Abundance and species composition of non-geniculate coralline red algae epiphytic on the South African populations of the rocky shore seagrass *Thalassodendron leptocaule* M.C. Duarte, Bandeira & Romeiras

Catherine M. Browne, Gavin W. Maneveldt, John J. Bolton, Robert J. Anderson

Abstract
Seagrasses support a great diversity of epiphytic organisms and new research has shown that non-geniculate coralline red algae are important occupiers of space on the fronds of seagrasses. Except for a few scant records, there are no detailed published accounts of non-geniculate coralline algae epiphytic on seagrasses in South Africa. The seagrass Thalassodendron leptocaule (previously known as Thalassodendron ciliatum) is unique among southern African seagrasses in that it occurs on exposed rocky outcrops along the Mozambique and north eastern South African coast; most other seagrasses are restricted to sheltered bays and estuaries. Here we present descriptions of three species of non-geniculate coralline red algae which we have identified growing epiphytically on this seagrass in northern KwaZulu-Natal: Hydrolithon farinosum, Pneophyllum amplexifrons and Synarthrophyton patena. Two of the corallines (P. amplexifrons and S. patena) were restricted to the seagrass' stems while the third (H. farinosum) occurred only on the leaves. Of the three coralline epiphytes, P. amplexifrons contributed most to the biomass (average wet weight per plant 0.6±1.18 g); its wet weight, however, varied between habitats. Hydrolithon farinosum and other smaller turf algae amounted to no more than 0.1 g (wet weight) per leaf. Synarthrophyton patena was far more sparsely evident and contributed to less than 0.1 g (wet weight) per stem. Pneophyllum amplexifrons and H. farinosum appear to be pioneer epiphytes and form additional surfaces onto which other seaweed epiphytes attach and grow. Distribution of these epiphytes is explained by the longevity of the stems and leaves of the seagrass.

Keywords: Sodwana Bay, rocky shore, *Hydrolithon farinosum*, *Pneophyllum amplexifrons*,
Synarthrophyton patena

Introduction
The coralline red algae (Corallinophycidae, Rhodophyta) are a unique group of algae and among the most abundant marine organisms found within the photic zone on rocky shores (Lee, 1967; Littler, 1973; Adey, 1978; Adey et al., 1982; Steneck, 1986; Maneveldt et al., 2008). Non-geniculate (encrusting)

coralline red algae, in particular, are wide- spread in all of the world's oceans (Adey and MacIntyre, 1973; Johansen, 1981; Littler and Littler, 2000, 2003. These corallines typically adhere to hard primary substrata (epilithic), but also grow: 1) as free-living rhodoliths; 2) endophytically or parasitically on other corallines; or 3) as epibionts on other plants (epiphytic) and animals (epizoic).

The South African rocky intertidal and shallow subtidal zones are rich in diversity of non-geniculate coralline algae (Maneveldt et al., 2008). Despite their widespread distribution in South Africa, limited detailed taxonomic work was conducted on them prior to 1993. Consequently coralline algal collection records are comparatively poor and their taxonomy is generally poorly understood in South Africa. Research on this group has, however, increased substantially over the past few years (e.g. Keats and Chamberlain, 1997; Keats et al., 2000; Maneveldt et al., 2007, 2008; Maneveldt and Van der Merwe, 2012).

Seagrasses support a great diversity of epiphytic macroalgae (Coppejans et al., 1992; Leliaert et al., 2001; Bandeira, 2002). Although Leliaert et al. (2001) reported non-geniculate corallines to be common epiphytes on the seagrasses around Zanzibar Island, Tanzania, they did not identify them. Bandeira (2002) on the other hand, reported P. amplexifrons growing abundantly on T. ciliatum in southern Mozambique, accounting for 80% of the dry weight biomass of epiphytes. These studies suggest that non-geniculate corallines are important occupiers of space on the fronds of seagrasses.

