like all members of the Corallinales, *Lithophyllum* and *Titanoderma* bear multiple zonately divided tetra/bisporangia in roofed conceptacles. Like all members of the Corallinaceae, tetra/bisporangia are produced in uniporate conceptacles that lack apical pore plugs. Like all members of the Lithophylloideae, contiguous vegetative filaments are joined primarily by secondary pit connections; cell fusions are absent or comparatively rare.

*Lithophyllum* is typified by *Lithophyllum incrustans* Philippi.

*Titanoderma* is typified by *Titanoderma pustulatum* (J.V.Lamouroux) Nägeli.

## 3.2. Identification key to the South African non-geniculate Lithophylloideae.

This identification key (modified from Maneveldt et al., 2008) is designed for South African specimen identification only and the characters used in the key are not necessarily diagnostic of the species to which they pertain.

1. Basal filaments composed of predominantly non-palisade cells; primary and regenerating thallus lacking a bistratose margin ....………………………..……................................. 2

   Basal filaments composed of predominantly palisade cells; primary and regenerating thallus possessing a bistratose margin .....……..……………..………………..…………...… 4

2. Tetra/bisporangial conceptacle pore lined with long, vertically orientated filaments ……………………….…………...……………….…........... *Lithophyllum neoatalayense*

   Tetra/bisporangial conceptacle pore unelaborated or lined with papillate cells orientated more or less parallel to roof surface ..………………………........................................ 3

3. Tetra/bisporangial conceptacle roof 3 - 5 cells thick, pore canal short, tapering markedly towards the pore …..……………………………………… *Lithophyllum acrocamptum*

   Tetra/bisporangial conceptacle roof 6 - 17 cells thick, pore canal long, with more or less parallel sides ….…………………………………..….……..... *Lithophyllum incrustans*

4. Thalli epilithic, lumpy, becoming massive and protuberant .......................................................................................... *Titanoderma polycephalum*

   Thalli mainly epiphytic, sometimes epilithic or epizoic, comprising thin, encrusting, featureless thalli ……………….……………………………………………..………….. 5

5. Tetra/bisporangial conceptacles more or less flush with surrounding thallus surface or only slightly raised above it, conceptacle floor immersed up to 7 cells deep in thallus ………………………………………………………..……….. *Titanoderma corallinae*

   Tetra/bisporangial conceptacles markedly raised above the surrounding thallus surface, conceptacle floor immersed no more than 3 cells deep in thallus ……………………..…………………………………………… *Titanoderma pustulatum*

### 3.3. ***Lithophyllum acrocamptum*** **Heydrich, 1902: 474**

(Figs. 1-13)

Basionym: *Lithophyllum acrocamptum* Heydrich, 1902: 474.

Synonyms: *Lithophyllum incrustans* f. *incrassatum* Foslie, 1900c: 28 (as f. *lobata*), 29 (as f. *incrassata*); *Lithophyllum incrassatum* (Foslie) Foslie, 1909: 18-20; *Lithothamnion incrassatum* (Foslie) Jadin, 1935: 171.

Holotype: PC unnumbered, slides 850-851. Fort-Dauphin (Taolanaro), Madagascar, collected by Ferlus, undated (Woelkerling, 1998: 299), illustrated in Printz (1929: pl. 57, fig. 14). Holotype fragments exist in TRH (A6-264) (see Woelkerling et al., 2005: 54).

Etymology: '*acrocamptum*' from the Greek words '*acros*', meaning at the tip, end or summit and '*camptos*', meaning bent or curved (Stearn, 1973). Heydrich (1902) did not explain the origin of the epithet, but twice makes reference to the distinctive curving of the tips of the protuberances. The epithet is therefore more than likely derived from this feature (Woelkerling *pers. com.*).

#### *3.3.1. Specimens examined*

In total, nine (9) specimens were examined, these representing our entire collection for this taxon.

South Africa. Western Cape Province: Struisbaai, epilithic on boulders in low shore tide pools (06.vii.2009, *G.W. Maneveldt & E. van der Merwe*, UWC 09/101; 07.vii.2009, *G.W. Maneveldt & E. van der Merwe*, UWC 09/128).

South Africa. Eastern Cape Province: Tsitsikamma, Grootbank, epilithic on primary bedrock in infratidal gullies (10.iv.2008, *G.W. Maneveldt & U. van Bloemestein*, UWC 08/39). Kei Mouth, epilithic on primary bedrock and boulders in mid shore tide pools

(11.vii.2010, *G.W. Maneveldt* & *E. van der Merwe*, UWC 10/215; 11.vii.2010, *G.W. Maneveldt & E. van der Merwe*, UWC 10/216). Morgan Bay, epilithic on boulders and primary bedrock in low shore gullies (12.vii.2010, *G.W. Maneveldt & E. van der Merwe*, UWC 10/220). Port Alfred, epilithic on primary bedrock in low shore gullies inundated with sand (07.iv.2011, *G.W. Maneveldt, E. van der Merwe & C. Padua*, UWC 11/28; 07.iv.2011, *G.W. Maneveldt, E. van der Merwe & C. Padua*, UWC 11/30). Qolorha, epilithic on primary bedrock in shallow subtidal gullies (13.vii.2010, *G.W. Maneveldt & E. van der Merwe*, UWC 10/231).

### *3.3.2. Distribution*

The species is reported from the western to the central Indian Ocean. See Guiry and Guiry (2015) for a detailed distribution with sources. In South Africa the species has been recorded from the Western Cape Province (Struisbaai) to the KwaZulu-Natal Province (Umdloti) (also see Maneveldt et al., 2008).

### *3.3.3. Habit*

Thalli are non-geniculate, and epilithic on the primary bedrock and on boulders. Thalli are loosely adherent, thick, easily removed from the substrate and are often invaded by burrowing organisms. Freshly collected living specimens are variable in colour ranging from grey-pink to maroon to brown; thalli are often also whitish due to epithallial shedding. Thalli vary from being encrusting (smooth) to lumpy to bearing knobbly protuberances (Fig. 1). Thalli measure up to 50 mm thick with protuberances that measure up to 7 mm in height and 10 mm in diameter.

### *3.3.4. Vegetative anatomy*

The thallus is pseudoparenchymatous, dorsiventrally organised and dimerous, and haustoria are absent (Fig. 2). The single basal layer comprises non-palisade cells that are slightly wider than they are long (Fig. 2). Cells of erect filaments are squat to square to rectangular and these arise from the basal layer, comprising the bulk of the thallus (Figs. 2-5). Cells of contiguous basal and erect filaments are joined by secondary pit connections (Figs. 3 and 4); cell fusions have not been observed. Subepithallial initials are squat to square to rectangular and are no different to cells subtending them (Figs. 4 and 5). Epithallial cells generally occur in a single layer (up to 3 when shedding) and are rounded to elliptical (Figs. 4 and 5). Data on measured vegetative characters are summarised in Table 1.

### *3.3.5. Reproductive anatomy*

Gametangial thalli are dioecious. Spermatangial (male) conceptacles are raised above the surrounding thallus surface (Fig. 6). Their chambers are wide and shallow to flask shaped. The conceptacle roof is formed from filaments that arise peripheral to the fertile area (Fig. 7), the terminal initials of which are more elongate than their inward derivatives. As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate. These cells project into the pore canal and are orientated more or less parallel or at a sharp angle to the conceptacle roof surface in fully developed conceptacles. Throughout the early development a protective layer of epithallial cells surrounds the young developing conceptacle; this protective layer is shed once the pore canal is fully developed. The pore opening in fully developed conceptacles is often occluded by a mucilage plug. Unbranched (simple) spermatangial systems develop only across the floor of mature male conceptacles (Fig. 6). Male conceptacles become buried, containing apparently viable spermatangial systems (Figs. 6 and 7).

Carpogonial (female) conceptacles are also raised above the surrounding thallus surface (Fig. 8). Their chambers are elliptical. Carpogonial conceptacle development is similar to that of the male conceptacles (Fig. 9). Carpogonial branches develop across the floor of the mature conceptacle chamber, and comprised a single support cell and a hypogynous cell bearing a carpogonium extended into a trichogyne (Fig. 8). Sterile cells are also present on the hypogynous cell.

After presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles (Fig. 10). Carposporangial conceptacles are comparatively large. Their chambers are rounded to elliptical, but with flattened bottoms presumably caused by the growth of the expanding gonimoblast filaments. The pore canal is lined by inflated papillate cells that project into the pore canal, but that do not occlude it (Fig. 10). The near solid central fusion cell is discontinuous, thick and narrow, and several-celled gonimoblast filaments (incl. a terminal carposporangium) develop along the periphery of the conceptacle chamber (Figs. 10 and 11). The remains of unfertilized carpogonia persist across the dorsal surface of the fusion cell. Senescent carposporangial conceptacles from our specimens appear to be shed as no buried conceptacles were observed.

Tetrasporangial conceptacles are uniporate, and are mostly flush to slightly raised to slightly sunken below the thallus surface (Fig. 12). Conceptacle primordia have not been observed. However, roof development appears to be from filaments both peripheral to the fertile area as well as from filaments interspersed amongst the developing tetrasporangia (Fig. 13). The conceptacle roof in mature conceptacles is 39-69 μm thick and composed of 3-5 (mostly 5, including an epithallial cell) cells (Fig. 12). Conceptacle chambers are more or less dumbbell-shaped as a result of an extensive central columella and zonately divided tetrasporangia occur peripherally around the central columella (Figs. 12 and 13). Pore canal cells are papillate, distinctly enlarged and balloon-like, and are orientated more or less parallel or at a sharp angle to the surrounding conceptacle roof structure (Fig. 12). Tetrasporangial conceptacles become buried in the thallus (Fig. 13). Data on measured reproductive characters are summarised in Table 2.

## 3.4. ***Lithophyllum incrustans* Philippi, 1837: 388**

Basionym: *Lithophyllum incrustans* Philippi, 1837: 388.

Synonyms: *Corallium cretaceum lichenoides* Ellis, 1755: 27; *Spongites confluens* Kützing, 1841: 32; *Lithothamnion polymorphum* f. *confluens* (Kützing) Vinassa, 1892: 59; *Lithothamnion incrustans* (Philippi) Foslie, 1895: 122; *Lithothamnion incrustans* f. *depressum* (P.Crouan and H.Crouan) Foslie, 1895:122 (as f. *depressa*); *Hyperantherella incrustans* (Philippi) Heydrich, 1901: 190; *Crodelia incrustans* (Philippi) Heydrich, 1911: 16.

Lectotype: L 943.10.34. Sicily, Mediterranean, on a shell (Chamberlain and Irvine, 1994: 75), illustrated in Printz (1929: pl. 58, fig. 11). Lectotype designated by Woelkerling (1983: 315, figs. 15-23).

Etymology: '*incrustans*' meaning incrusting (Stearn, 1973). Philippi (1837) did not explain the origin of the epithet, but presumably it makes reference to the encrusting nature of the species on the shell from which the species was first described.

### *3.4.1. Specimens examined*

Despite extensive collections along rocky shores of the Eastern Cape Province, we were unable to find specimens that matched this species. The species is therefore extremely rare, or was perhaps misidentified by Chamberlain (1996). Chamberlain (1996: 209) based her description of South African *L. incrustans* on a single specimen (YMC 88/62) and stated that it strongly resembled European *L. incrustans*. We have not examined YMC 88/62, probably now residing in the British Museum, and so cannot confirm or deny the existence of *L. incrustans* in South Africa. Until such time as this specimen can be examined, or until DNA sequence data proves otherwise, we will presume that the Chamberlain (1996) record for South Africa is correct.

### *3.4.2. Distribution*

The species is reported from the tropical to temperate northeastern Atlantic Ocean, the Mediterranean region, the southwestern Indian Ocean and Japan. See Guiry and Guiry (2015) for a detailed distribution with sources. In South Africa the species has been recorded from only one location (Coffee Bay) in the Eastern Cape Province (Chamberlain, 1996).

### *3.4.3. Description*

See Chamberlain (1996) for a description of the species. Data on vegetative and reproductive characters are summarised in Tables 1 and 2.

## 3.5. ***Lithophyllum neoatalayense*** **Masaki, 1968: 34**

(Figs. 14-25)

Basionym: *Lithophyllum neoatalayense* Masaki, 1968: 34.

Synonyms: None.

Holotype: HAK, unnumbered. Kominato Town, Chiba Prefecture, Japan. T. Masaki, 2.vi.1961, on stones.

Etymology: derived from ‘*neo*’ meaning new and ‘*atalayense*’. Masaki (1968) gave the name in recognition of the species’ similarity to *Lithophyllum atalayense* Me.Lemoine from Patagonia.

### *3.5.1. Specimens examined*

In total, twelve (12) specimens were examined, these representing our entire collection for this taxon.

South Africa. Western Cape Province: Holbaaipunt, epilithic on primary bedrock and boulders in shallow sublittoral gullies (21.v.1993, *D.W. Keats*, UWC 93/51; 17.iii.1995, *D.W. Keats*, UWC 95/17; 21.vi.1993, *D.W.Keats*, UWC 93/67). Cape Agulhas, Stinkbaai, epilithic on pebbles and small boulders in mid to low shore tide pools (08.vii.2009, *G.W. Maneveldt & E. van der Merwe*, UWC 09/134, UWC 09/138; 15.vi.2010, *G.W. Maneveldt & E. van der Merwe*, UWC 10/130, UWC 10/135, UWC 10/136, UWC 10/138, UWC 10/139, 19.iii.2011, *G.W. Maneveldt*, UWC 11/20).

South Africa. Eastern Cape Province: Port Alfred, Shark Bay, epilithic on primary bedrock in low shore tide pools inundated with sand (07.iv.2011, *G.W. Maneveldt, E. van der Merwe & C. Padua*, UWC 11/29).

### *3.5.2. Distribution*

The species is reported from the temperate southeastern Atlantic Ocean and Japan. See Guiry and Guiry (2015) for a detailed distribution with sources. In Southern Africa the species has been recorded from Namibia (8 km south of Torra Bay) to the Eastern Cape Province (Port Alfred Bay) of South Africa (Chamberlain, 1996, Maneveldt et al., 2008).

### *3.5.3. Habit*

Thalli are non-geniculate, and epilithic on the primary bedrock, pebbles, and small boulders (Fig. 14). Freshly collected living specimens are variable in colour ranging from purplish-pink to brown to blueish and greyish-pink. Thalli vary from being encrusting (smooth) to lumpy and are generally loosely adherent. Margins are raised and often convoluted.

Conceptacles are easily visible on dried specimens and shed conceptacles appear as tiny craters. Thalli measure up to 1725 µm thick with convoluted margins measuring up to a further 1.5 mm thick and with protuberances that measure up to 6 mm in height and 3 mm in diameter.

### *3.5.4. Vegetative anatomy*

The thallus is pseudoparenchymatous, dorsiventrally organised and dimerous, and haustoria are absent (Fig. 15). The single basal layer comprises non-palisade cells that are slightly wider than they are long (Fig. 15). Cells of erect filaments are squat to square to mostly rectangular and these arise from the basal layer, comprising the bulk of the thallus (Figs. 15-17). Cells of contiguous basal and erect filaments are joined by secondary pit connections (Fig. 16); cell fusions have not been observed. Subepithallial initials are squat to square to rectangular and are no different to cells subtending them (Fig. 17). Epithallial cells occur in multiple layers (2-5) and are rounded to elliptical (Fig. 17). Data on measured vegetative characters are summarised in Table 1.

### *3.5.5. Reproductive anatomy*

Gametangial thalli are dioecious. Spermatangial (male) conceptacles vary from being flush with, to raised above the surrounding thallus surface (Figs. 18 and 19). Their chambers are wide and shallow to flask shaped. The conceptacle roof is formed from filaments that arise peripheral to the fertile area (Fig. 19), the terminal initials of which are more elongate than their inward derivatives. As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate (Fig. 20). These cells project somewhat into the pore canal and are orientated more or less parallel or at a sharp angle to the conceptacles roof surface in fully developed conceptacles. Throughout the early development a protective layer of epithallial cells surrounds the young developing conceptacle

(Fig. 19); this protective layer is shed once the pore canal is fully developed. The pore opening in fully developed conceptacles is often occluded by a mucilage plug (Fig. 20). Unbranched (simple) spermatangial systems develop only across the floor of mature male conceptacles (Figs. 18-20). Male conceptacles become buried, containing apparently viable spermatangial systems (Fig. 18).

Carpogonial (female) conceptacles are also raised above the surrounding thallus surface (Fig. 21). Their chambers are generally elliptical with the developing pore canal resembling a cone-shaped structure. Carpogonial conceptacle development is similar to that of the male conceptacles and the conceptacle pore is occluded by a protruding mucilage plug (Fig. 21). Carpogonial branches develop across the floor of the conceptacle chamber, and comprised a single support cell and a hypogynous cell bearing a carpogonium extended into a trichogyne (Fig. 21 insert). Sterile cells are also present on the hypogynous cell.

After presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles (Fig. 22). Carposporangial conceptacles are comparatively large. Their chambers are rounded to elliptical, but with flattened bottoms presumably caused by the growth of the expanding gonimoblast filaments. The conceptacle pore is occluded by a mucilage plug. The pore canal is lined by inflated papillate cells that project into the pore canal, but that does not occlude it. At the base of the pore canal is a ring of enlarged cells (Fig. 22). The near solid central fusion cell is discontinuous, thick and narrow, and several-celled gonimoblast filaments (incl. a terminal carposporangium) develop along the periphery of the conceptacle chamber (Figs. 22 and 23). The remains of unfertilized carpogonia persist across the dorsal surface of the fusion cell. Senescent carposporangial conceptacles from our specimens appear to be shed as no buried conceptacles were observed.

Tetrasporangial conceptacles are uniporate, and are mostly flush to slightly raised (Fig. 24) to slightly sunken below the thallus surface. Conceptacle primordia have not been observed.

However, roof development appears to be from filaments both peripheral to the fertile area as well as from filaments interspersed amongst the developing tetrasporangia (Fig. 24). The conceptacle roof in mature conceptacles is 39-59 μm thick and composed of 5-7 cells, including multiple layers of epithallial cells (Fig. 24). Conceptacle chambers are elliptical to slightly dumbbell-shaped as a result of an extensive central columella that appears to become progressively diminished as the conceptacle matures, and zonately divided tetrasporangia occur peripherally around the weakly calcified central columella (Fig. 24). The pore opening is occluded by a mucilage plug and the pore canal is lined by a single layer of enlarged papillate cells that are orientated more or less perpendicularly to the roof surface (Figs. 24 and 25). Senescent tetrasporangial conceptacles from our specimens appear to be shed as no buried conceptacles were observed. Data on measured reproductive characters are summarised in Table 2.

### 3.6. ***Titanoderma corallinae*** **(P.Crouan & H.Crouan) Woelkerling, Y.M.Chamberlain & P.C.Silva, 1985: 333**

(Figs. 26-37)

Basionym: *Melobesia corallinae* P.Crouan & H.Crouan, 1867: 150, 252.

Synonyms: *Lithophyllum corallinae* (P.Crouan & H.Crouan) Heydrich, 1897: 47; *Dermatolithon corallinae* (P.Crouan & H.Crouan) Foslie in Børgesen, 1903: 402; *Lithophyllum pustulatum* f. *corallinae* (P.Crouan & H.Crouan) Foslie, 1905a: 118, 127; *Lithophyllum macrocarpum* f. *corallinae* (P.Crouan & H.Crouan) Foslie, 1909: 47; *Tenarea corallinae* (P.Crouan & H.Crouan) Notoya, 1974: 47 (invalid).

Lectotype: CO, unnumbered; Banc du Chateau et Baie de la Ninon, Rade de Brest, France. Epiphytic on *Corallina officinalis* Linnaeus. Designated by and illustrated in Chamberlain

(1991: 67, fig. 208 as *Titanoderma*); also illustrated in Woelkerling and Campbell (1992: 43, fig. 22A as *Lithophyllum*).

Etymology: Crouan and Crouan (1867) did not explain the origin of the epithet, but '*corallinae*' almost certainly in reference to the host alga *Corallina officinalis* from which the type material was sampled (Woelkerling and Campbell, 1992).

*3.6.1. Specimens examined*

In total, three (3) specimens were examined, these representing our entire collection for this taxon.

South Africa. Western Cape Province: Dalebrook, False Bay, epiphytic on *Bifacaria brassicaeformis* in the low shore intertidal zone (21.xi.1991, *D.W. Keats*, UWC 91/202). Stilbaai, Skulpiesbaai, epilithic on medium-sized boulder in large tide pool (12.vi.2010, *G.W. Maneveldt & E. van der Merwe*, UWC 10/111).

South Africa. Eastern Cape Province: Kei Mouth, epizoic on mussel shell (11.vii.2010, *J.J. Bolton*, UWC 10/201).

*3.6.2. Distribution*

The species is reported from the tropical to subtropical Atlantic Ocean, temperate north Atlantic Ocean, the southwestern Indian Ocean and the western Pacific Ocean. See Guiry and Guiry (2015) for a detailed distribution with sources. In South Africa the species has been recorded from the Western Cape Province (Kommetjie) to the KwaZulu-Natal Province (Durban) (also see Maneveldt et al., 2008; Chamberlain and Norris, 1994).

### *3.6.3. Habit*

Thalli are non-geniculate, mainly epiphytic, but also epilithic on the primary bedrock and on boulders (Fig. 26), and also epizoic. Thalli are firmly adherent and thin with individual thalli producing marginal upgrowths when they meet. Freshly collected living specimens are bright pink in colour. Thalli vary from being encrusting (smooth) to warty. Thalli measure up to 368 µm.

### *3.6.4. Vegetative anatomy*

The thallus is pseudoparenchymatous, dorsiventrally organised and dimerous, and haustoria are absent (Fig. 27). Margins are characteristically bistratose comprising a single basal cell and a single epithallial cell (Fig. 28). The single basal layer comprises predominantly palisade cells that are wider than they are long (Figs. 27 and 29). Cells of erect filaments are square to mostly palisade and these arise from the basal layer, comprising the bulk of the thallus (Fig. 27). Cells of contiguous basal and erect filaments are joined by secondary pit connections (Figs. 29 and 30); cell fusions have not been observed. Subepithallial initials are square to palisade and are no different to the cells subtending them (Fig. 30). Epithallial cells occur in a single layer and are generally rounded to elliptical, but also triangular-shaped in bistratose sections. Data on measured vegetative characters are summarised in Table 3.

### *3.6.5. Reproductive anatomy*

Gametangial thalli appear to be dioecious. Spermatangial (male) conceptacles vary from being flush with to raised above the surrounding thallus surface (Fig. 31). Their chambers are wide and shallow to elliptical. The conceptacle roof is formed from filaments that arise peripheral to the fertile area (Fig. 33), the terminal initials of which are more elongate than their inward derivatives. As they divide, the newly forming filaments curve inwards to form the roof and pore, with the terminal initials along the pore canal becoming papillate (Fig. 31). These cells project into the pore canal and are orientated more or less parallel or at a sharp angle to the conceptacle roof surface in fully developed conceptacles. Throughout the early development a protective layer of epithallial cells surrounds the young developing conceptacle (Fig. 33); this protective layer is shed once the pore canal is fully developed. The pore opening in fully developed conceptacles is often occluded by a mucilage plug (Fig. 31). Unbranched (simple) spermatangial systems develop only across the floor of mature male conceptacles (Figs. 31-33). Senescent male conceptacles from our specimens appear to be shed as no buried conceptacles were observed.

No carpogonial (female) conceptacles were observed.

After presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles (Fig. 34). Carposporangial conceptacles are comparatively large. Their chambers are rounded to elliptical. The pore canal is lined by inflated papillate cells that project into the pore canal, but do not occlude it. The near solid fusion cell is discontinuous, thick and narrow, and several-celled gonimoblast filaments (incl. a terminal carposporangium) develop along the periphery of the conceptacle chamber (Figs. 34 and 35). The remains of unfertilized carpogonia persist across the dorsal surface of the fusion cell. Senescent carposporangial conceptacles from our specimens appear to be shed as no buried conceptacles were observed.

Tetrasporangial conceptacles are uniporate, and flush to raised above the surrounding thallus surface (Fig. 36). Roof development is both from filaments peripheral to the fertile area as well as from filaments interspersed amongst the sporangial initials (Fig. 37). The conceptacle roof in mature conceptacles is 34-69 μm thick and composed of 3-5 cells, including a single layer of epithallial cells (Fig. 36). Conceptacle chambers are more or less dumbbell-shaped as a result of an extensive central columella and zonately divided tetrasporangia occur peripherally around the central columella (Fig. 36). The pore opening is occluded by a mucilage plug and the pore canal is lined by enlarged papillate cells that are orientated more or less perpendicularly to the roof surface (Fig. 36). Senescent tetrasporangial conceptacles from our specimens appear to be shed as no buried conceptacles were observed. Data on measured reproductive characters are summarised in Table 4.

### 3.7. ***Titanoderma polycephalum*** **(Foslie) Woelkerling, Y.M.Chamberlain & P.C.Silva, 1985: 333**

(Figs. 38-43)

Basionym: *Lithophyllum polycephalum* Foslie, 1905b: 16.

Synonyms: *Dermatolithon polycephalum* (Foslie) Foslie, 1909: 58; *Tenarea polycephala* (Foslie) W.H.Adey, 1970: 7; *Goniolithon polycephalum* (Foslie) Afonso-Carrillo, 1984: 139.

Holotype: TRH (A19-1256). St. Vincent, Cape Verde Islands, Vanhöffen, 1901 (see Printz, 1929, pl. LXXII, fig. 18). Woelkerling (1993) reported that most of the specimen depicted in Printz (1929) is absent from TRH. See Chamberlain (1996, figs. 70, 71) for a depiction of the remaining holotype fragments.

Etymology: '*polycephalum*' from the Greek words '*poly*', meaning many or numerous and '*cephalus*', meaning headed. Foslie (1905b) did not explain the origin of the epithet but it presumably makes reference to the lumpy nature of the specimen (see Chamberlain, 1996: 219, figs. 70, 71).

#### *3.7.1. Specimens examined*

In total, two (2) specimens were examined, these representing our entire collection for this taxon.

South Africa. Western Cape Province: Holbaaipunt, Betty's Bay, epilithic on primary bedrock in mid to shallow subtidal zone (10.vi.1990, *D.W. Keats & I. Mathews*, UWC COR 16; 16.ii.1991, *D.W. Keats*, UWC COR 185).

### *3.7.2. Distribution*

The species is reported only from the Atlantic Ocean (Canary Islands, Cape Verde Islands, South Africa). See Guiry and Guiry (2015) for a detailed distribution with sources. In South Africa the species has been recorded only from the Western Cape Province (False Bay to Cape Agulhas) (Chamberlain, 1996).

### *3.7.3. Habit*

Thalli are non-geniculate, and epilithic on the primary bedrock (Fig. 38). Thalli are loosely adherent, thick and easily removed from the substrate. Freshly collected living specimens are variable in colour ranging from bluish mauve to pink. Thalli vary from being encrusting (smooth) to lumpy and protuberant. Thalli measure up to 10 mm thick with protuberances that measure up to 20 mm in length and 10 mm in diameter.

### *3.7.4. Vegetative anatomy*

The thallus is pseudoparenchymatous, dorsiventrally organised and dimerous, and haustoria are absent (Fig. 39). Margins are characteristically bistratose comprising a single basal cell and a single epithallial cell (Fig. 40). The single basal layer comprises predominantly palisade cells that are wider than they are long (Fig. 39). Cells of erect filaments are square to mostly palisade and these arise from the basal layer, comprising the bulk of the thallus (Fig. 39). Cells of contiguous basal and erect filaments are joined by secondary pit connections (Fig. 41); cell fusions have not been observed. Subepithallial initials are mostly rectangular to palisade and are no different to the cells subtending them (Fig. 41). Epithallial cells occur in a single layer and are generally rounded to elliptical, but also triangular-shaped in bistratose sections. Data on measured vegetative characters are summarised in Table 3.

### *3.7.5. Reproductive anatomy*

Gametangial conceptacles were not observed.

Tetrasporangial conceptacles are uniporate and raised above the surrounding thallus surface (Fig. 42). No conceptacle primordia were observed and so roof development is unknown. The conceptacle roof in mature conceptacles is 39-64 μm thick and composed of 3-5 cells, including a single layer of epithallial cells. Conceptacle chambers are flask-shaped and bear an extensive central columella. Zonately divided tetrasporangia occur peripherally around the central columella (Fig. 42). The pore opening is unoccluded and the base of the pore canal is lined by enlarged papillated cells that are orientated more or less perpendicularly to the roof surface (Fig. 43). In most conceptacles observed, however, these enlarged cells were not present. It appears that they are only weakly calcified (denoted by the light stain intensity) and are probably lost in the histological preparation. Senescent tetrasporangial conceptacles from our specimens appear to be shed as no buried conceptacles were observed. Data on measured reproductive characters are summarised in Table 4.

### 3.8. ***Titanoderma pustulatum* (J.V.Lamouroux) Nägeli, 1858: 532**

(Figs. 44-54)

Basionym: *Melobesia pustulata* J.V.Lamouroux, 1816: 315.

Synonyms: *Melobesia verrucata* J.V.Lamouroux, 1816: 316; *Melobesia pustulata* var. *canellata* Kützing, 1849: 696 (as β *canellata*); *Melobesia macrocarpa* Rosanoff, 1866: 74; *Melobesia confinis* P.Crouan & H.Crouan, 1867: 150; *Melobesia hapalidioides* P.Crouan & H.Crouan, 1867: 150; *Melobesia simulans* P.Crouan & H.Crouan, 1867: 149; *Lithophyllum hapalidioides* (P.Crouan & H.Crouan) Hariot, 1889: 84; *Lithothamnion adplicitum* Foslie, 1897: 17; *Dermatolithon pustulatum* f. *macrocarpum* (Rosanoff) Foslie, 1898: 11; *Dermatolithon hapalidioides* (P.Crouan & H.Crouan) Foslie, 1898: 11; *Dermatolithon pustulatum* (J.V.Lamouroux) Foslie, 1898: 11; *Dermatolithon hapalidioides* f. *confine* (P.Crouan & H.Crouan) Foslie, 1900d: 12 (as f. *confinis*); *Dermatolithon macrocarpum* (Rosanoff) Foslie,1900d: 14; *Melobesia caspica* Foslie, 1900a: 131; *Dermatolithon adplicitum* (Foslie) Foslie, 1900b: 22; *Dermatolithon macrocarpum* f. *faeroënsis* Foslie, 1900d: 15; *Lithophyllum macrocarpum* (Rosanoff) Foslie, 1905a: 128; *Lithophyllum pustulatum* (J.V.Lamouroux) Foslie, 1905a: 117; *Litholepis caspica* (Foslie) Foslie, 1905c: 6; *Lithophyllum hapalidioides* f. *confinis* (P.Crouan & H.Crouan) Foslie, 1905a: 128; *Lithophyllum macrocarpum* f. *faroense* (Foslie) Foslie, 1905a: 128 (as f. *faeröensis*); *Lithophyllum pustulatum* f. *intermedium* Foslie, 1905a: 117 (as f. *intermedia*); *Lithophyllum macrocarpum* f. *intermedium* (Foslie) Foslie, 1905a: 128 (as f. *intermedia*); *Lithophyllum pustulatum* f. *macrocarpum* (Rosanoff) Foslie, 1905a: 117; *Lithophyllum pustulatum* var. *australe* Foslie, 1905a: 117 (as f. *australis*); *Lithophyllum pustulatum* f. *ascripticium* Foslie, 1907: 34 (as f. *ascripticia*); *Lithophyllum pustulatum* f. *similis* Foslie, 1909: 47; *Lithophyllum pustulatum* var. *macrocarpum* (Rosanoff) Me.Lemoine, 1913: 142; *Epilithon pustulatum*

(J.V.Lamouroux) Me.Lemoine, 1921: 10; *Lithophyllum hapalidioides* var. *confinis* (P.Crouan & H.Crouan) Me.Lemoine, 1913: 136; *Dermatolithon macrocarpum* f. *intermedium* (Foslie) Foslie ex De Toni, 1924: 666; *Dermatolithon pustulatum* f. *ascripticium* (Foslie) Foslie ex De Toni, 1924: 665; *Lithophyllum adplicitum* (Foslie) L.Newton, 1931: 306; *Fosliella ascripticia* (Foslie) G.M.Smith, 1944: 224; *Fosliella intermedia* (Foslie) G.M.Smith, 1944: 226; *Dermatolithon pustulatum* f. *similis* (Foslie) Hamel & Me.Lemoine, 1953: 60; *Tenarea pustulata* (J.V.Lamouroux) W.H.Adey, 1965: 88 (invalid); *Dermatolithon caspicum* (Foslie) Zaberzhinskaya ex A.D.Zinova, 1967: 227; *Tenarea ascripticia* (Foslie) W.H.Adey, 1970: 6; *Tenarea caspica* (Foslie) W.H.Adey, 1970: 7; *Tenarea confinis* (P.Crouan & H.Crouan) W.H.Adey & P.J.Adey, 1973: 393; *Tenarea hapalidioides* (P.Crouan & H.Crouan) W.H.Adey & P.J.Adey, 1973: 394; *Dermatolithon confinis* (P.Crouan & H.Crouan) C.Boudouresque, Perret-Boudouresque & Knoepffler-Peguy, 1984: 46; *Titanoderma ascripticium* (Foslie) Woelkerling, Y.M.Chamberlain & P.C.Silva, 1985: 333; *Titanoderma caspica* (Foslie) Woelkerling, 1986: 257; *Titanoderma confinis* (P.Crouan & H.Crouan) J.H.Price, D.M.John & G.W.Lawson, 1986: 86; *Titanoderma hapalidioides* (P.Crouan & H.Crouan) J.H.Price, D.M.John & G.W.Lawson, 1986: 86; *Titanoderma macrocarpum* (Rosanoff) Y.M.Chamberlain, 1986: 203; *Titanoderma verrucatum* (J.V.Lamouroux) Y.M.Chamberlain, 1986: 201; *Titanoderma pustulatum* var. *canellatum* (Kützing) Y.M.Chamberlain, 1991: 61; *Titanoderma pustulatum* var. *confine* (P.Crouan & H.Crouan) Y.M.Chamberlain, 1991: 50; *Titanoderma pustulatum* var. *macrocarpum* (Rosanoff) Y.M.Chamberlain, 1991: 33.

Lectotype: CN, unnumbered. France (location unknown). Epiphytic on *Chondrus crispus*. Designated by Woelkerling et al. (1985: 325). Illustrated in Woelkerling et al. (1985: figs. 29-39) and Woelkerling and Campbell (1992: fig. 50A-C).

Etymology: '*pustulatum*' from '*pustulatus*' meaning having pustules (blisters, pimples) or blister-shaped (Stearn, 1973). Lamouroux (1816) did not explain the origin of the epithet, but presumably it makes reference to the "pustulose" appearance of the conceptacles on the thallus surface (Woelkerling and Campbell, 1992).

### *3.8.1. Specimens examined*

In total, ten (10) specimens were examined, these representing our entire collection for this taxon.

South Africa. Western Cape Province: Cape Point Nature Reserve, Olifantsbos, epiphytic on *Gigartina* sp. in tide pool (13.vii.1993, *D.W. Keats*, UWC 93/87). Holbaaipunt, epiphytic on a kelp holdfast in the shallow subtidal zone (25.x.1991, *D.W. Keats*, UWC 91/101). Struisbaai, epiphytic on *Spongites yendoi* in mid eulittoral zone gullies (06.vii.2009, *G.W. Maneveldt & E. van der Merwe*, UWC 09/112). Knysna Heads, epilithic on primary bedrock and on small to large boulders in high to mid shore tide pools (07.iv.2008, *G.W. Maneveldt & U. van Bloemestein*, UWC 08/26).

South Africa. Eastern Cape Province: Kei Mouth, epiphytic on *Codium extricatum* in low shore tide pool (11.vii.2010, J.J. *Bolton*, UWC 10/200). Morgan Bay, epiphytic on *Codium extricatum* in shallow subtidal zone (12.vii.2010, *G.W. Maneveldt & E. van der Merwe*, UWC 10/223). Qolorha, epiphytic on stipes of *Ecklonia radiata* in subtidal gullies (13.vii.2010, *G.W. Maneveldt & E. van der Merwe*, UWC 10/226; UWC 10/228).

South Africa. KwaZulu-Natal Province: Durban, Brighton Beach, epiphytic on *Codium duthrae* in intertidal pool (11.viii.1991, *D.W. Keats*, UWC 91/192). Sodwana Bay, 7-Mile Reef, epiphytic on the seagrass *Thalassodendron leptocaule* in low shore tide pools (11.iv.1991, *D.W. Keats*, UWC 91/120).

### *3.8.2. Distribution*

The species is widely reported throughout all of the world's oceans. See Guiry and Guiry (2015) for a detailed distribution with sources. In South Africa the species has been reported from the Northern Cape Province with increasing abundance toward the KwaZulu-Natal Province (Sodwana Bay) where it is particularly abundant (Maneveldt et al., 2008).

### *3.8.3. Habit*

Thalli are non-geniculate, epilithic on the primary bedrock and on pebbles, but mostly epiphytic on other algae (Fig. 44) and on seagrasses. Thalli are strongly adherent and thin. Freshly collected living specimens are variable in colour ranging from deep purple to pink to maroon. Thalli are encrusting (smooth) and measure up to 1360 µm thick.

### *3.8.4. Vegetative anatomy*

The thallus is pseudoparenchymatous, dorsiventrally organised and dimerous, and haustoria are absent (Fig. 45). Margins are characteristically bistratose comprising a single basal cell and a single epithallial cell (Fig. 46). The single basal layer comprises predominantly palisade cells that are wider than they are long (Figs. 45 and 47). Cells of erect filaments are more or less square to mostly palisade and these arise from the basal layer, comprising the bulk of the thallus (Fig. 45). Cells of contiguous basal and erect filaments are joined by secondary pit connections (Fig. 47); cell fusions have not been observed. Subepithallial initials are rectangular to palisade and are no different to the cells subtending them. Epithallial cells occur in a single layer and are generally rounded to elliptical, but also triangular-shaped in bistratose sections. Data on measured vegetative characters are summarised in Table 3.

### *3.8.5. Reproductive anatomy*

Gametangial thalli are dioecious. Spermatangial (male) conceptacles are raised above the surrounding thallus surface (Fig. 48). Their chambers are roughly elliptical in shape. Conceptacle primordia have not been observed. In fully developed conceptacles, the pore canal is lined by papillate cells that project into the pore canal (Fig. 48). These cells are orientated more or less parallel or at a sharp angle to the conceptacle roof surface. The pore opening is unoccluded. Unbranched (simple) spermatangial systems develop only across the floor of mature male conceptacles (Figs. 48 and 49). Senescent male conceptacles conceptacles from our specimens appear to be shed as no buried conceptacles were observed.

Carpogonial (female) conceptacles are only slightly raised above the surrounding thallus surface, but are anatomically similar to spermatangial conceptacles (Fig. 50). Carpogonial branches develop across the floor of the mature conceptacle chamber, and comprised a single support cell and a hypogynous cell bearing a carpogonium extended into a trichogyne (Fig. 50 insert). Sterile cells are also present on the hypogynous cell.

After presumed karyogamy, carposporophytes develop within female conceptacles and form carposporangial conceptacles (Fig. 51). Carposporangial conceptacles are comparatively large. Their chambers are rounded to elliptical. The pore opening is occluded by a mucilage plug and the pore canal is lined by inflated papillate cells that project into the pore canal (Fig. 51). The near solid central fusion cell is discontinuous, thick and narrow, and distinctly raised well above the chamber floor (Figs. 51 and 52). Several-celled gonimoblast filaments (incl. a terminal carposporangium) develop along the periphery of the conceptacle chamber (Fig. 52). The remains of unfertilized carpogonia persist across the dorsal surface of the fusion cell. Senescent carposporangial conceptacles from our specimens appear to be shed as no buried conceptacles were observed.

Tetrasporangial conceptacles are uniporate, and raised well above the surrounding thallus surface (Fig. 53). Conceptacle primordia have not been observed. However, roof development appears to be from filaments both peripheral to the fertile area as well as from filaments interspersed amongst the developing tetrasporangia (Fig. 54). The conceptacle roof in mature conceptacles is 39-69 μm thick and composed of 2-4 (mostly 3, including an epithallial cell) cells (Figs. 53 and 54). Conceptacle chambers are elliptical bearing an extensive central columella that appears to become progressively diminished as the conceptacle matures, and zonately divided tetrasporangia occur peripherally around the central columella (Figs. 53 and 54). The pore opening is occluded by a mucilage plug and the pore canal is lined by enlarged cells that are orientated more or less perpendicularly to the roof surface (Fig. 54). Senescent tetrasporangial conceptacles from our specimens appear to be shed as no buried conceptacles were observed. Data on measured reproductive characters are summarised in Table 4.

## 4. Discussion

*Titanoderma*, as delimited by Chamberlain and Irvine (1994: 88), is a genus of non-geniculate coralline red algae in the subfamily Lithophylloideae that: 1) possesses a bistratose dimerous thallus margin (comprising a single palisade and a single epithallial cell only); and 2) bears predominantly palisade basal filament cells. This contrasts with *Lithophyllum* in which the basal layer consists of predominately non-palisade cells and no bistratose margin, as the thallus begins to thicken immediately behind the primary meristematic cell (Chamberlain, 1996). Our data supports this characterisation, and as with other published accounts (e.g. Chamberlain et al., 1991; Chamberlain and Irvine, 1994; Chamberlain, 1996; Keats, 1997), we found no difficulty in assigning species to either *Titanoderma* or *Lithophyllum* on the basis of these two characters (Table 5).

While the majority of the South African non-geniculate Lithophylloideae have previous been described in detail, the predominantly epiphytic *T. corallinae* and *T. pustulatum* are here described in detail for the first time. Similarly (with the exception of *L. incrustans* that we cannot at this stage verify) for species of *Lithophyllum* here reported, new data (female and carposporangial) is presented for the first time, providing a more complete view of the South African species assigned to this genus. Specimens of all species presented here compare favourably to those reported from Australia and the British Isles.

Although morphology and vegetative anatomy are widely considered to be very variable characters (Woelkerling, 1984; Chamberlain, 1986; Woelkerling and Campbell, 1992; Farr et al., 2009), often these characters are useful at a regional level for distinguishing species (see e.g. Maneveldt and van der Merwe, 2012). For South African species of *Titanoderma* morphology is a useful character, and the growth form and habit (epiphytic vs. epilithic) in particular provides a good initial means for separating species (Table 5). Within the South

African species of *Lithophyllum*, however, morphology is not a reliable character at all, although the number of epithallial cell layers is a useful anatomical character once the genus name has been identified; in *Titanoderma*, the number of epithallial cell layers is not a useful character for separating species.

It is now widely accepted that reproductive anatomy is far more reliable as distinguishing features for delimiting taxa (Johansen, 1976, 1981; Turner and Woelkerling, 1982; Penrose and Woelkerling, 1988, 1991, 1992; Woelkerling, 1988; Penrose, 1991, 1992a, 1992b). Among South African species within both *Lithophyllum* and *Titanoderma*, the structure of the tetra/bisporangial conceptacle pore canal as well as the shape of the cells lining the pore canal are useful characters for distinguishing among the species here under investigation (Table 5). It is important to note here that Chamberlain (1996: 219) commented that *T. polycephalum* "lacks differentiated pore cells". In Chamberlain's (1996) fig 68, however, there clearly is an enlarged cell lining the base of the left side of the pore canal, which happens to be orientated perpendicular to the roof surface. This illustration is consistent with our findings. In many of our observations, these enlarged papillated cells were absent, presumably due to them being weakly calcified (evident by the light stain intensity). Since Chamberlain (see Chamberlain 1993 for a description of her methodology) used predominantly a freeze microtome, it was very likely that weakly calcified structures would become lost during the process. In addition, although the roof thickness (in μm) per se is not a reliable character, the number of cells in the tetra/bisporangial conceptacle roof from species of *Lithophyllum*, is a useful character for separating species.

The nature of the dimerous margin (bistratose vs. non-bistratose) and the cells of the basal layer (predominantly palisade vs. predominantly non-palisade) are currently regarded as the distinguishing characters separating species of *Lithophyllum* from *Titanoderma*. During the course of this study we found a distinct difference in the depth of the tetra/bisporangial conceptacle floor between the two genera (Table 5), suggesting a third possible distinguishing feature. An examination of the depth of the conceptacle floor might imply that conceptacle initiation is adventitious (deep) within the thallus in *Lithophyllum* and superficial (in the subepithallial layer) within the thallus in *Titanoderma*, but as Chamberlain et al. (1991) had demonstrated for *L. orbiculatum*, all conceptacle types originate in the subepithallial layer[4], the conceptacles quickly becoming immersed in the thallus due to overgrowth of the surrounding erect filaments. Conceptacle initiation aside, an examination of the literature pertaining to detailed accounts of species from both genera (e.g. Chamberlain et al., 1991; Woelkerling and Campbell, 1992; Chamberlain and Irvine, 1994; Chamberlain, 1996; Womersley, 1996, Harvey et al., 2009) supports the use of the depth of the mature tetra/bisporangial conceptacle floor as a distinguishing feature. Woelkerling and Campbell (1992) and Harvey et al. (2009) already went as far as to include the depth of the tetra/bisporangial conceptacle chamber floor relative to the surrounding thallus surface as diagnostically reliable for delimiting southern and south-eastern Australian species of *Lithophyllum* respectively (which includes species recognised as belonging to *Titanoderma* under the Chamberlain and Irvine (1994) characterisation). This suggestion of the depth of the tetra/bisporangial conceptacle floor as a third diagnostic character for separating species of *Lithophyllum* (well below the surrounding thallus surface) from *Titanoderma* (superficial), will need to be verified once this feature is reported for all species.

In conclusion, with the exception of *L. incrustans* that we cannot at this stage verify, all specimens reported on in this account compare favourably to specimens of the same species reported from Australia and the British Isles. As with other published accounts (e.g. Chamberlain et al., 1991; Chamberlain and Irvine, 1994; Chamberlain, 1996; Keats, 1997), our data supports the characterisation of the genus *Titanoderma* separate from *Lithophyllum*

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[4] Based on information at that time, Townsend (1981) had hypothesised that conceptacle initiation in *Lithophyllum* was characteristically in the subepithallial layer.

as we found no difficulty in assigning species to either genus on the basis of either the nature of the dimerous margin (bistratose vs. non-bistratose), or the cells of the basal layer (predominantly palisade vs. predominantly non-palisade). As with previous accounts (e.g. Woelkerling and Campbell, 1992; Harvey et al., 2009) we consider the structure of the tetra/bisporangial conceptacle pore canal, the number of cells lining the tetra/bisporangial conceptacle roof, and the depth of the tetra/bisporangial conceptacle chamber floor to be the principal diagnostically reliable characters for use in delimiting South African species of Lithophylloideae. Secondarily, and to a lesser extent, the number of epithallial cells (in *Lithophyllum*), and the growth form and habit (epiphytic vs. epilithic) (in *Titanoderma*) could prove useful.

## Acknowledgements

We thank the Department of Biodiversity and Conservation Biology at the University of the Western Cape (UWC) for providing funding and research equipment, and the South African National Research Foundation (NRF) for a research grant to GWM. William J. Woelkerling is gratefully acknowledged for providing a translation of the Heydrich description and for assisting in resolving the epithet '*acrocamptum*'. We thank the reviewers for their invaluable comments.

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## TABLES

**Table 1.** A comparison of the habit and vegetative features of the species of *Lithophyllum* reported to occur in South Africa compared against those of previously published records. "ND" = No data provided.

| **Character** | ***L. acrocamptum*** (this study) | ***L. acrocamptum*** (South Africa: Chamberlain 1996, as *L. incrassatum*) | ***L. incrustans*** (South Africa: Chamberlain 1996) | ***L. neoatalayense*** (this study) | ***L. neoatalayense*** (South Africa: Chamberlain 1996) |
|---|---|---|---|---|---|
| Substrate | epilithic on primary bedrock and boulders | epilithic on primary bedrock and boulders | epilithic on a boulder | epilithic on primary bedrock, pebbles small boulders | epilithic on the primary bedrock and boulders, epiphytic on other corallines, and also forming subtidal rhodoliths. |
| Growth form | encrusting (smooth) to lumpy to bearing knobbly protuberances | encrusting (smooth) to lumpy with broad protuberances | encrusting (smooth) to lumpy to bearing knobbly protuberances | encrusting (smooth) to lumpy bearing knobbly protuberances | encrusting (smooth), to lumpy bearing knobbly protuberances |
| Margin | not bistratose | ND | ND | not bistratose | ND |
| Thallus thickness | to 50 mm, protuberances to 7 mm | to 500 µm, protuberances to 20 mm | to 1000 µm, protuberances to 10 mm (dead thalli up to 30 mm thick) | to 1725 µm, protuberances to 6 mm | mostly to 2000 µm (may reach up to 30 mm thick), protuberances to 30 mm |
| Basal filaments cell length | 5-29 µm | 9-22 µm | 4-6 µm | 4-17 µm | 9-11 µm |

| | | | | | |
|---|---|---|---|---|---|
| Basal filaments cell diameter | 12-32 µm | 9-22 µm | 12-50 µm | 5-20 µm | 9-11 µm |
| Erect filaments cell length | 6-32 µm | 6-12 µm | 5-40 (78) µm | 6-17 µm | 6-15 µm |
| Erect filaments cell diameter | 5-12 µm | 6-13 µm | 3-8 µm | 5-10 µm | 3-10 µm |
| Subepithallial cell length | 5-17 µm | ND | ND | 3-15 µm | ND |
| Subepithallial cell diameter | 7-12 µm | ND | ND | 6-10 µm | ND |
| Epithallial cell number | 1 (up to 3 when shedding) | 1 | 1-4 | 2-5 | up to 5 |
| Epithallial cell length | 4-7 µm | 3-5 µm | 3-4 µm | 3-6 µm | 2-5 µm |
| Epithallial cell diameter | 7-12 µm | 5-12 µm | 3-4 µm | 5-11 µm | 4-6 µm |

**Table 2.** A comparison of the reproductive features of the species of *Lithophyllum* reported to occur in South Africa compared against those of previously published records. "ND" = No data provided; "–" = feature not observed.

| **Character** | ***L. acrocamptum*** (this study) | ***L. acrocamptum*** (South Africa: Chamberlain 1996, as *L. incrassatum*) | ***L. incrustans*** (South Africa: Chamberlain 1996) | ***L.neoatalayense*** (this study) | ***L. neoatalayense*** (South Africa: Chamberlain 1996) |
|---|---|---|---|---|---|
| Gametangial thalli | dioecious | dioecious | – | dioecious | dioecious |
| Spermatangial thalli | | | | | |
| Conceptacle placement | raised above surrounding thallus surface | slightly sunken to flush to slightly raised above surrounding thallus surface | – | flush to raised above surrounding thallus surface | slightly sunken below surrounding thallus surface |
| External conceptacle diameter | 255-417 µm | ND | – | 180-260 µm | ND |
| Conceptacle chamber diameter | 162-211 µm | 156-269 µm | – | 123-172 µm | 130-221 µm |
| Conceptacle chamber height | 44-83 µm | 33-52 µm | – | 29-49 µm | 39-73 µm |
| Conceptacle roof thickness | 22-47 µm | 23-33 µm | – | 17-34 µm | 21-29 µm |
| Carpogonial thalli | | | | | |
| Conceptacle placement | raised above the surrounding thallus surface | – | – | raised above the surrounding thallus surface | immersed below the surrounding thallus surface |
| External conceptacle | 150-380 µm | – | – | 200-350 µm | ND |

| | | | | | |
|---|---|---|---|---|---|
| diameter | | | | | |
| Conceptacle chamber diameter | 103-127 µm | – | – | 130-159 µm | ND |
| Conceptacle chamber height | 22-42 µm | – | – | 27-64 µm | ND |
| Conceptacle roof thickness | 37-51 µm | – | – | 51-66 µm | ND |
| Carposporangial thalli | | | | | |
| Conceptacle placement | flush with to raised above the surrounding thallus surface | – | – | flush with to raised above the surrounding thallus surface | – |
| External conceptacle diameter | 600-650 µm | – | – | 290-450 µm | – |
| Conceptacle chamber diameter | 162-198 µm | – | – | 201-240 µm | – |
| Conceptacle chamber height | 59-83 µm | – | – | 76-130 µm | – |
| Conceptacle roof thickness | 27-37 µm | – | – | 27-49 (69) µm | – |
| No of cells in gonimoblast filament | 4-5 | – | – | 4-7 | – |
| Carpospore length | 29-54 µm | – | – | 25-44 (49) µm | – |
| Carpospore diameter | 29-56 µm | – | – | 17-56 µm | – |
| Tetrasporangial thalli | | | | | |
| Conceptacle placement | mostly flush with to slightly raised to | mostly flush with the surrounding thallus | flush with the surrounding thallus | mostly flush to slightly raised above to slightly | flush with, to sunken below the surrounding |

| | | | | | |
|---|---|---|---|---|---|
| | slightly sunken below the surrounding thallus surface | surface | surface | sunken below surrounding thallus surface | thallus surface |
| External conceptacle diameter | 370-760 µm | ND | ND | 280-450 µm | ND |
| Conceptacle chamber diameter | 274-377 µm | 208-364 µm | 203-390 µm | 216-279 µm | 229-252 µm |
| Conceptacle chamber height | 81-140 µm | 52-130 µm | 104-156 µm | 81-140 µm | 83-177 µm |
| Conceptacle roof thickness | 39-69 µm | 26-62 µm | 65-104 µm | 39-59 µm | 44-57 µm |
| No. of cells in conceptacle roof (incl. epithallial cell[s]) | 3-5 (mostly 5) | 3-4 | 6-17 | 5-7 | 6-10 |
| Tetra/bisporangium length | 39-110 µm | 46-65 µm | 65-104 µm | 64-115 (145) µm | 65-91 µm |
| Tetra/bisporangium diameter | 9-54 µm | 27-38 µm | 31-52 µm | 37-61 µm | 26-34 µm |

**Table 3.** A comparison of the habit and vegetative features of the species *Titanoderma* reported to occur in South Africa compared against those of previously published records. "ND" = No data provided.

| **Character** | ***T. corallinae*** (this study) | ***T. corallinae*** (British Isles: Chamberlain, 1991; Chamberlain and Irvine, 1994) | ***L. corallinae*** (Australia: Woelkerling and Campbell, 1992; Womersley, 1996; Harvey et al., 2009) | ***T. polycephalum*** (this study) | ***T. polycephalum*** (South Africa: Chamberlain, 1996) | ***T. pustulatum*** (this study) | ***T. pustulatum*** (British Isles: Chamberlain, 1991; Chamberlain and Irvine, 1994) | ***L. pustulatum*** (Australia: Woelkerling and Campbell, 1992; Womersley, 1996; Harvey et al., 2009) |
|---|---|---|---|---|---|---|---|---|
| Substrate | mainly epiphytic, but also epilithic on primary bedrock and on boulders, but also epizoic | epiphytic | epiphytic, epizoic, epilithic or epigenous | epilithic on primary bedrock | epilithic on primary bedrock | mostly epiphytic, but also epilithic on primary bedrock and on pebbles | mostly epiphytic, but also epilithic on primary bedrock | epiphytic |
| Growth form | encrusting (smooth) to warty | encrusting (smooth) | encrusting (smooth) to warty to lumpy to fruticose | encrusting (smooth) to lumpy and protuberant | encrusting (smooth) to lumpy to massively protuberant and turreted | encrusting (smooth) | encrusting (smooth) | encrusting (smooth) to layered to rarely warty or lumpy |
| Thallus thickness | to 368 µm | to 370 µm | to 32 mm | to 10 mm, protuberances up to 20 mm in length | to 50 mm | to 1360 µm | to 500 µm | to 2.5 mm |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Thallus construction | dimerous | dimerous | dimerous or dimerous and monomerous | dimerous | dimerous | dimerous | dimerous | dimerous |
| Monomerous filaments cell length | – | – | 5-35 (55) µm | – | – | – | – | – |
| Monomerous filaments cell diameter | – | – | 5-14 µm | – | – | – | – | – |
| Basal filaments cell length | 7-22 µm | 7-16 µm | 5-20 µm | 10-33 µm | 9-28 µm | 2-15 µm | 8-21 µm | 5-25 µm |
| Basal filaments cell diameter | 5-123 µm | 7-98 µm | (13)20-65(82) µm | 34-61 µm | 20-55 µm | 17-110 µm | 13-190 µm | (12) 25-75 (100) µm |
| Erect filaments cell length | 7-83 µm | 10-63 µm | 5-40(55) µm | 7-54 µm | 4-60 µm | 9-110 µm | 8-118 µm | (5) 15-80 µm |
| Erect filaments cell diameter | 4-15 µm | 5-20 µm | 5-16 µm | 6-20 µm | 5-15 µm | 2-15 µm | 6-22 µm | 5-20 µm |
| Subepithallial cell length | 15-34 µm | ND | ND | 12-49 µm | ND | 34-66 µm | ND | ND |
| Subepithallial cell diameter | 5-10 µm | ND | ND | 6-12 µm | ND | 5-11 µm | ND | ND |
| Epithallial cell number | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Epithallial cell length | 4-10 µm | ND | 2-6 µm | 5-9 µm | 3-4 µm | 4-9 µm | ND | 2-8 µm |
| Epithallial cell diameter | 6-10 µm | ND | 4-10 µm | 6-12 µm | 3-6 µm | 6-12 µm | ND | 3-12 µm |

**Table 4.** A comparison of the reproductive features of the species of *Titanoderma* reported to occur in South Africa compared against those of previously published records. “ND” = No data provided; “–” = feature not observed.

| **Character** | ***T. corallinae*** (South Africa: this study) | ***T. corallinae*** (British Isles: Chamberlain, 1991; Chamberlain and Irvine, 1994) | ***L. corallinae*** (Australia: Woelkerling and Campbell, 1992; Womersley, 1996; Harvey et al., 2009) | ***T. polycephalum*** (this study) | ***T. polycephalum*** (South Africa: Chamberlain, 1996) | ***T. pustulatum*** (South Africa: this study) | ***T. pustulatum*** (British Isles: Chamberlain, 1991; Chamberlain and Irvine, 1994) | ***L. pustulatum*** (Australia: Woelkerling and Campbell, 1992; Womersley, 1996; Harvey et al., 2009) |
|---|---|---|---|---|---|---|---|---|
| Gametangial thalli | dioecious | monoecious or dioecious | monoecious or dioecious | – | – | dioecious | – | dioecious |
| Spermatangial thalli | | | | | | | | |
| Conceptacle placement | flush with to raised above surrounding thallus surface | ND | flush with to slightly raised above the surrounding thallus surface | – | – | raised above the surrounding thallus surface | – | raised above the surrounding thallus surface |
| External conceptacle diameter | 200-490 µm | ND | ND | – | – | 360-520 µm | – | ND |
| conceptacle chamber diameter | 142-368 µm | 78-130 µm | 110-145 µm | – | – | 167-245 µm | – | (53) 110-450 µm |
| Conceptacle chamber height | 34-81 µm | 39-52 µm | 30-50 µm | – | – | 74-98 µm | – | 25-90 µm |
| Conceptacle roof thickness | 27-59 µm | ND | 25-40 µm | – | – | 37-49 µm | – | ND |
| Carpogonial thalli | | | | | | | | |
| Conceptacle | – | ND | – | – | – | slightly raised | – | raised above |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| placement | | | | | | above the surrounding thallus surface | | the surrounding thallus surface |
| External conceptacle diameter | – | ND | – | – | – | 430-600 µm | – | ND |
| Conceptacle chamber diameter | – | 90-104 µm | – | – | – | 123-172 µm | – | ND |
| Conceptacle chamber height | – | 39-59 µm | – | – | – | 44-69 µm | – | ND |
| Conceptacle roof thickness | – | ND | – | – | – | 27-42 µm | – | ND |
| Carposporangial thalli | | | | | | | | |
| Conceptacle placement | raised above the surrounding thallus surface | slightly raised above the surrounding thallus surface | flush with to slightly raised above the surrounding thallus surface | – | – | raised above the surrounding thallus surface | – | raised above the surrounding thallus surface |
| External conceptacle diameter | 350-450 µm | ND | ND | – | – | 470-620 µm | – | ND |
| Conceptacle chamber diameter | 198-238 µm | 182 µm | 170-305 µm | – | – | 186-274 µm | – | 220-300 µm |
| Conceptacle chamber height | 113-130 µm | 130 µm | 60 -110 (140) µm | – | – | 83-123 µm | – | 85-110 (177) µm |
| Conceptacle roof thickness | 29-47 µm | 47 µm | 50-115 µm | – | – | 37-51 µm | – | 60-100 µm |
| Type of fusion cell | discontinuous | continuous[1] | discontinuous[2] | – | – | discontinuous | – | discontinuous[2] |
| No of cells in gonimoblast filament | 5-6 | up to 5 | up to 7 | – | – | 4-5 | – | up to 5 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Carpospore length | 29-59 µm | ND | ND | – | – | 20-71 µm | – | ND |
| Carpospore diameter | 29-61 µm | ND | 27-40 (57) µm | – | – | 12-54 µm | – | 30-75 µm |
| Tetrasporangial thalli | | | | | | | | |
| Conceptacle placement | flush with to raised above the surrounding thallus surface | completely immersed to somewhat raised above the surrounding thallus surface | flush with to raised above the surrounding thallus surface | raised above the surrounding thallus surface | flush with to raised above the surrounding thallus surface | raised well above the surrounding thallus surface | raised above the surrounding thallus surface | raised above the surrounding thallus |
| External conceptacle diameter | 400-670 µm | 150-200 µm | 235-330 (419) µm | 400-700 µm | ND | 480-700 µm | 400-800 µm | 390-690 (890) µm |
| Conceptacle chamber diameter | 216-333 µm | 169-235 µm | (140) 160-260 (340) µm | 320-500 µm | 302-442 µm | 167-343 µm | 156-468 µm | (162) 280-500 (556) µm |
| Conceptacle chamber height | 81-132 µm | 75-117 µm | 55-105 (136) µm | 74-216 µm | 78-182 µm | 93-157 µm | 78-234 µm | 80-180 µm |
| Conceptacle roof thickness | 34-69 µm | 26-52 µm | ND | 39-64 µm | 36-52 µm | 39-69 µm | 23-73 µm | ND |
| No. of cells in conceptacle roof (incl. epithallial cell) | 3-5 | varying numbers | (2) 3-4 | 3-5 | 3-5 | 2-4 (mostly 3) | 3 | (2) 3-4 (7) |
| Tetra/bisporangium length | 44-120 µm | 50-87 µm | (35) 50-95 (125) µm | 39-191 µm | 46-72 µm | 49-145 µm | 72-156 µm | 70-140 µm |
| Tetra/bisporangium diameter | 17-76 µm | 39-59 µm | (15) 25-60 (95) µm | 10-78 µm | 26-39 µm | 17-76 µm | 33-104 µm | 25-85 µm |

[1] Chamberlain (1991) and Chamberlain and Irvine (1994) did not comment on the type of fusion cell, but their drawings depict a continuous central fusion cell.

[2] Woelkerling and Campbell (1992 ), Womersley (1996) and Harvey et al. (2009) did not comment on the type of fusion cell, but their images clearly show a discontinuous central fusion cell.

**Table 5.** Comparison of the characters collectively considered diagnostic of the species of *Lithophyllum* and *Titanoderma* reported to occur in South Africa. "ND" = No data provided.

| **Character** | ***L. acrocamptum*** | ***L. incrustans*** | ***L. neoatalayense*** | ***T. corallinae*** | ***T. polycephalum*** | ***T. pustulatum*** |
|---|---|---|---|---|---|---|
| Substrate | epilithic on primary bedrock and on boulders | epilithic on a boulder | epilithic on primary bedrock, pebbles and small boulders | mainly epiphytic, but also epilithic on primary bedrock and on boulders, but also epizoic | epilithic on primary bedrock | mostly epiphytic, but also epilithic on primary bedrock and on pebbles |
| Growth form | encrusting (smooth) to lumpy to bearing knobbly protuberances | encrusting (smooth) to lumpy to bearing knobbly protuberances | encrusting (smooth) to lumpy | encrusting (smooth) to warty | encrusting (smooth) to lumpy to bearing knobbly protuberances | encrusting (smooth) |
| Thallus thickness | to 50 mm, protuberances to 7 mm | to 1000 µm, protuberances to 10 mm | to 1725 µm, protuberances to 6 mm | to 368 µm | to 10 mm, protuberances up to 20 mm | to 1360 µm |
| Margin | not bistratose | not bistratose | not bistratose | bistratose | bistratose | bistratose |
| Basal filament cells | predominantly non-palisade | predominantly non-palisade | predominantly non-palisade | predominantly palisade | predominantly palisade | predominantly palisade |
| No. of epithallial cell layers | 1 (up to 3 when shedding) | 1-4 | 2-5 | 1 | 1 | 1 |
| No. of cells in gonimoblast filament (incl. terminal carpospores) | 4-5 | ND | 4-7 | 5-6 | ND | 4-5 |
| Depth of | 10-16 | 12-17 | 11-14 (17) | 7-9 | 5-9 (mostly 5-6) | 3 |

| | | | | | | |
|---|---|---|---|---|---|---|
| tetrasporangial conceptacle floor (no. of cells below surface) | | | | | | |
| Tetrasporangial conceptacle roof (no. of cells) | 3-5 (mostly 5) | 6-17 | 5-7 | 3-5 | 3-5 | 2-4 (mostly 3) |
| Tetra/bisporangial conceptacle pore canal structure | pore canal short, tapering markedly towards the pore | pore canal long, with more or less parallel sides | pore canal short, not tapering markedly towards the pore | pore canal short, tapering towards the pore | pore canal short, not tapering towards the pore | pore canal short, not tapering towards the pore |
| Tetra/bisporangial conceptacle pore canal cells | papillate, enlarged and balloon-like, orientated more or less parallel or at a sharp angle to the surrounding roof structure | ND | papillate and enlarged, orientated more or less perpendicular to the roof surface | papillate and enlarged, orientated more or less perpendicular to the roof surface | papillate and enlarged, orientated more or less perpendicular to the roof surface. These cells are often not present due to presumable weak calcification | non-papillate and enlarged, orientated more or less perpendicular to the roof surface |

## FIGURE CAPTIONS

**Figs 1-5.** Morphology and vegetative anatomy of *L. acrocamptum.*

**Fig. 1.** Typical encrusting to lumpy growth form (UWC 10/220). Scale bar = 20 mm.

**Fig. 2.** Vertical section of the ventral region of the thallus showing a dimerous construction with non-palisade basal filament cells (b) (UWC 09/101). Scale bar = 20 µm.

**Fig. 3.** Vertical section of the central region of the thallus showing secondary pit connections (arrows) between cells of adjacent erect filaments (UWC 10/231). Scale bar = 20 µm.

**Fig. 4.** Vertical section of the dorsal region of the thallus showing a single layer of epithallial cells (e), subepithallial initials (i) and secondary pit connections between cells of adjacent erect filaments (arrows) (UWC 10/231). Scale bar = 20 µm.

**Fig. 5.** Vertical section of the dorsal region of the thallus showing multiple layers of epithallial cells (e) and subepithallial initials (i) (UWC 10/220). Scale bar = 20 µm.

**Figs 6-11.** Gametangial anatomy of *L. acrocamptum.*

**Fig. 6.** Vertical section through a spermatangial (male) conceptacle showing unbranched spermatangial systems restricted to the floor of the conceptacle chamber (black arrows). Note the buried conceptacle bearing apparently viable spermatangial systems (white arrow) (UWC 10/220). Scale bar = 50 µm.

**Fig. 7.** Vertical section through a young developing spermatangial conceptacle showing peripheral roof development (black arrowheads). Note the protective layer of epithallial cells (E) and buried conceptacles (white arrows) bearing apparently viable spermatangial systems (UWC 10/220). Scale bar = 50 µm.

**Fig. 8.** Vertical section through a mature carpogonial conceptacle showing carpogonial branches bearing a carpogonium (white arrowhead) extended into a trichogyne (t). Note the sterile

cell (black arrowhead), hypogynous cell (black arrow) and supporting cell (white arrow) (UWC 09/101). Scale bar = 20 µm.

**Fig. 9.** Vertical section through a young developing carpogonial conceptacle showing roof development from the periphery (arrowheads). Note the protective layer of epithallial cells (E) (UWC 09/101). Scale bar = 50 µm.

**Fig. 10.** Vertical section through a carposporangial conceptacle showing peripherally arranged gonimoblast filaments each terminating in a carposporangium (g). The remains of unfertilised carpogonial branches (arrow) persist across the dorsal surface of the central fusion cell. Note the inflated papillate cells (arrowheads) that project into the pore canal (UWC 09/101). Scale bar = 50 µm.

**Fig. 11.** Magnified view of the floor of a carposporangial conceptacle showing a discontinuous central fusion cell (arrowheads) bearing a peripherally arranged gonimoblast filament (1-4) terminating in a carposporangium (5). The remains of unfertilised carpogonial branches (arrow) persist across the dorsal surface of the central fusion cell (UWC 09/101). Scale bar = 20 µm.

**Figs 12-13.** Tetrasporangial anatomy of *L. acrocamptum* (UWC 10/231).

**Fig. 12.** Vertical section through a flush conceptacle bearing tetrasporangia (t) distributed peripherally around a conspicuous central columella (C). Scale bar = 50 µm.

**Fig. 13.** Vertical section through a buried immature tetrasporangial conceptacle bearing tetrasporangial initials (t) distributed peripherally around a conspicuous central columella (C). Note the remains of the interspersed filaments (arrowheads) that gave rise to the conceptacle roof. Scale bar = 50 µm.

**Figs 14-17.** Morphology and vegetative anatomy of *L. neoatalayense* (UWC 11/20).

**Fig. 14.** Typical encrusting to lump growth form with convoluted margins. Scale bar = 20 mm.

**Fig. 15.** Vertical section of the ventral region of the thallus showing a dimerous construction with non-palisade basal filament cells (b). Scale bar = 20 µm.

**Fig. 16** Vertical section of the central region of the thallus showing secondary pit connections (arrows) between cells of adjacent erect filaments. Scale bar = 20 µm.

**Fig. 17.** Vertical section of the dorsal region of the thallus showing multiple epithallial cell layers (e) and subepithallial initials (i). Scale bar = 20 µm.

**Figs 18-23.** Gametangial anatomy of *L. neoatalayense*.

**Fig. 18.** Vertical section through a spermatangial (male) thallus showing conceptacles both at the surface (S) and buried in the thallus (arrows) (UWC 10/138). Scale bar = 100 µm.

**Fig. 19.** Vertical section through a young developing spermatangial conceptacle showing peripheral roof development (black arrowheads) and unbranched spermatangial systems restricted to the floor (white arrowheads) of the conceptacle chamber. Note the protective layer of epithallial cells (E) (UWC 10/138). Scale bar = 50 µm.

**Fig. 20.** Magnified view of a spermatangial conceptacle showing papillate cells lining the pore canal (arrowheads) and unbranched spermatangial systems (arrow) restricted to the conceptacle floor (UWC 10/138). Scale bar = 20 µm.

**Fig. 21.** Vertical section through a carpogonial (female) conceptacle showing the cone-shaped pore canal structure and occlusion of the pore opening (arrow) (UWC 10/135). Scale bar = 40 µm.

**Fig. 21 insert.** Magnified view of the carpogonial branches bearing a carpogonium (white arrowhead) extended into a trichogyne (t), the sterile cell (black arrowhead), hypogynous cell (black arrow) and supporting cell (white arrow) (UWC 10/135). Scale bar = 10 µm.

**Fig. 22.** Vertical section through a carposporangial conceptacle showing peripherally arranged gonimoblast filaments each terminating in a carposporangium (g). The pore opening is occluded by a mucilage plug (arrow). Note the inflated, papillate pore canal cells (black arrowheads) that project into the pore canal and the ring of enlarged cells (white arrowheads) at the base of the pore canal (UWC 10/138). Scale bar = 60 µm.

**Fig. 23.** Magnified view of the floor of a carposporangial conceptacle showing a discontinuous central fusion cell (arrowheads) bearing a peripherally arranged gonimoblast filament (1-6) terminating in a carposporangium (7). The remains of unfertilised carpogonial branches (arrow) persist across the dorsal surface of the central fusion cell (UWC 10/138). Scale bar = 20 µm.

**Figs 24-25.** Tetrasporangial anatomy of *L.neoatalayense* (UWC 10/138).

**Fig. 24.** Vertical section through a raised conceptacle bearing tetrasporangia (t) distributed peripherally around a weakly calcified central columella (C). Note the occluded pore opening (arrow) and the remains of the interspersed filaments (arrowheads) that gave rise to the conceptacle roof. Scale bar = 50 µm.

**Fig. 25.** Magnified view through a conceptacle pore canal showing single layer of enlarged papillate cells (arrowheads) that are orientated more or less perpendicularly to the roof surface. Scale bar = 20 µm.

**Figs 26-30.** Morphology and vegetative anatomy of *T. corallinae*.

**Fig. 26.** Typical encrusting growth form showing many thin individual crusts with upgrowing margins (UWC 10/111). Scale bar = 20 mm

**Fig. 27.** Vertical section of the dimerous thallus showing a basal layer of sinuous palisade cells (b) (UWC 10/201). Scale bar = 80 µm.

**Fig. 28.** Vertical section of a dimerous bistratose margin showing the terminal initial (i), the basal filament cells (b) and a single layer of epithallial cells (e) (UWC 10/111). Scale bar = 20 µm.

**Fig. 29**. Magnified view of the ventral region of the thallus showing a basal layer of sinuous palisade cells (b). Note the secondary pit connections between cells of adjacent filaments (arrows) (UWC 10/201). Scale bar = 20 µm.

**Fig. 30.** Magnified view of the dorsal region of the thallus showing a single layer of epithallial cells (e), subepithallial initials (i) and secondary pit connections between cells of adjacent erect filaments (arrows) (UWC 10/201). Scale bar = 20 µm.

**Figs 31-35.** Gametangial anatomy of *T. corallinae*.

**Fig. 31.** Vertical section through a spermatangial (male) conceptacle showing unbranched spermatangial systems restricted to the floor of the conceptacle chamber (arrow). The pore opening is occluded by a mucilage plug (arrowhead) (UWC 10/201). Scale bar = 50 µm.

**Fig. 32.** Magnified view of the floor showing the unbranched spermatangial systems (arrow) (UWC 10/201). Scale bar = 20 µm.

**Fig. 33.** Vertical section through an immature spermatangial conceptacle showing peripheral roof development (arrowheads) and a protective layer of epithallial cells (E) (UWC 10/111). Scale bar = 50 µm.

**Fig. 34**. Vertical section through a carposporangial conceptacle showing peripherally arranged gonimoblast filaments each terminating in a carposporangium (g). Note the inflated papillate cells (arrowheads) lining the pore canal (UWC 10/111). Scale bar = 50 µm.

**Fig. 35.** Magnified view of the floor of a carposporangial conceptacle showing a discontinuous central fusion cell (arrowheads) bearing a peripherally arranged gonimoblast filament (1-5) terminating in a carposporangium (6). The remains of unfertilised carpogonial branches (arrow) persist across the dorsal surface of the central fusion cell (UWC 10/111). Scale bar = 20 µm.

**Figs 36-37.** Tetrasporangial anatomy of *T. corallinae* (UWC 10/111).

**Fig. 36** Vertical section through a raised conceptacle bearing tetrasporangia (t) distributed peripherally around a large conspicuous central columella (C). The pore opening is occluded by a mucilage plug (arrow). Scale bar = 50 µm.

**Fig. 37.** Magnified view through a young developing conceptacle showing peripherally distributed tetrasporangial initials (t), the developing central columella (C), the roof development both from filaments peripheral to the fertile area as well as from filaments interspersed amongst the developing sporangial initials (arrowheads), and the protective layer of epithallial cells (E). Scale = 20 µm.

**Figs 38-41.** Morphology and vegetative anatomy of *T. polycephalum*.

**Fig. 38**. A typical lumpy growth form (UWC COR 185). Scale bar = 20 mm.

**Fig. 39**. Vertical section of the ventral region of the thallus showing a dimerous construction with a basal layer of sinuous palisade cells (b). Note the secondary pit connections (arrows) between cells of adjacent filaments (UWC COR 16). Scale bar = 20 µm.

**Fig. 40** Vertical section of a dimerous bistratose margin showing the terminal initial (i), the basal filament cells (b) and a single layer of epithallial cells (arrowheads) (UWC COR 185). Scale bar = 20 µm.

**Fig. 41**. Magnified view of the dorsal region of the thallus showing a single layer of epithallial cells (e), subepithallial initials (i) and secondary pit connections between cells of adjacent erect filaments (arrows) (UWC COR 16). Scale bar = 20 µm.

**Figs 42-43.** Tetrasporangial anatomy of *T. polycephalum* (UWC COR 16).

**Fig. 42** Vertical section through a raised, near senescent conceptacle bearing tetrasporangia (t) distributed peripherally around a conspicuous central columella (C). Scale bar = 100 µm.

**Fig. 43.** Magnified view through an unoccluded conceptacle pore canal showing enlarged papillated cells (arrowheads) lining the base of the pore canal. Scale bar = 20 µm.

**Figs 44-47.** Morphology and vegetative anatomy of *T. pustulatum*.

**Fig. 44**. Encrusting thalli epiphytic on the stipe of *Ecklonia radiata* (UWC 10/226). Scale bar = 20 mm

**Fig. 45.** Vertical section of the dimerous thallus showing a basal layer of sinuous palisade cells (b), subepithallial initials (i) and a single layer of epithallial cells (arrowhead) (UWC 10/223). Scale bar = 50 µm.

**Fig. 46.** Vertical section of a dimerous bistratose margin showing the terminal initial (i), the basal filament cells (b) and a single layer of epithallial cells (arrowheads) (UWC 10/200). Scale bar = 20 µm.

**Fig. 47.** Magnified view of the ventral region of the thallus showing a basal layer of sinuous palisade cells (b). Note the secondary pit connections between cells of adjacent filaments (arrows) (UWC 10/223). Scale bar = 20 µm.

**Figs 48-52**. Gametangial anatomy of *T. pustulatum*.

**Fig. 48.** Vertical section through a spermatangial (male) conceptacle showing unbranched spermatangial systems restricted to the floor of the conceptacle chamber (arrow) (UWC 10/223). Scale bar = 50 µm.

**Fig. 49**. Magnified view of the floor of a spermatangial conceptacle showing the unbranched spermatangial systems (arrow) (UWC 10/223). Scale bar = 20 µm.

**Fig. 50.** Vertical section through a near fully developed carpogonial (female) conceptacle showing carpogonial branches distributed across the conceptacle floor (UWC 10/200). Scale bar = 50 µm.

**Fig. 50 insert.** Magnified view of the carpogonial branches bearing a carpogonium (white arrowhead) extended into a trichogyne (t), the sterile cell (black arrowhead), hypogynous cell (black arrow) and supporting cell (white arrow) (UWC 10/200). Scale bar = 10 µm.

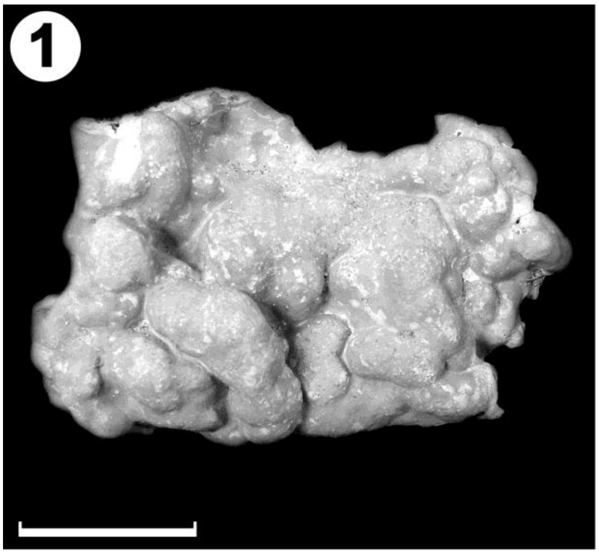
**Fig. 51.** Vertical section through a carposporangial conceptacle showing a raised central fusion cell (white arrows) bearing peripherally arranged gonimoblast filaments each terminating in a carposporangium (g). Note that the pore opening is occluded by a mucilage plug (white arrowhead) and the pore canal is lined by inflated papillate cells (black arrowheads). The remains of unfertilised carpogonial branches (black arrow) persist across the dorsal surface of the central fusion cell (UWC 10/200). Scale bar = 50 µm.

**Fig. 52**. Magnified view of the floor of a carposporangial conceptacle showing a distinctly raised (white arrows) discontinuous central fusion cell (black arrowheads) bearing a peripherally arranged gonimoblast filament (1-4) terminating in a carposporangium (5). The remains of unfertilised carpogonial branches (black arrow) persist across the dorsal surface of the central fusion cell (UWC 10/200). Scale bar = 20 µm.

**Figs 53-54.** Tetrasporangial anatomy of *T. pustulatum* (UWC 10/223).

**Fig. 53** Vertical section through a raised conceptacle bearing tetrasporangia (t) distributed peripherally around a weakly calcified central columella (C). Note the utricles (H) of the host alga, *Codium extricatum*. Scale bar = 100 µm.

**Fig. 54**. Magnified view through a conceptacle showing the peripherally distributed tetrasporangia (t), the weakly calcified central columella (C), the occluded pore opening (white arrow) and the enlarged cells (black arrows) lining the pore canal. Note the remains of the interspersed filaments (black arrowheads) that gave rise to the conceptacle roof. Scale = 50 µm**.**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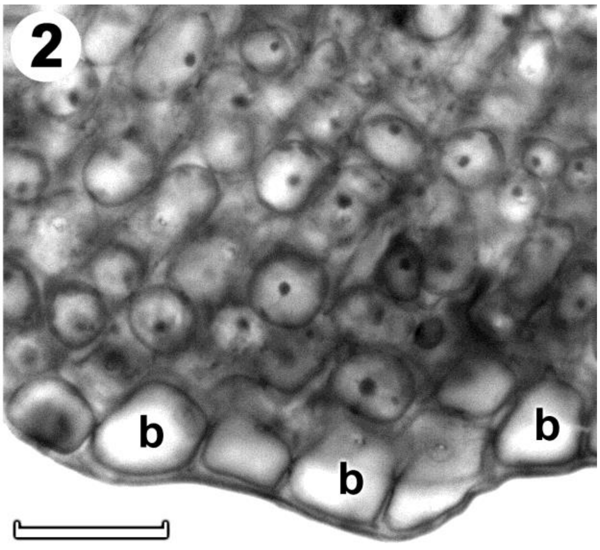
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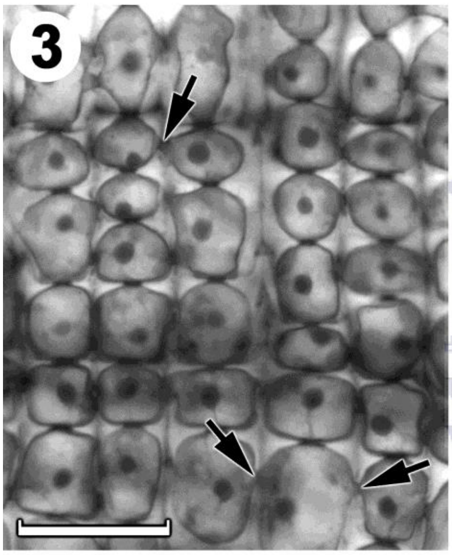
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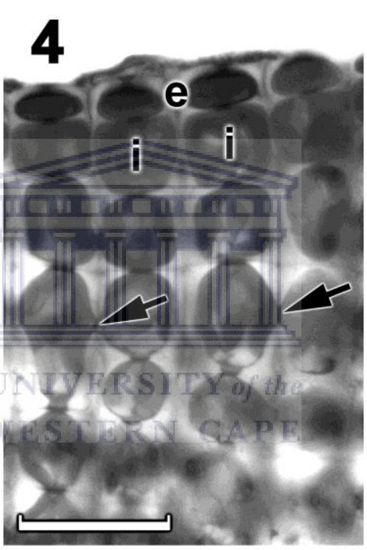
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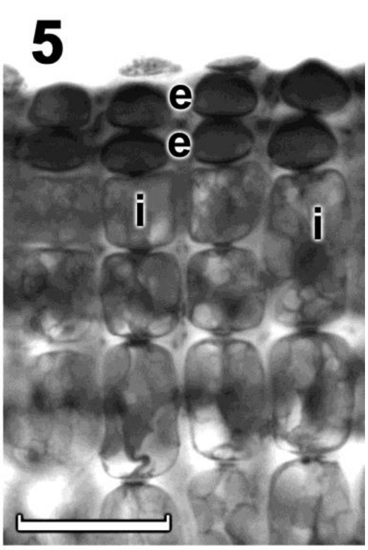
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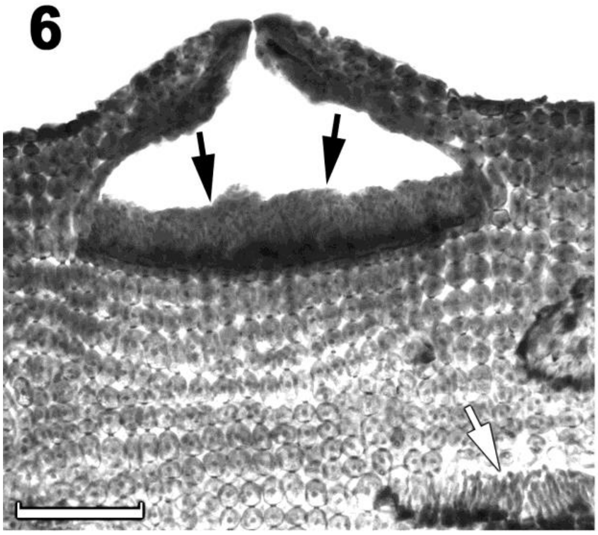
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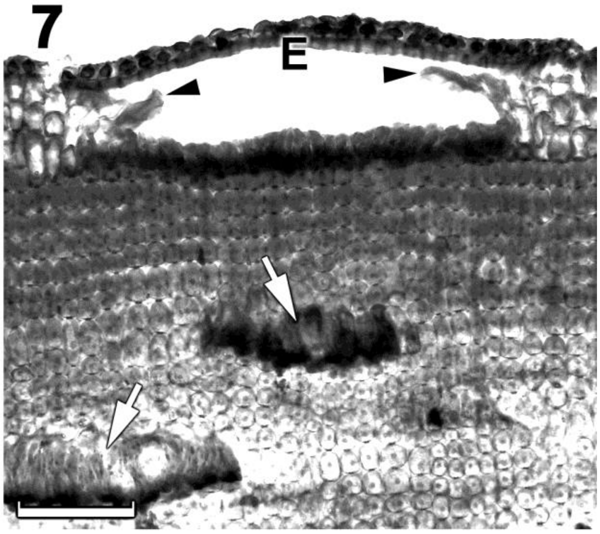
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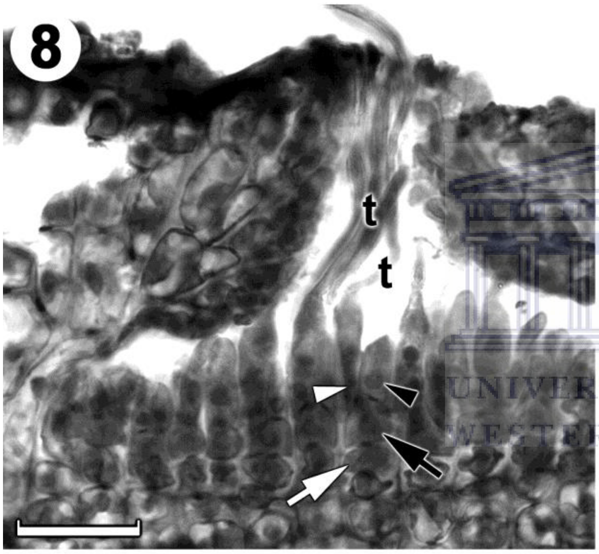
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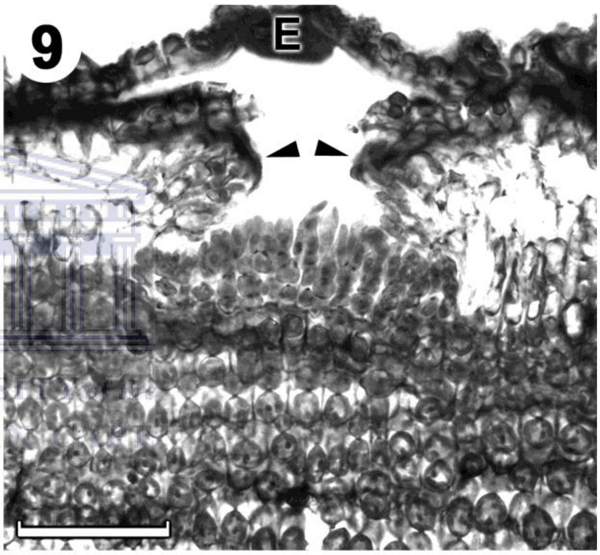
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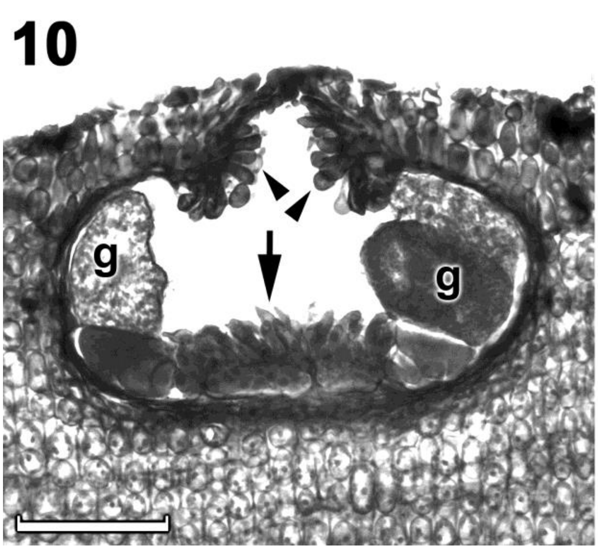
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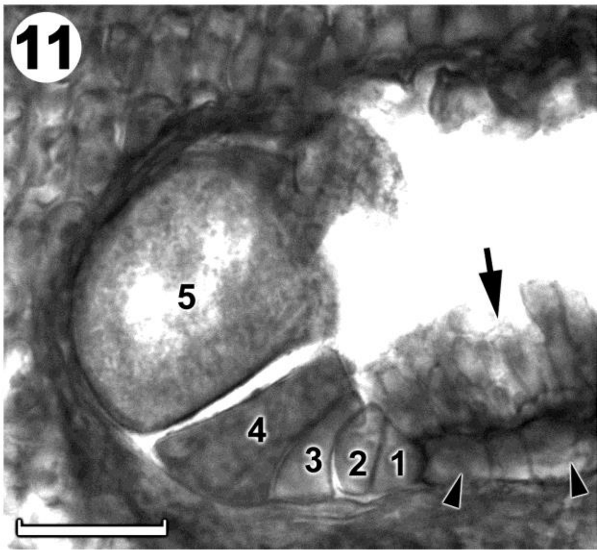
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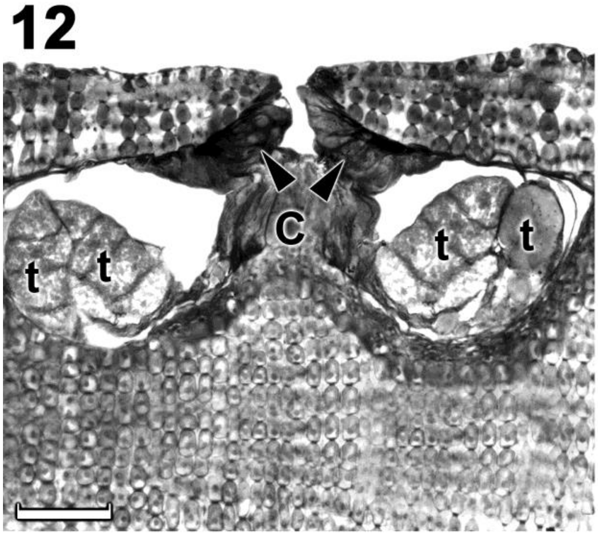
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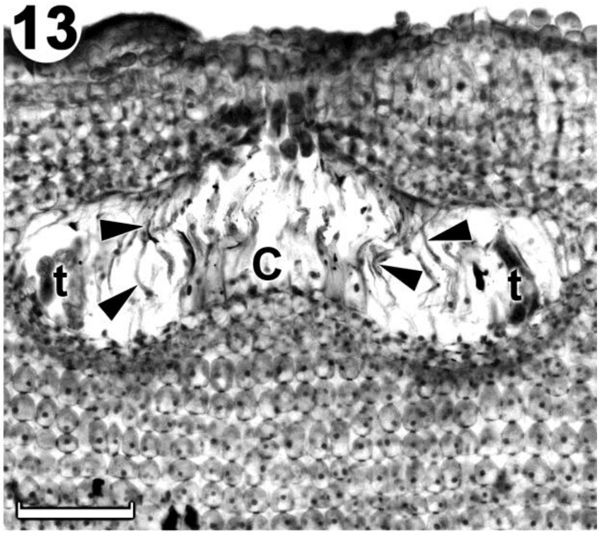
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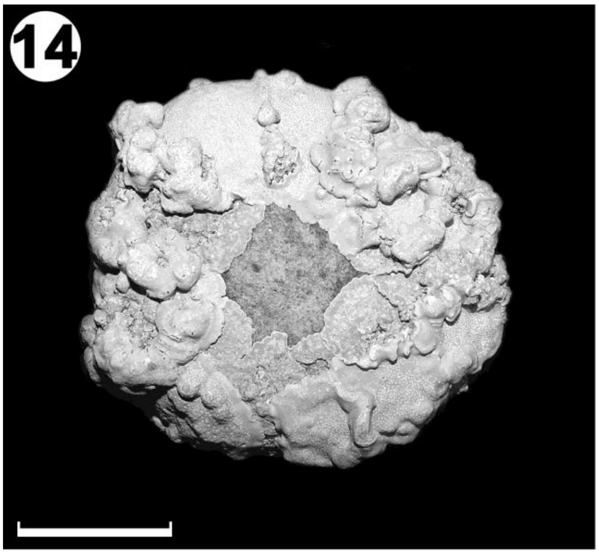
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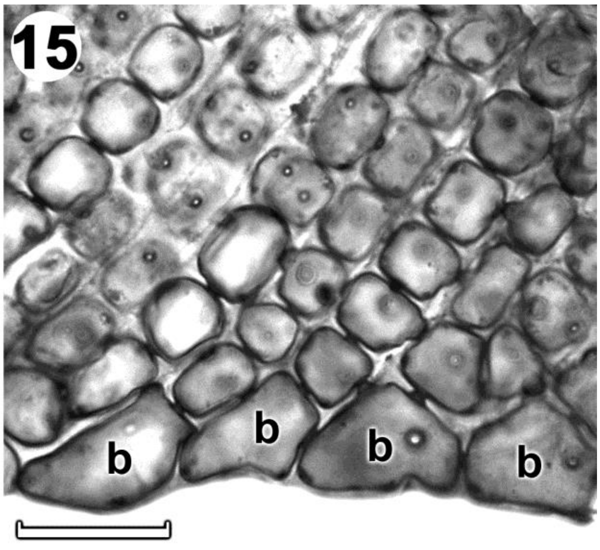
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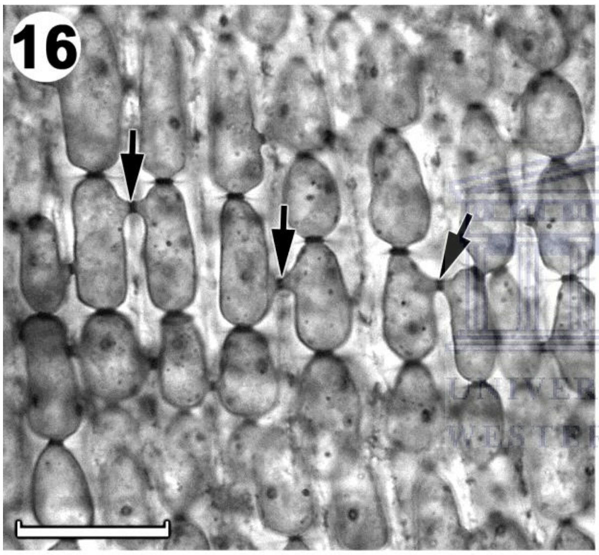
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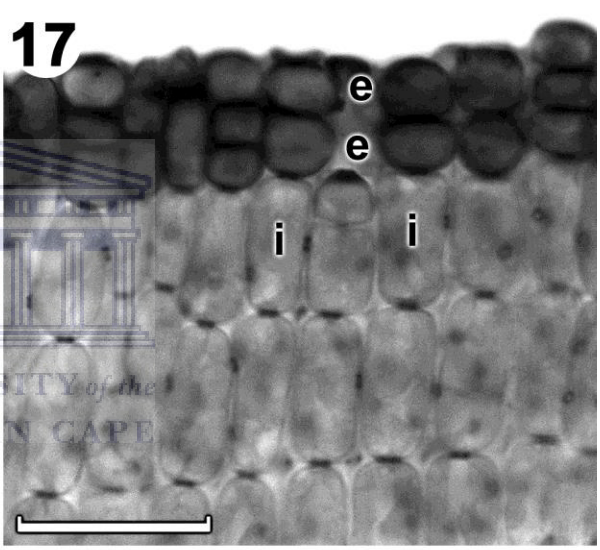
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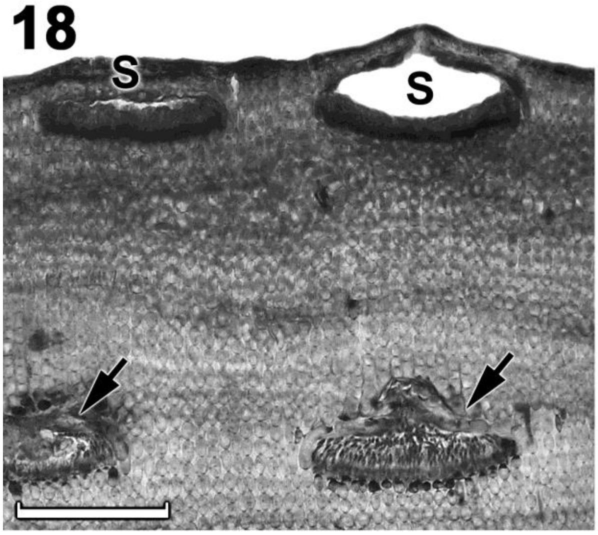

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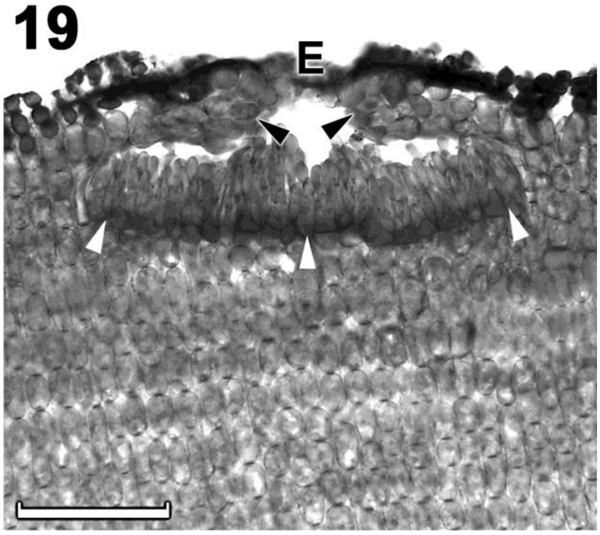

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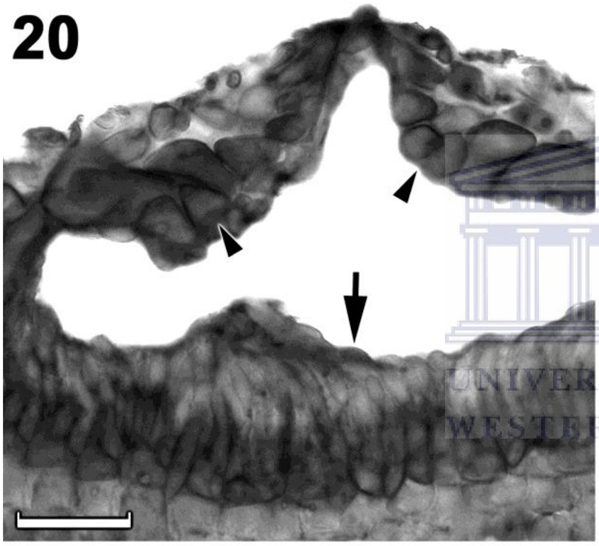

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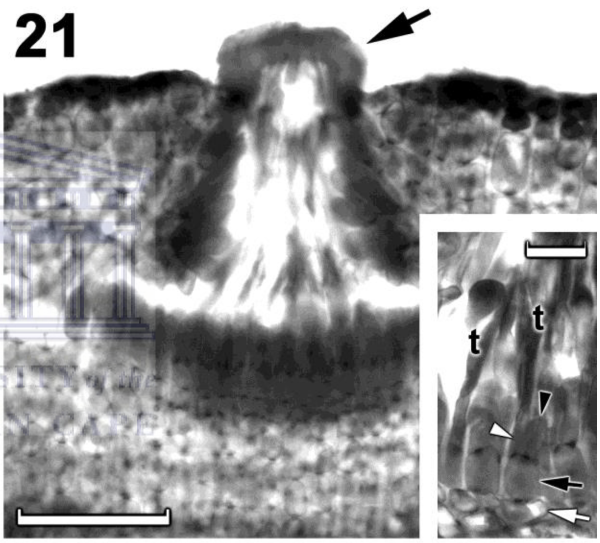

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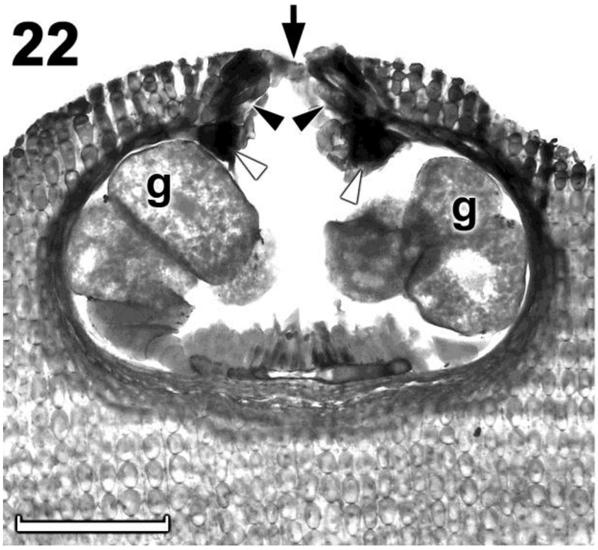

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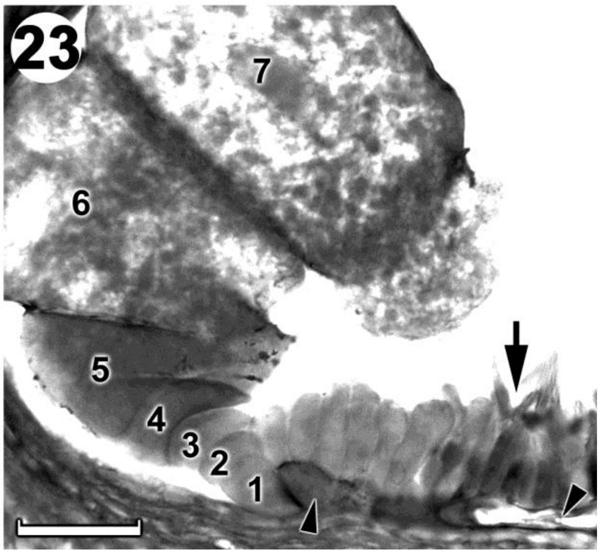

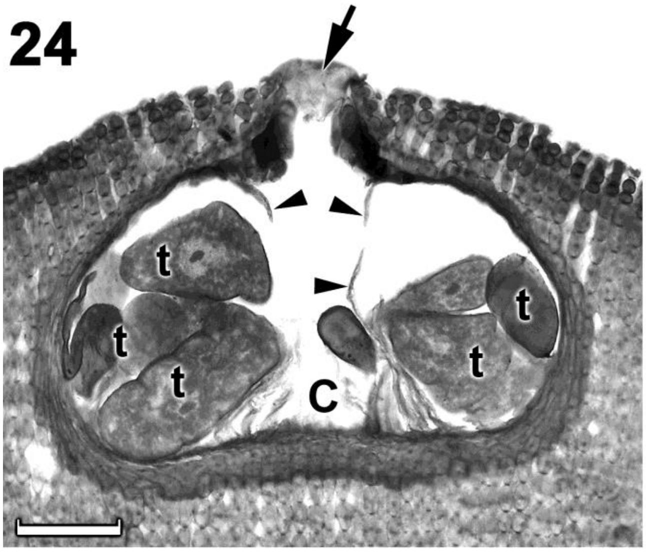
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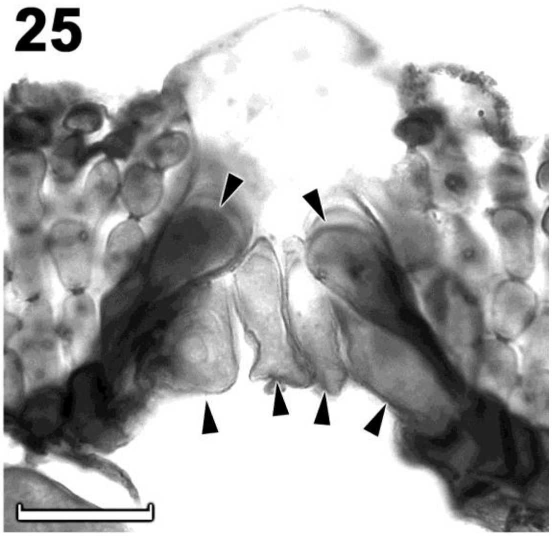
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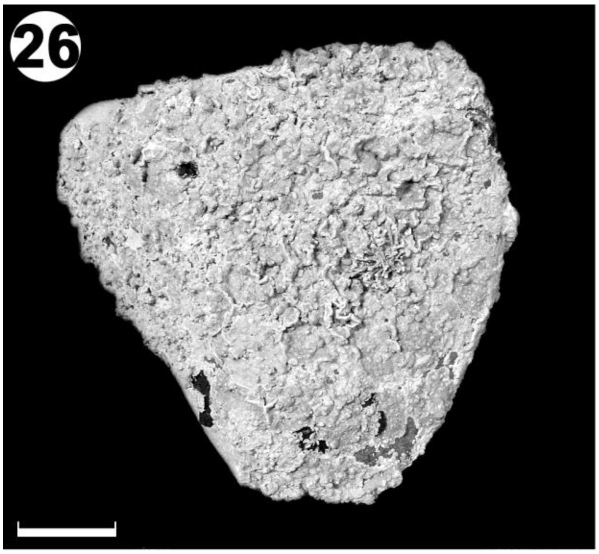
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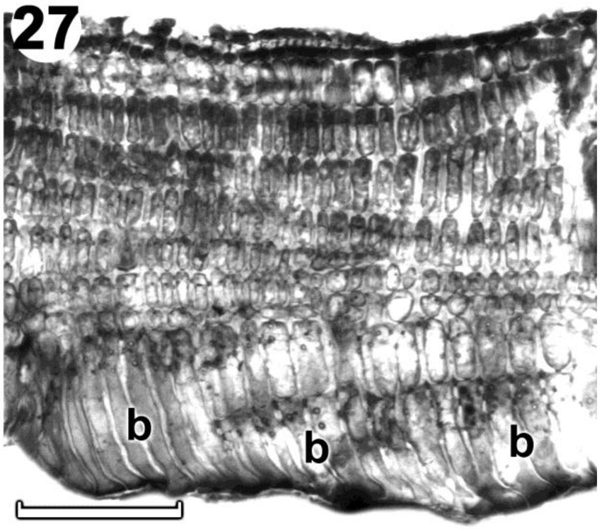
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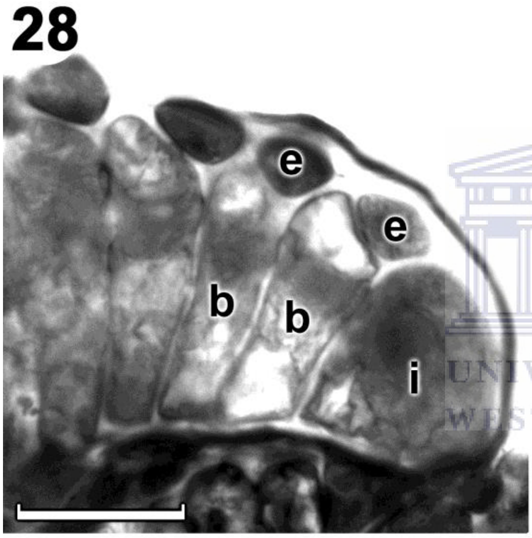
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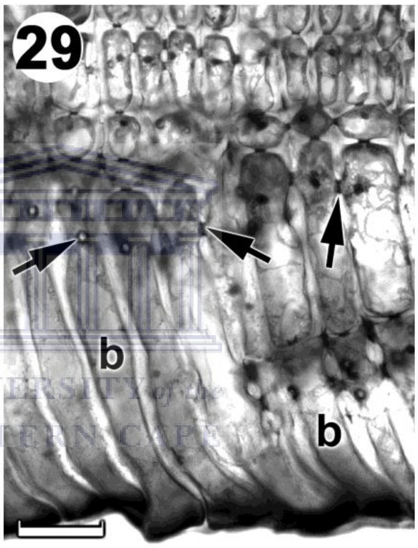
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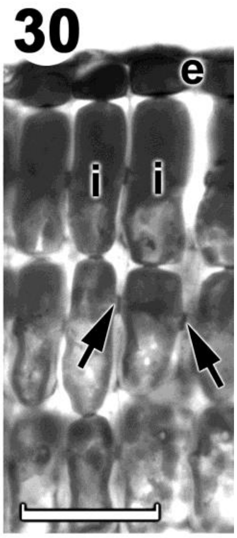
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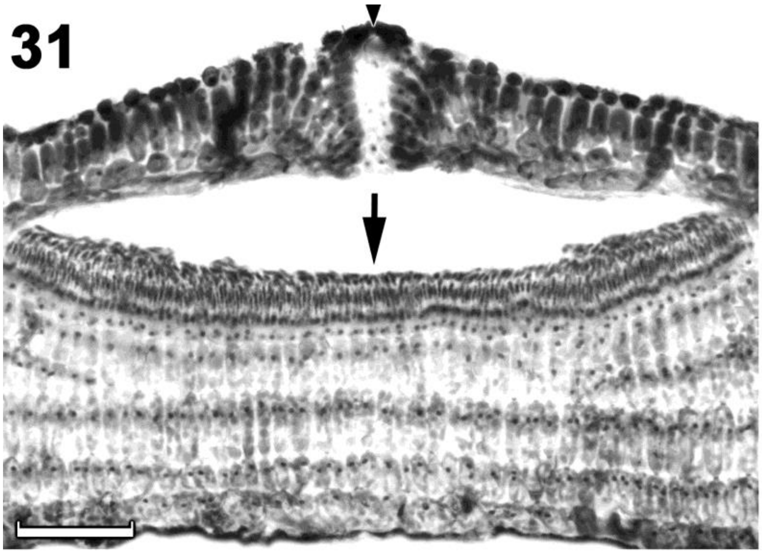
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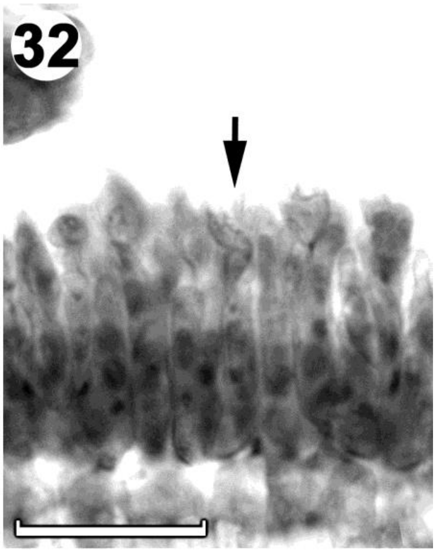
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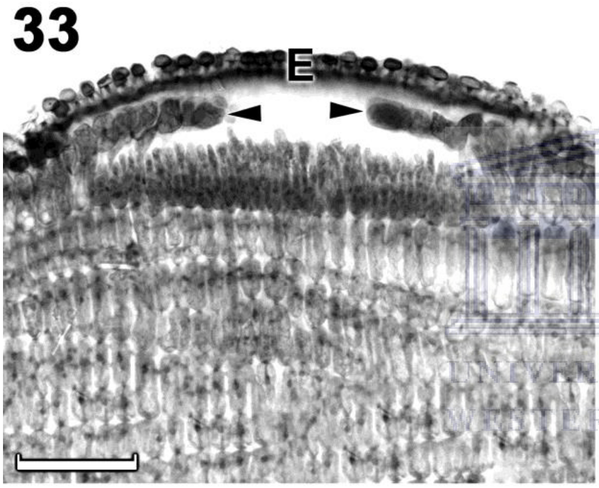
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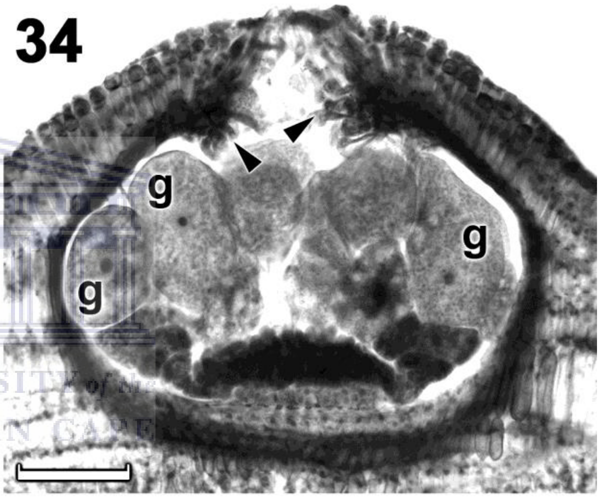
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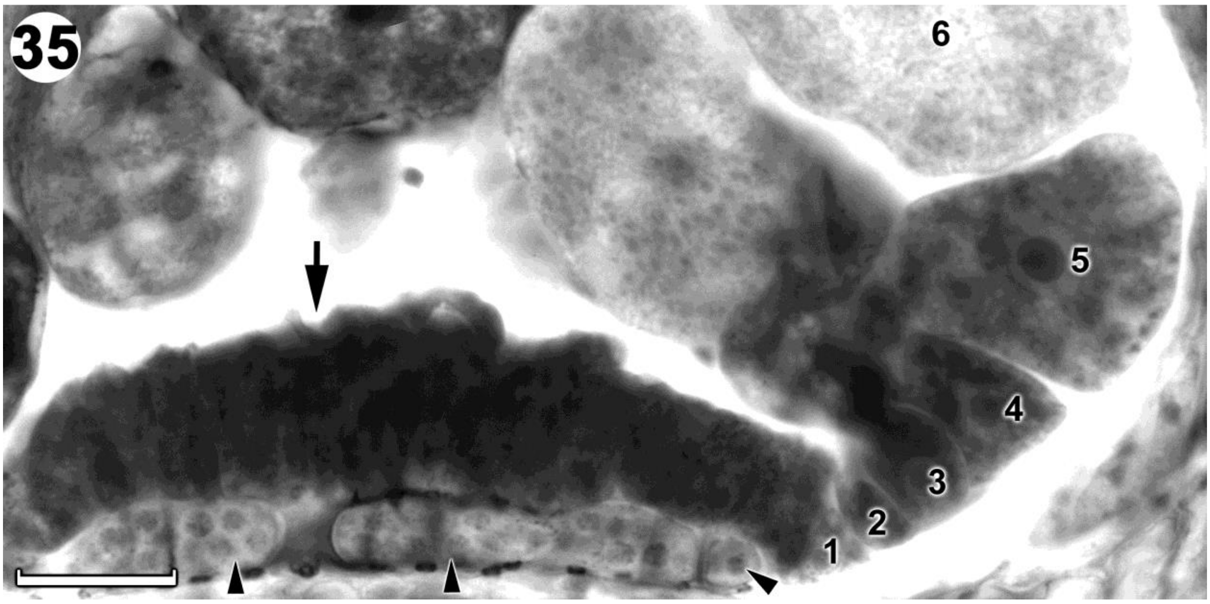
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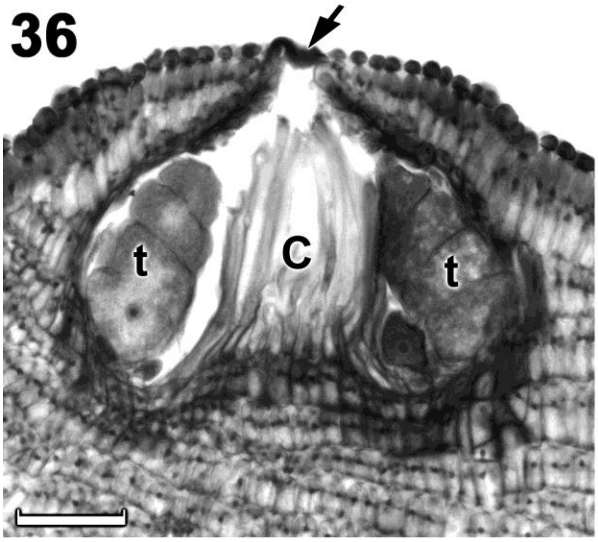
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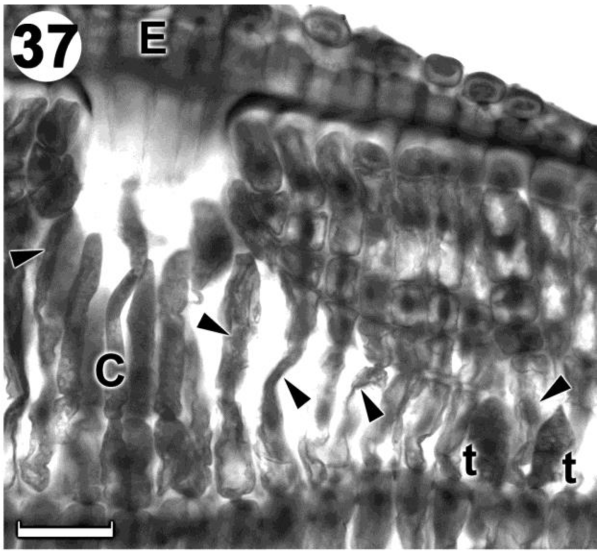
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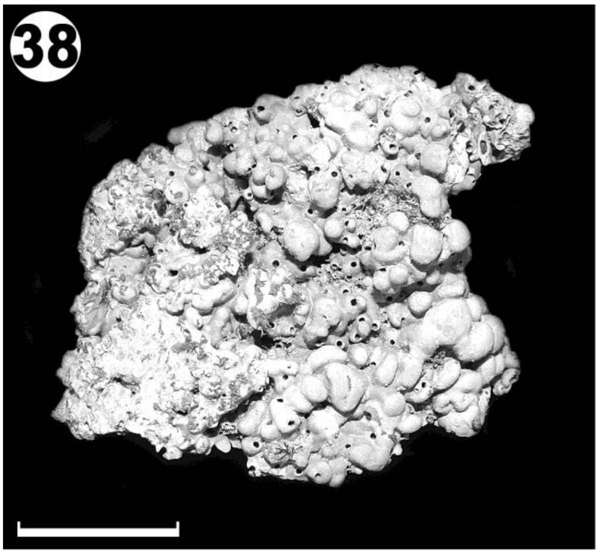
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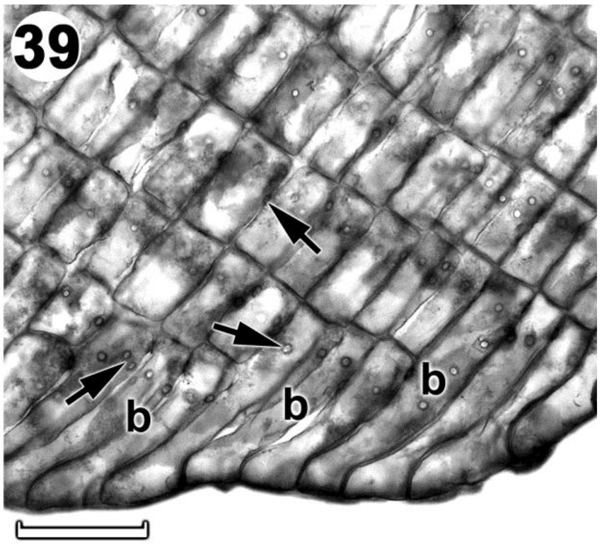
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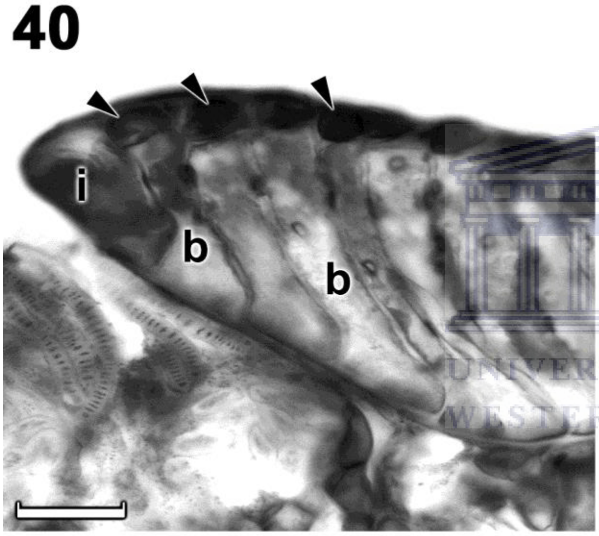
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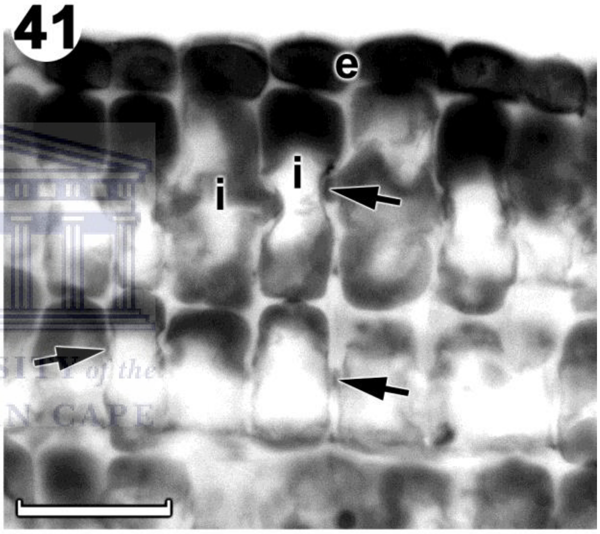
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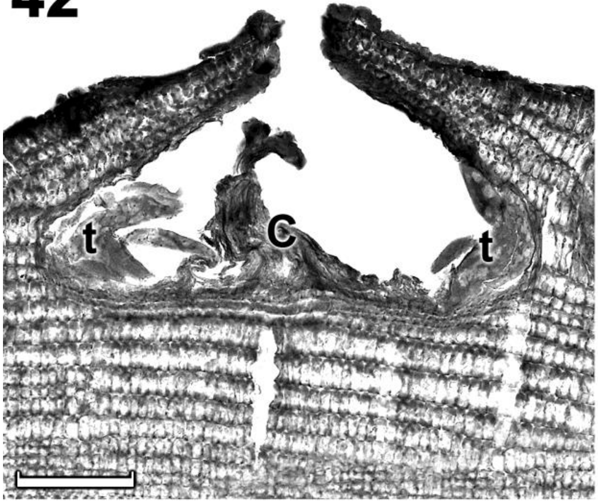

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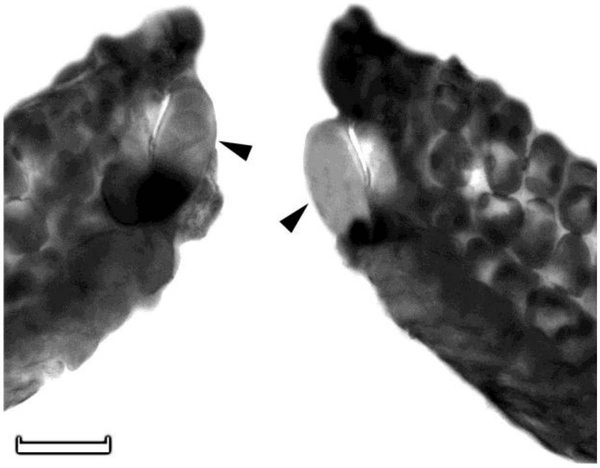


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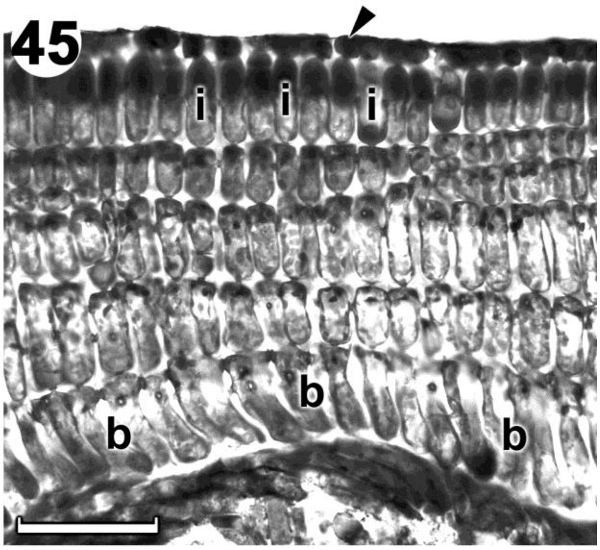
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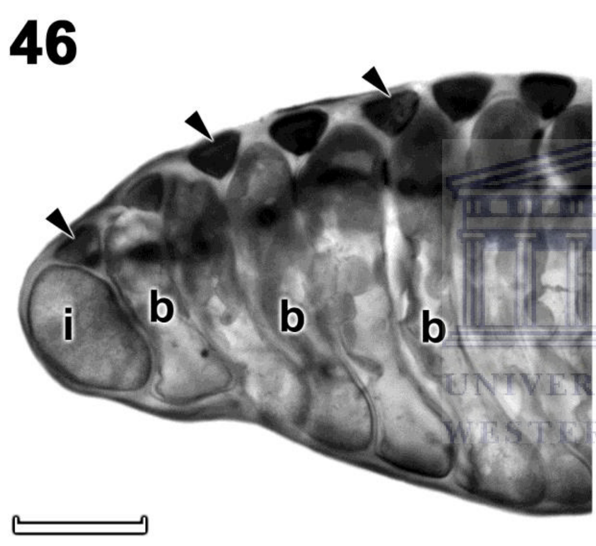
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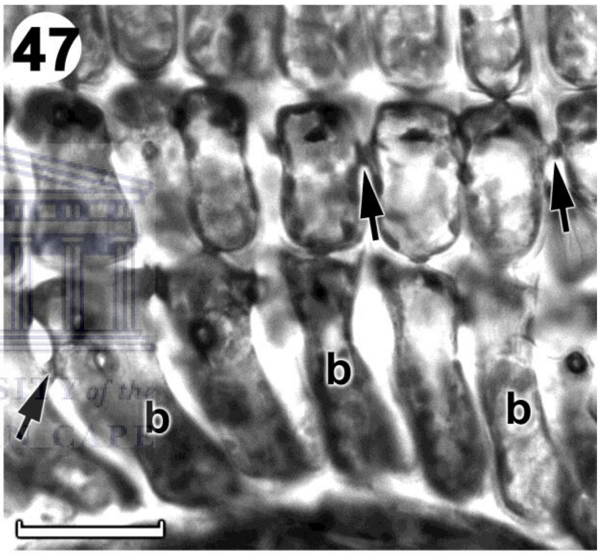
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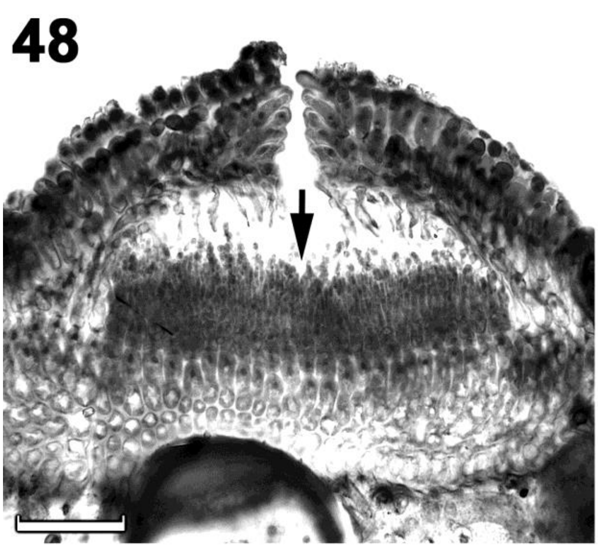

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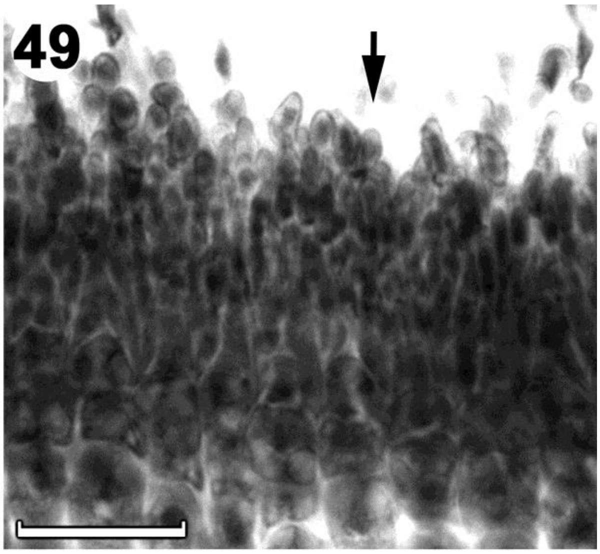

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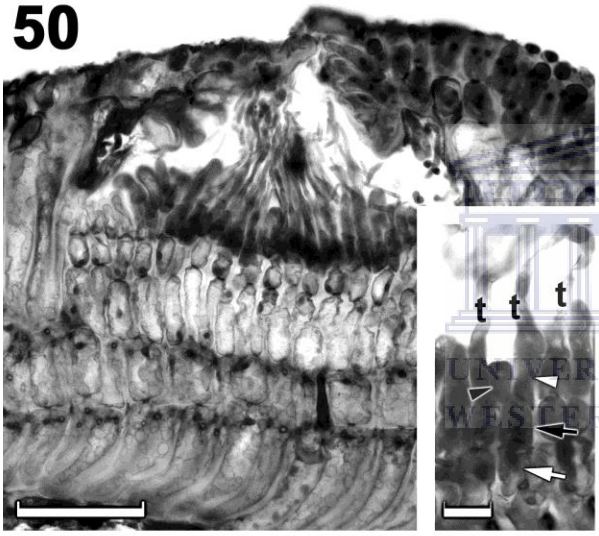

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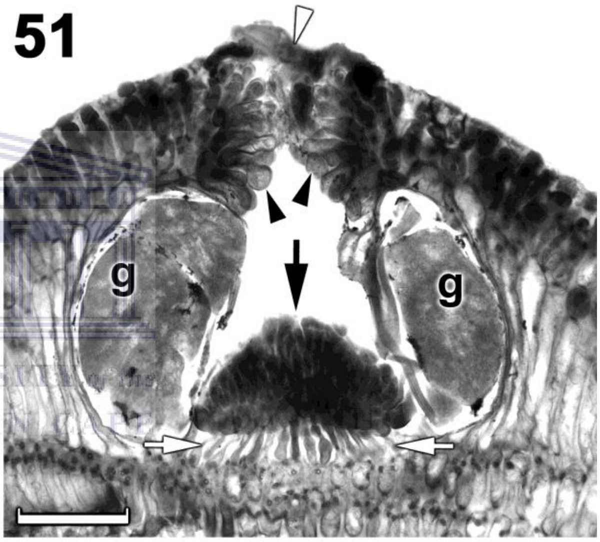

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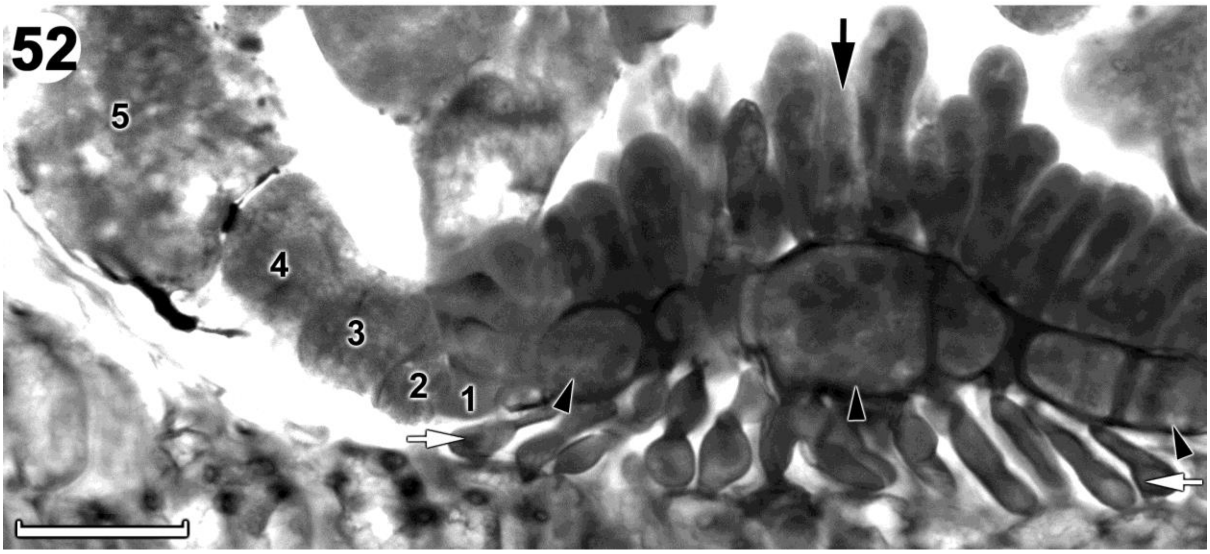

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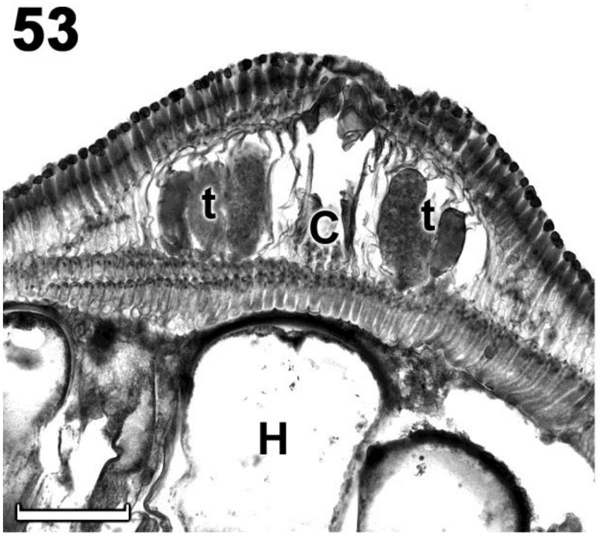

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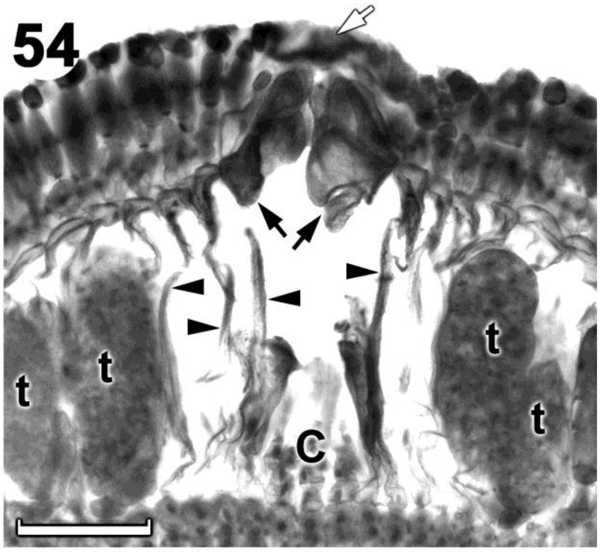

## 6.1. The current state of non-geniculate coralline algal diversity in South Africa

### 6.1.1. Between 2008 and the present

The catalogue with keys by Maneveldt *et al*. (2008) represents the most up to date assimilated account of the non-geniculate coralline algae for South Africa. In that account, references to papers published between 1993 and 2000, as well as the older records, were gathered to document the well delimited families (3), subfamilies (4), genera (17) and species (43) then known to exist for the country. Since the account by Maneveldt *et al*. (2008), and largely as a consequence of the use of molecular tools to supplement taxonomic reporting, much has changed with regards the systematics of the coralline algae. Most notably was the establishment of the subclass Corallinophycideae (Le Gall and Saunders, 2007), the recognition of the orders Sporolithales (Le Gall *et al*., 2010) and Hapalidiales (Nelson *et al*., 2015), and various subfamilies (e.g. Hydrolithoideae, Neogoniolithoideae, Porolithoideae) within the family Corallinaceae (Kato *et al*., 2011). As a consequence of the changes proposed over the past eight years, many amendments (e.g. Mastophoroideae, Kato *et al*., 2011; Corallinales, Nelson *et al*., 2015) have been affected and many genera resurrected (e.g. *Porolithon*, Bittner *et al*., 2011, Kato *et al*., 2011) re-defined (e.g. *Mesophyllum*, Athanasiadis and Ballantine, 2014), and still other new genera proposed (e.g. *Melyvonnea*, Athanasiadis and Ballantine, 2014; *Corallinapetra*, Nelson *et al*., 2015).

In light of the sampling gap in the Maneveldt *et al*. (2008, 558; see map of the sampling locations), the aim of this study was to document the intertidal and shallow subtidal species of non-geniculate coralline red algae from the South Africa south coast. As a consequence of more focused collections along the South African south coast, currently 45 species of non-geniculate coralline red algae, belonging to three orders (Corallinales, Hapalidiales, Sporolithales), three families (Corallinaceae, Hapalidiaceae, Sporolithaceae), seven subfamilies (Choreonematoideae, Hydrolithoideae, Lithophyloideae, Mastophoroideae, Melobesioideae, Neogoniolithoideae, Porolithoideae) and 17 genera (*Choreonema*, *Clathromorphum*, *Heydrichia*, *Hydrolithon*, *Lithophyllum*, *Lithothamnion*, *Melobesia*, *Mesophyllum*, *Metamastophora*, *Neogoniolithon*, *Phymatolithon* , *Pneophyllum*, *Porolithon*, *Spongites*, *Sporolithon*, *Synarthrophyton* , *Titanoderma*) are now known to occur along the South African coast (Table 6.5.1.). Based solely on the findings from the current study, this represents an addition of two species new to science (*H. cerasina*, *S. agulhensis*), the formal transfer of all species previously ascribed to *Leptophytum* to the genus *Phymatolithon*, and a revision of the species ascribed to the subfamily Lithophylloideae in which we retain the genera *Lithophyllum* and *Titanoderma*.

However, although only two species have been added to the diversity of South African non-geniculate coralline red algae, our molecular evidence has pointed to a large number of cryptic species (Figure 6.6.1.), suggesting that the true species diversity for South Africa could be as much as two times what we currently recognise based solely on anatomy and morphology. Maneveldt *et al*. (2008) commented on the high diversity of non-geniculate coralline red algae for the South African coastline in comparison to other regions where comparable research investment has been made, but cautioned on the merits of this statement in light of the significant ongoing taxonomic revisions to the group at that time. Based on recent molecular data (not just from this study, but also from across the globe) it appears that we have highly underestimated the diversity of the non-geniculate coralline algae.

Other findings from the current research include the following.

1. *Phymatolithon repandum* (Maneveldt *et al*. (2008), *Titanoderma corallinae* (Chamberlain and Norris, 1994: 14, Chamberlain, 1996: 219) and *T. pustulatum* (Barton, 1893: 202, Adey and Lebednik, 1967: 38, Seagrief, 1984: 39, Farrell *et al*., 1993: 152, Chamberlain and Norris, 1994: 292, Chamberlain, 1996: 219) were previously only listed as occurring along the South Africa coastline. The current research represents the first study to provide detailed descriptions of these species that have previously been reported for Australia, Great Britain and New Zealand.
2. We have documented range extensions for a number of species including *Heydrichia groeneri, Lithophyllum neoatalayense, Phymatolithon foveatum, Pneophyllum coronatum, Spongites discoidea, Synarthrophyton eckloniae, Synarthrophyton munimentum*, and *Synarthrophyton papillatum* (Table 6.5.2.).

### 6.1.2. The genus *Phymatolithon*

The status and generic disposition of those South African species (*L. acervatum, L. ferox, L. foveatum*) previously ascribed to the genus *Leptophytum* have remained unresolved ever since Düwel and Wegeberg (1996) determined from a study of relevant types and other specimens that *Leptophytum* Adey was a heterotypic synonym of *Phymatolithon* Foslie. *Phymatolithon*, as delimited by Harvey *et al*. (2003), is the only known genus in the family Hapalidiaceae that: 1) possesses subepithallial initials that are as short as or shorter than the cells immediately subtending them; and 2) produces both branched (dendroid) and unbranched (simple) spermatangial filaments in male conceptacles. In addition to the other family characteristics, South African *P. acervatum, P. ferox* and *P. foveatum*, possess these characters currently considered diagnostic of *Phymatolithon* and so rightly belong in the genus. The current research has shown that features used to segregate the genus *Leptophytum* from *Phymatolithon* do not stand up to scrutiny and are unreliable for generic delimitation. We reiterate that the name *Leptophytum* is not available for use as a result of the study of Düwel and Wegeberg (1996).

### 6.1.3. The genera *Lithophyllum* and *Titanoderma*

Within the Lithophylloideae, the non-geniculate genera *Lithophyllum* and *Titanoderma* have probably been the most contentious in recent years. While some authors (Campbell and Woelkerling, 1990, Woelkerling and Campbell, 1992) consider *Titanoderma* to be a heterotypic synonym of *Lithophyllum* (arguing that the morphological criteria proposed to separate the two genera do not stand up to rigorous testing), others (Chamberlain and Irvine, 1994a, Chamberlain, 1996, Keats, 1997) consider *Titanoderma* to be a distinct genus from *Lithophyllum*. Molecular evidence currently available (e.g. Bailey, 1999; Bittner et al., 2011) supports the placing of type species of *Lithophyllum* and *Titanoderma* in separate genera. Our data supports this latter view as we have found no difficulty in assigning species to either *Titanoderma* or *Lithophyllum* on the basis of the characters proposed to separate them.

## 6.2 Keys to the non-geniculate coralline algae of South Africa

Here a key (modified from Maneveldt *et al*., 2008) to the South African species of non-geniculate coralline algae is presented. This key is designed for South African specimen identification only and the characters used in the key are not necessarily diagnostic of the species to which they pertain. In this key, thallus terminology follows Chamberlain (1990) and growth-forms terminology follows Woelkerling *et al*. (1993).

### 6.2.1. Key to the orders of Corallinophycidae

1. Tetra/bisporangia cruciately divided, borne singly within calcified compartments in diffuse sori …...…..………………………………………………………. Sporolithales

   Tetra/bisporangia zonately divided, multiple tetra/bisporangia borne in roofed conceptacles ..…….……………………………………………………………......… 2

2. Tetra/bisporangia borne in uniporate conceptacles that lack apical plugs ……………………………………………...…………………..….. Corallinales

   Tetra/bisporangia borne in multiporate conceptacles that bear apical plugs ……………………………………………………………………….. Hapalidiales

The orders Corallinales, Hapalidiales and Sporolithales currently comprise only one family each namely Corallinaceae, Hapalidiaceae[5] and Sporolithaceae respectively. Except for the genus *Corallinapetra* within the Hapalidiaceae (see footnote), these family names conform to the characterisation of the orders.

### 6.2.2. Key to the subfamilies of Corallinaceae

1. Secondary pit connections predominant; cell fusions absent or comparatively rare .……………………………………………………………………….. Lithophylloideae

   Cell fusions predominant; secondary pit connections absent or comparatively rare ……………………………………………………………………………...….…… 2

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[5] Nelson *et al*. (2015) recently raised the Hapalidiaceae to ordinal level and described a new genus (*Corallinapetra*) and species (*C. novaezelandiae*). *Corallinapetra novaezelandiae*, however, does not conform to the characterisation of the Hapalidiaceae and a new family and subfamily still needs to be established to accommodate the new genus and species.

2. Basal layer consisting of predominantly palisade cells …….……….…… Mastophoroideae[6]

   Basal layer consisting of predominantly non-palisade cells …………………..........…. 3

3. Trichocytes present in large tightly packed horizontal fields ………..….. Porolithoideae

   Trichocytes absent in large tightly packed horizontal fields ………………..……..…… 4

4. Tetra/bisporangial conceptacles formed by filaments peripheral to the fertile area as well as interspersed among the tetra/bisporangial initials; spermatangia restricted to the floor of the male conceptacle ……………………………………...……….. Hydrolithoideae

   Tetra/bisporangial conceptacles formed only by filaments peripheral to the fertile area; spermatangia developing on the floor, walls and roof of the male conceptacle ……………………………………………………………………….. Neogoniolithoideae

### 6.2.3. 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 predominant, secondary pit connections absent or comparatively rare; tetra/bisporangial conceptacle pore plate composed of cells at maturity …..……………………………………………………………………….….. Melobesioideae

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[6] Within the modern characterisation of the Corallinaceae (Kato *et al*., 2011), the genera *Spongites* and *Pneophyllum* still remains unresolved with regards their placement in a subfamily.

### 6.2.4. Key to the genera of Sporolithaceae, Corallinaceae and Hapalidiaceae

1. Tetra/bisporangia cruciately divided, borne singly within calcified compartments in diffuse sori ................................................ 2

Tetra/bisporangia zonately divided, multiple tetra/bisporangia borne in roofed conceptacles ................................................ 3

2. Tetra/bisporangia with a single stalk cell ................................ *Sporolithon*

Tetra/bisporangia with up to 5 stalk cells ................................ *Heydrichia*

3. Tetra/bisporangial conceptacles uniporate ................................ 4

Tetra/bisporangial conceptacles multiporate ................................ 11

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 predominantly non-palisade cells; primary and regenerating thallus lacking a bistratose margin ................................ *Lithophyllum*

Basal filaments composed of predominantly palisade cells; primary and 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 surrounded at their base by a ring of enlarged, vertically orientated cells ................................ 8

Tetra/bisporangial conceptacle pores lined by small papillate cells initially lying more or less parallel to roof surface, sometimes later becoming long and filamentous ................ 9

8. Trichocytes present in large tightly packed horizontal fields ................ *Porolithon*

Trichocytes absent in large tightly packed horizontal fields ................ *Hydrolithon*

9. Tetra/bisporangial conceptacles formed by filaments peripheral to the fertile area as well as interspersed among the tetra/bisporangial initials ……….…………….….. *Pneophyllum*

   Tetra/bisporangial conceptacles formed only by filaments peripheral to the fertile area ……………………………………………………………………..........……...…… 10

10. Spermatangia restricted to the floor of the male conceptacle; gonimoblast filaments arising only from the margins of the fusion cell in carposporangial conceptacles ………………..……..…………………..……................……………………. *Spongites*

    Spermatangia developing on the floor, walls and roof of the male conceptacle; gonimoblast filaments arising dorsally from fusion cells in carposporangial conceptacles ………………………………….................................….……….. *Neogoniolithon*

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

    Vegetative thallus epiphytic, epilithic and/or epizoic, but not endophytic ..……....….. 12

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

    Thallus monomerous, conceptacles not characteristically dark-centred ..……........... 13

13. Epithallial cells with flared outer walls ……….………............….….…..... *Lithothamnion*

    Epithallial cells without flared outer walls ..……………………........….………….. 14

14. Spermatangial systems simple throughout …..……....................................................... 15

    Spermatangial systems dendroid …………………………………………….………… 16

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 (deep) within the thallus from ordinary vegetative cells; subepithallial cells as short as or shorter than subtending cells ……………………………...................................................................…….. *Phymatolithon*

    Tetra/bisporangial conceptacles initiated superficially within the subepithallial layer; subepithallial cells usually as long as or longer than subtending cells ………….............................................................................................. *Synarthrophyton*

### 6.2.5. Key to the 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 mostly encrusting (smooth), but also lumpy, generally occurring on boulders and the primary bedrock ……………………………………………………………………….. 4

   Thallus warty, occurring only on small (ranging from 10–40 mm along the long axis) pebbles ……………………………………………..………...…... *Heydrichia cerasina*
4. Thallus thin, less than 1 mm thick ………………………………….. *Heydrichia groeneri*

   Thallus very thick (up to 15 mm) and generally massively discoid in appearance ……………………………………………………….…………. *Heydrichia woelkerlingii*

### 6.2.6. Key to the Hydrolithoideae

1. Thalli thin, epiphytic; with dimerous internal construction ……………..……..……… 2

   Thalli thin to thick, epilithic; with predominantly monomerous internal construction … 3

2. Thalli to 150 µm thick; reproductively mature thalli no more than 2-5 cells thick ............……………………………………………………..……..... *Hydrolithon farinosum*

   Thalli to 370 µm thick; reproductively mature thalli more than 5 cells thick ....................…………………………………………….....……….. *Hydrolithon pellire*

3. 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*

   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; colour of living thalli gleaming dark red ...……………….……….......…....…. *Hydrolithon samöense*

### 6.2.7. Key to the Lithophylloideae

1. Basal filaments composed of predominantly non-palisade cells; primary and regenerating thallus lacking a bistratose margin ………………………………………………........... 2

   Basal filaments composed of predominantly palisade cells; primary and regenerating thallus margin bistratose ………………….……………….......................……………. 4

2. Tetra/bisporangial conceptacle pore lined with long, vertically orientated filaments …………………………………………..……………….. *Lithophyllum neoatalayense*

Tetrasporangial conceptacle pore unelaborated or lined with papillate cells orientated more or less parallel to roof surface ………………………………………...……….. 3

3. Tetra/bisporangial conceptacle roof 3-5 cells thick, pore canal short, tapering markedly towards the pore …………………………………...………. *Lithophyllum acrocamptum*

   Tetra/bisporangial conceptacle roof 6-17 cells thick, pore canal long, with more or less parallel sides …………………………………......……………...... *Lithophyllum incrustans*

4. Thalli epilithic, lumpy, becoming massive and protuberant .......................................................................................... *Titanoderma polycephalum*

   Thalli mainly epiphytic, sometimes epilithic or epizoic, comprising thin, encrusting, featureless thalli ............................................................................................................ 5

5. Tetra/bisporangial conceptacles more or less flush with surrounding thallus surface or slightly raised above it, conceptacle floor immersed up to 7 cells deep in thallus …..................................................................................….…..... *Titanoderma corallinae*

   Tetra/bisporangial conceptacles markedly raised above the surrounding thallus surface, conceptacles with floor immersed no more than 3 cells deep in thallus ………………………………...............................……...…. *Titanoderma pustulatum*

### 6.2.8. Key to the Mastophoroideae[7]

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

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[7] Within the modern characterisation of the Corallinaceae (Kato *et al*., 2011), the genera *Spongites* and *Pneophyllum* still remains unresolved with regards their placement in a subfamily. For this reason, the two genera have been maintained in the key under the Mastophoroideae in which subfamily they had previously been assigned.

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

   Thallus thin to thick, epiphytic, epilithic, or epizoic ……………………….............….. 3

3. Thallus epiphytic, encrusting on *Ecklonia maxima* stipes and/or holdfasts and various red algae ……………………...…………………………...……………………………... 4

   Thalli epilithic or epizoic ............…………………………………………..……..…... 6

4. Thalli with very prominent raised conceptacles, only known on *Ecklonia* ……………………………………………………………….…. *Pneophyllum coronatum*

   Thalli with flush conceptacles ..……………...……………………………………...….. 5

5. Thalli epiphytic on *Ecklonia* and red algal hosts; with a single layer of epithallial cells; subepithallial initials only slightly elongate ………………………...... *Pneophyllum fragile*

   Thalli epiphytic only on *Ecklonia*; with up to 4 layers of epithallial cells; subepithallial initials markedly elongate ……………………..……………..………... *Pneophyllum keatsii*

6. Thalli forming a band on the mid-shore; surface wrinkled like an elephant's skin, crusts becoming thick and encrusting; margins often growing back-to-back to form convoluted crests; colour of living thalli yellowish to beige ……………….……….. *Spongites impar*

   Thalli thin and encrusting; margins not growing back-to-back to form convoluted crests, but merging ………….……………………………………….…………….........…… 7

7. Thalli initially thin and encrusting, but giving rise to thick, discoid to crested crusts on top of thin crusts …………………………..….........………...... *Spongites discoideus*

   Thalli primarily and uniformly thin and encrusting to only slightly warty ...................... 8

8. Colour of living thalli brownish-pink; individuals usually easily discernible, not coalescing (fusing); predominant on high to mid shore ……….….. *Spongites agulhensis*

Colour of living thalli greyish to beigish to blueish mauve; individual crusts coalescing to form large indistinguishable expanses; predominant on mid- to low shore, especially together with the limpet *Scutellastra cochlear* …………………..….... "*Spongites yendoi*"[8]

### 6.2.9. Key to the Neogoniolithoideae

The genus *Neogoniolithon* is represented by only one species in South Africa. The features diagnostic of the subfamily and genus (see above) therefore can be used to distinguish this species from others ...……..............................…….………. *Neogoniolithon brassica-florida*

### 6.2.10. Key to the Porolithoideae

The genus *Porolithon* is represented by only one species in South Africa. The features diagnostic of the subfamily and genus (see above) therefore can be used to distinguish this species from others ……………...………………………..................…… *Porolithon onkodes*

### 6.2.11. Key to the 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 (see above) therefore can be used to distinguish this species from others …..........… *Choreonema thuretii*

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[8] "*Spongites yendoi*" is used in inverted commas here because current molecular evidence suggests that this species in South Africa comprises at least five different cryptic species.

### 6.2.12. Key to the Melobesioideae

1. Thalli thin, with dimerous internal construction; usually epiphytic ….......................................................................................… *Melobesia membranacea*

   Thalli thin to thick, with monomerous internal 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 crispatum*

   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 encrusting; 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.; crusts distinctly discoid; conceptacle roof raised and dome-like, 750-1300 µm in diameter ……………….................. *Synarthrophyton patena*

   Epiphytic on *Gelidium capense*; crusts not distinctly discoid; conceptacles truncated and conical with sunken pore plate, 450-900 µm in diameter …........… *Mesophyllum capense*

8. Thalli thin and encrusting; surface pitted with sunken conceptacles ................................ 9

   Thalli thick and encrusting, or protuberant, or layered ……………….……………….. 10

9. Thalli mostly epilithic on pebbles and small boulders in intertidal rock pools; living specimens bright pink in colour; thallus surface mat-like with a pitted appearance ………...………..………………………………..........……... *Phymatolithon acervatum*

   Thalli epilithic on the primary bedrock in the low intertidal zone, living specimens brownish-pink in colour; thallus glossy and covered in secondary margins giving the thallus an imbricate appearance …………………..........………. *Phymatolithon foveatum*

10. Thalli loosely adherent on the primary bedrock and on worm tubes; living specimens mauvish grey in colour; thalli mostly warty to lumpy and producing numerous secondary margins that form mouth-like structures were they meet .................. *Phymatolithon ferox*

    Thalli firmly adherent on the primary bedrock; living specimens variable in colour from reddish to brownish to purplish; thalli encrusting to fruticose without conspicuous secondary margins that form mouth-like structures …...................................….….…….. 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 encrusting with minute, low, irregularly domed papillae fused into scroll-like patterns, conceptacles 185-330 µm in external diameter, with shallowly depressed pore plate ......................................................................................... *Synarthrophyton robbenense*

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

13. Tetra/bisporangial conceptacles arising adventitiously (deep) 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 superficially within the subepithallial initials, subepithallial initials as long as or longer than subtending cells ................................... 14

14. Male conceptacles with only simple spermatangial systems ......................................... 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 in diameter), conceptacle roof composed of filaments 7-10 cells long …………...……......….. *Mesophyllum funafutiense*

Tetra/bisporangial conceptacles rarely exceeding 600 µm in diameter, conceptacle 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*

Tetra/bisporangial conceptacles low-domed, thalli adherent, but later producing free, overlapping lamellae, usually epilithic subtidally …...…. *Synarthrophyton magellanicum*

## 6.3. Future Research

The current study has accumulated over 300 specimens, 155 of which have been reported on in this thesis. While a large number of specimens were not able to be positively identified, largely because they were either infertile or did not have enough reproductive characters, a substantial number of specimens belonging to the genera *Clathromorphum*, *Hydrolithon Lithothamnion*, *Melobesia*, *Mesophyllum*, *Pneophyllum*, *Spongites*, *Synarthrophytum*, and *Heydrichia*, which are not documented here, were also encountered. The majority of the specimens positively identified, which are not reported on in this thesis, belong to taxa that have been already well documented for South Africa (e.g. Keats and Chamberlain, 1993, 1994a, 1994b, 1995, 1997; Chamberlain and Norris, 1994; Townsend *et al*., 1994; Chamberlain *et al*., 1995; Keats and Maneveldt, 1997a, 1997b; Keats *et al*., 2000; Maneveldt *et al*., 2007), and so have not been repeated. This said, much new data, particularly pertaining to gametangial material, has been obtained for already well-documented species and these would provide the basis for further monographic accounts of the genera and subfamilies of non-geniculate coralline algae for South Africa.

The genus most notably presenting much opportunity for future research in South African is the genus *Spongites*. While anatomy, ecology and distributions are useful in separating the South African species of *Spongites*, DNA sequence data has forced us to question the practice of placing into synonymy geographically widely separated specimens (and species) of non-geniculate coralline algae. For example, *psb*A sequences deposited in GenBank from 28 specimens called *S. yendoi* from New Zealand are not the same species as South African material called *S. yendoi*. Furthermore, several specimens we have sequenced, which initially were classified as *S. yendoi*, proved to be genetically different from the ecological (the species is characteristically found as the basal coralline on the low shore intertidal zone in the *Scutellastra cochlear* zone) concept of *S. yendoi* in South Africa (Figure 6.6.1). Consequently, we find that we must question whether any of the sequenced material from either South Africa or New Zealand called *S. yendoi* is conspecific with type (or ‘topotype’) material, which incidentally has yet to be sequenced. This suggests that there exists a large number of cryptic species posing under the name of *S. yendoi* in South Africa and probably also New Zealand, and also provides ample opportunities for future research.

### 6.4. Concluding Remarks

The current research has resulted in a number of new additions to the studies on the biodiversity of the South African non-geniculate coralline red algae. First, two species (*Heydrichia cerasina* and *Spongites agulhensis*) new to science, which appear to be range-restricted endemics, have been documented and described. Second, for the first time, detailed descriptions are provided for species only previously reported for the South African coastline. Third, the current research has documented range extensions for a number of already well-known species. Fourth, the status and generic disposition of South African species previously ascribed to the genus *Leptophytum* have now been resolved and all species have been formally transferred to the genus *Phymatolithon*. In addition, new data on gametangial material, ecological and morphological/anatomical comparisons, and a review of the information on the various features previously used to separate *Leptophytum* and *Phymatolithon*, are also provided. Fifth, a detailed modern account is provided of the South African species ascribed to the Lithophylloideae with comparisons from other geographic localities where the same species have been described in detail. Lastly, updated keys to all the currently recognised taxa of non-geniculate coralline algae for South Africa are provided. Probably the most exciting outcome of the current research are the opportunities for future research particularly that proposed by our DNA sequencing data that has suggested a large degree of cryptism within the non-geniculate coralline algae. This study has re-affirmed South Africa as a region rich in coralline algal diversity.

## 6.5. Tables

**Table 6.5.1. Species of non-geniculate coralline red algae currently recognized for South Africa.**

| **Corallinales** |
|---|
| *Hydrolithon farinosum* (J.V.Lamouroux) Penrose & Y.M.Chamberlain |
| *Hydrolithon pellire* Y.M.Chamberlain & R.E.Norris |
| *Hydrolithon samoënse* (Foslie) Keats & Y.M.Chamberlain |
| *Hydrolithon superficiale* Keats & Y.M.Chamberlain |
| *Lithophyllum acrocamptum* Heydrich |
| *Lithophyllum incrustans* Philippi |
| *Lithophyllum neoatalayense* Masaki |
| *Metamastophora flabellata* (Sonder) Setchell |
| *Neogoniolithon brassica-florida* (Harvey) Setchell & L.R.Mason |
| *Pneophyllum amplexifrons* (Harvey) Y.M.Chamberlain & R.E.Norris |
| *Pneophyllum coronatum* (Rosanoff) Penrose |
| *Pneophyllum fragile* Kützing |
| *Pneophyllum keatsii* Y.M.Chamberlain |
| *Porolithon onkodes* (Heydrich) Foslie |
| *Spongites agulhensis* Maneveldt, E.Van der Merwe & P.W.Gabrielson |
| *Spongites discoideus* (Foslie) Penrose & Woelkerling |
| *Spongites impar* (Foslie) Y.M.Chamberlain |
| *Spongites yendoi* (Foslie) Y.M.Chamberlain |
| *Titanoderma corallinae* (P.L.Crouan & H.M.Crouan) Woelkerling, Y.M.Chamberlain & P.C.Silva |
| *Titanoderma polycephalum* Woelkerling, Y.M.Chamberlain & P.C.Silva |
| *Titanoderma pustulatum* (J.V.Lamouroux) Nägeli |
| **Hapalidiales** |
| *Choreonema thuretii* (Bornet) F.Schmitz |
| *Clathromorphum tubiforme* Y.M.Chamberlain, R.E.Norris, Keats & Maneveldt |
| *Lithothamnion crispatum* Hauck |
| *Lithothamnion muelleri* Lenormand ex Rosanoff |
| *Melobesia membranacea* (Esper) J.V.Lamouroux |

*Mesophyllum capense* (Rosanoff) Y.M.Chamberlain

*Mesophyllum engelhartii* (Foslie) Adey

*Mesophyllum erubescens* (Foslie) Me.Lemoine

*Mesophyllum funafutiense* (Foslie) Verheij

*Phymatolithon acervatum* (Foslie) Adey

*Phymatolithon ferox* (Foslie) Maneveldt & E.Van der Merwe

*Phymatolithon foveatum* (Y.M.Chamberlain & Keats) Maneveldt & E.Van der Merwe

*Phymatolithon repandum* (Foslie) Wilks & Woelkerling

*Synarthrophyton eckloniae* (Foslie) Keats & Y.M.Chamberlain

*Synarthrophyton magellanicum* (Foslie) Keats & Y.M.Chamberlain

*Synarthrophyton munimentum* Keats & Maneveldt

*Synarthrophyton papillatum* Maneveldt, Keats & Y.M.Chamberlain

*Synarthrophyton patena* (J.D.Hooker & Harvey) R.A.Townsend

*Synarthrophyton robbenense* Keats & Maneveldt

**Sporolithales**

*Heydrichia cerasina* Maneveldt & E.Van der Merwe

*Heydrichia groeneri* Keats & Y.M.Chamberlain

*Heydrichia woelkerlingii* R.A.Townsend, Y.M.Chamberlain & Keats

*Sporolithon episporum* (M.A.Howe) E.Y.Dawson

*Sporolithon ptychoides* Heydrich

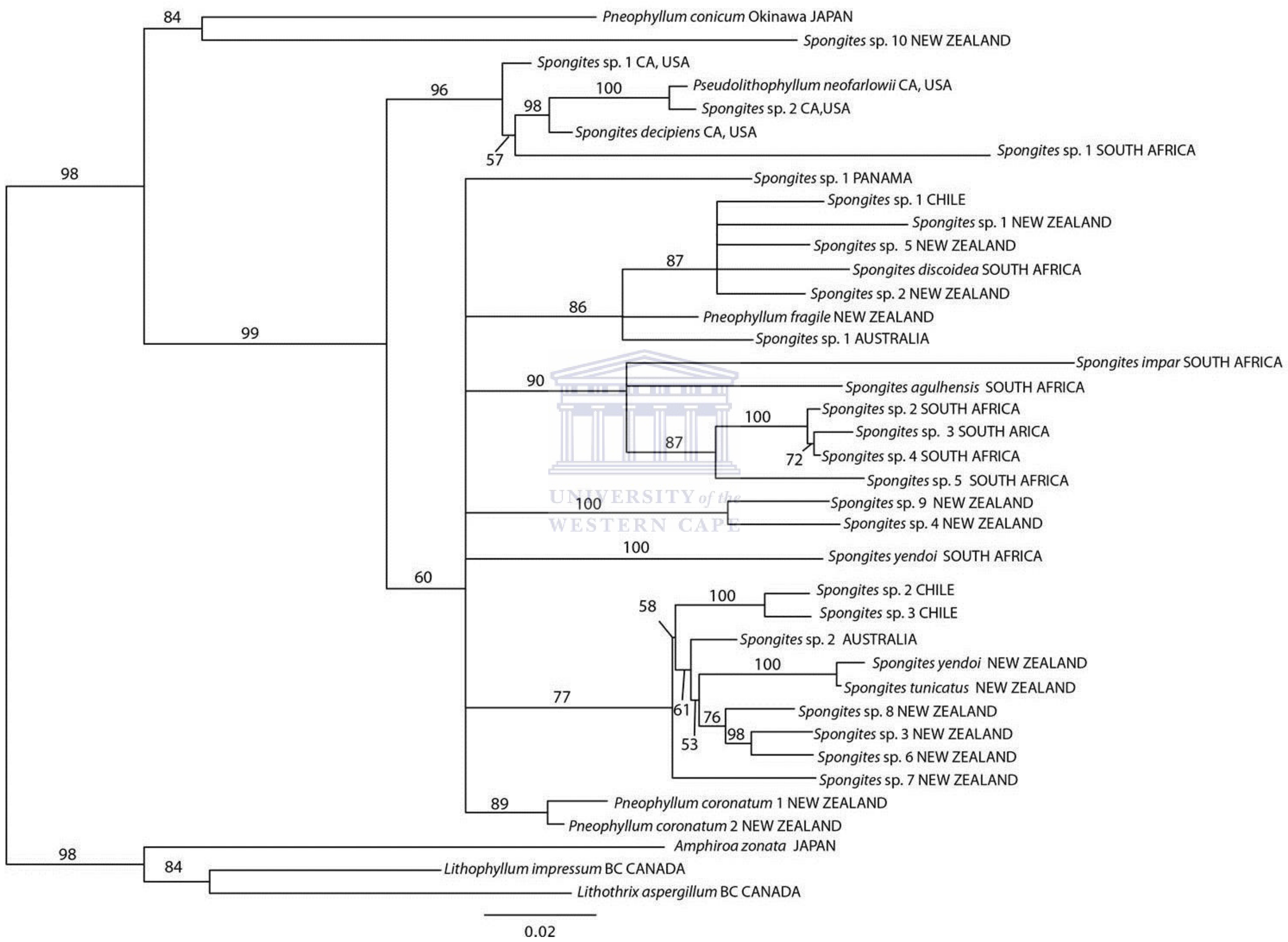
**Table 6.5.2. Species distributions along the South African coastline (adopted from Maneveldt *et al.* 2008). Highlighted cells denote recently described species and species with range extensions. Biogeographic delimitations follow Anderson *et al.* (2009).**

| **West Coast**<br>(West of Cape Agulhas) | **South Coast**<br>(East of Cape Agulhas to southern border of Kwazulu-Natal | **East Coast**<br>(East of southern border of Kwazulu-Natal) |
|---|---|---|
| *Choreonema thuretii* | *Choreonema thuretii* | *Choreonema thuretii* |
| *Clathromorphum tubiforme* | *Clathromorphum tubiforme* | |
| | *Heydrichia cerasina* | |
| *Heydrichia groeneri* | *Heydrichia groeneri* | |
| *Heydrichia woelkerlingii* | *Heydrichia woelkerlingii* | |
| | | *Hydrolithon farinosum* |
| | *Hydrolithon pellire* | *Hydrolithon pellire* |
| *Hydrolithon samoënse* | *Hydrolithon samoënse* | *Hydrolithon samoënse* |
| | | *Hydrolithon superficiale* |
| *Lithothamnion crispatum* | *Lithothamnion crispatum* | |
| *Lithothamnion muelleri* | | |
| | *Lithophyllum acrocamptum* | |
| | *Lithophyllum incrustans* | |
| *Lithophyllum neoatalayense* | *Lithophyllum neoatalayense* | |
| *Melobesia membranacea* | *Melobesia membranacea* | *Melobesia membranacea* |
| *Mesophyllum capense* | *Mesophyllum capense* | *Mesophyllum capense* |
| *Mesophyllum engelhartii* | *Mesophyllum engelhartii* | |
| *Mesophyllum erubescens* | *Mesophyllum erubescens* | *Mesophyllum erubescens* |
| | | *Mesophyllum funafutiense* |
| | | *Metamastophora flabellata* |
| | *Neogoniolithon brassica-florida* | |
| | | *Porolithon onkodes* |
| *Phymatolithon acervatum* | *Phymatolithon acervatum* | *Phymatolithon acervatum* |
| *Phymatolithon ferox* | *Phymatolithon ferox* | *Phymatolithon ferox* |
| *Phymatolithon foveatum* | *Phymatolithon foveatum* | |
| *Phymatolithon repandum* | | |
| | | *Pneophyllum amplexifrons* |

| | | |
|---|---|---|
| *Pneophyllum coronatum* | *Pneophyllum coronatum* | |
| *Pneophyllum fragile* | | |
| *Pneophyllum keatsii* | | |
| | *Spongites agulhensis* | |
| *Spongites discoidea* | *Spongites discoidea* | |
| *Spongites impar* | | |
| *Spongites yendoi* | *Spongites yendoi* | *Spongites yendoi* |
| *Sporolithon episporum* | *Sporolithon episporum* | *Sporolithon episporum* |
| | | *Sporolithon ptychoides* |
| *Synarthrophyton eckloniae* | *Synarthrophyton eckloniae* | |
| *Synarthrophyton magellanicum* | | |
| *Synarthrophyton munimentum* | *Synarthrophyton munimentum* | |
| *Synarthrophyton papillatum* | *Synarthrophyton papillatum* | |
| *Synarthrophyton patena* | *Synarthrophyton patena* | *Synarthrophyton patena* |
| *Synarthrophyton robbenense* | | |
| *Titanoderma corallinae* | *Titanoderma corallinae* | *Titanoderma corallinae* |
| *Titanoderma polycephalum* | | |
| *Titanoderma pustulatum* | *Titanoderma pustulatum* | *Titanoderma pustulatum* |

## 6.6. Figure Caption

**Fig. 6.6.1.** Consensus maximum likelihood tree inferred from concatenated *rbc*L and *psb*A sequences. Numbers above nodes are bootstrap values.


84
Pneophyllum conicum Okinawa JAPAN
Spongites sp. 10 NEW ZEALAND
Spongites sp. 1 CA, USA
96
100
Pseudolithophyllum neofarlowii CA, USA
98
Spongites sp. 2 CA,USA
Spongites decipiens CA, USA
57
Spongites sp. 1 SOUTH AFRICA
98
Spongites sp. 1 PANAMA
Spongites sp. 1 CHILE
Spongites sp. 1 NEW ZEALAND
Spongites sp. 5 NEW ZEALAND
87
Spongites discoidea SOUTH AFRICA
Spongites sp. 2 NEW ZEALAND
86
Pneophyllum fragile NEW ZEALAND
99
Spongites sp. 1 AUSTRALIA
Spongites impar SOUTH AFRICA
90
Spongites agulhensis SOUTH AFRICA
Spongites sp. 2 SOUTH AFRICA
100
Spongites sp. 3 SOUTH ARICA
87
72
Spongites sp. 4 SOUTH AFRICA
Spongites sp. 5 SOUTH AFRICA
100
Spongites sp. 9 NEW ZEALAND
Spongites sp. 4 NEW ZEALAND
100
Spongites yendoi SOUTH AFRICA
60
Spongites sp. 2 CHILE
58
100
Spongites sp. 3 CHILE
Spongites sp. 2 AUSTRALIA
100
Spongites yendoi NEW ZEALAND
Spongites tunicatus NEW ZEALAND
77
61
76
Spongites sp. 8 NEW ZEALAND
98
Spongites sp. 3 NEW ZEALAND
53
Spongites sp. 6 NEW ZEALAND
Spongites sp. 7 NEW ZEALAND
89
Pneophyllum coronatum 1 NEW ZEALAND
Pneophyllum coronatum 2 NEW ZEALAND
98
Amphiroa zonata JAPAN
84
Lithophyllum impressum BC CANADA
Lithothrix aspergillum BC CANADA
0.02

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KRAMMER K. & LANGE-BERTALOT H. 1986. *Bacillariophyceae 1. Teil: Naviculaceae*. In: *Süsswasserflora von Mitteleuropa* (Ed. by H. Ettl, J. Gerloff, H. Heynig & D. Mollenhauer), vol. 2/1. G. Fischer, Stuttgart & New York. 876 pp.

HOEK C. VAN DEN, MANN D.G. & JAHNS H.M. 1995. *Algae: an introduction to phycology*. Cambridge University Press, Cambridge. 623 pp.

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GUIRY M.D. & GUIRY G.M. 2012. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; searched on 13 January 2012.

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**Examples:** Type: South Africa. Western Cape, Beaufort West (3222): 'Renosterkopf' [Renosterkop] (-BB), 1850, *Zeyher 854* (TCD, lecto.-image!, here designated; SAM!, P - image! [2 sheets], isolecto.).

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Specimens examined are cited under each species treatment and arranged into paragraphs by country and within these paragraphs by Province. Within each Province the specimens are ordered according to the quarter-degree grid regerence system (Leistner and Morris 1976) [see paragraph below]

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**EXAMPLES:**

**Additional specimens examined.**
Botswana. **2615 (Luderitz)**: Diamond Area No. 1, Sperrgebiet, south of Rotkuppe gate (-CD), 2 Aug 2001, *Mannheimer 1391* (WIND); Road to Grillental from Kaukausib, Blue ridge (-DC), 5 Sep 2002, *Mannheimer 2200* (WIND). **2715 (Bogenfels)**: Diamond Area No. 1, en route from Tsabiams to Grillenthal (-BA), 5 Sep 2002, *Bartsch, Loots and Mannheimer 1028* (WIND); Approach to Kaukausib Plain to south (-BA), 5 Sep 2002, *Mannheimer 2195* (WIND); Sandy-gravel plain east of Kaukausib Fountain (-BA), 12 Sep 2005, *Mannheimer 2769*(WIND, JRAU); Karas district, Sperrgebiet, Kaukausib Drainage (-BA), 3 Mar 2007, *Burke 7001* (PRE).
South Africa. WESTERN CAPE: **3218 (Clanwilliam)**: Near Eendekuil, western foot of Piekenierskloof Pass (-DB), 28 Aug 2009, *Magee, Boatwright, Manning and Goldblatt 161* (NBG, PRE, K, BOL). **3319 (Worcester)**: Tulbagh (-AC), Sep 1919, *Bolus 16734* (BOL); roadside near Gouda (-AC), 9 Sep 1951, *Esterhuysen 18840* (BOL [3 sheets], K, PRE).

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I thank the Department of Biodiversity and Conservation Biology at the University of the Western Cape (UWC) for providing funding and research equipment, and the South African National Research Foundation (NRF) for a research grant to GWM. Thanks to all the undergraduate research students that contributed towards the preparation of histological slides. A special word of thanks to all the amazing people sharing moments, giving smiles, hugs, time, and just being there for me throughout my study period. I thank my supervisors, Prof. Gavin W. Maneveldt and Prof Alan Channing, great mentors, assisting me with continuous dedication on this path of tremendous growth, both professionally and personally. May God bless and keep them always in his hands. A final word of thanks goes to all the examiners who are gratefully acknowledged for their contributions in strengthening this dissertation. May God bless them abundantly.