South African records of non-geniculate coralline red algae are increasing (e.g. Maneveldt et al., 2007; Maneveldt and Van der Merwe, 2012) and many species still remain to be documented from most other similar regions (Maneveldt et al., 2008). This is particularly true in light of ongoing molecular studies (e.g. Bittner et al., 2011; that are proposing substantial reassessment of the taxonomy of the coralline algae globally. Furthermore, most taxonomic advances have focused on the more abundant species (Maneveldt et al., 2008) and often the less abundant and cryptic species (easily mistaken for other encrusting organisms such as corals, sponges, and even other corallines) have been overlooked. Maneveldt and Van der Merwe (2012) for example, demonstrated that range-restricted endemics that typically have a very narrow distribution range, are able to provide key taxonomic information. Also, the coralline algae as a group have not been well studied globally and species-rich areas such as Brazil and the tropics (e.g. Amado-Filho et al., 2010; Villas-Boas et al., 2009;

Amado-Filho et al., 2010; Bahia et al., 2011) may prove to hold very high coralline algal diversity. Finally, most detailed descriptions of coralline algae are based on the collections from intertidal and generally relatively shallow-water epilithic and epizoic habitats. With increased sampling of deeper mesophotic habitats (e.g. Amano-Filho et al., 2007; Villas-Boas et al., 2009; Bahia et al., 2011), coralline diversity is likely to be higher than previously thought.

Except for the very brief comments by Chamberlain and Norris (1994) and De Clerck et al. (2005) of Pneophyllum epiphytic on seagrasses, there are no detailed published accounts of non-geniculate coralline algae epiphytic on seagrasses in South Africa. Thalassodendron leptocaule is unique among southern African seagrasses in that it occurs on exposed rocky outcrops along the Mozambique and north eastern coast of South Africa; most other seagrasses are restricted to sheltered bays and estuaries. This species was previously known as Thalassodendron ciliatum (Forsskål) den Hartog, but it has recently been shown that rocky shore material in Mozambique and South Africa is of a different species, newly described (Duarte et al., 2012). True T. ciliatum occurs in more sheltered habitats in Mozambique, but has not been recorded in South Africa (Janine Adams, Botany Dept., Nelson Mandela Metropolitan University, pers. comm.). T. leptocaule reaches its southwestern distribu- tional limit on the southeast African tropical coastal areas from Xai-Xai (Gaza Province) and Ponta do Ouro (Maputo Province, type locality) in southern Mozambique, extending to Boteler Point (KwaZulu-Natal Province) in South Africa (Duarte et al., 2012). It is very common on east African coasts, where populations appear to be stable. It is not well studied outside of this region. The distribution of T. leptocaule (as T. ciliatum) on the South African coast was mapped by Ward (1962) who found the species to be restricted to rocky shores along the coast of northern KwaZulu-Natal in the intertidal and shallow subtidal zones, and recent collections by Browne (2012) have confirmed this.

The current study examined South African populations of T. leptocaule to document the relative abundance of the non-geniculate coralline red algae found to occur epiphytically on the seagrass.

1. Materials and methods

1.1. Specimen collection and preparation

In situ collections of T. leptocaule were made in 2010 from open rocky shores at Sodwana Bay (27°32′23″S 32°40′49″E) and Maphelane (28˚24′27″S 32°25′36″E) on the northern coast of KwaZulu-Natal, South Africa. The seagrass beds at Sodwana Bay (Jesser Point) were located in the subtidal fringe (that part of the extreme low intertidal only exposed at spring low tide), to subtidal depths of 2 m, and in per- manent pools. Fifteen samples were taken, using haphazardly placed 25 × 25 cm quadrats, from each of these habitats during each of the two collection trips to Jesser Point. Five replicate samples were collected from each of the three different habitats. Collecting was done somewhat differently at Maphelane owing to the scarcity of the seagrass at this site and the homogeneity of the habitat. Ten 25 × 25 cm quadrats were placed haphazardly and the seagrass collected, scraping samples to bare rock where possible. Plants were examined as far as possible when fresh, or preserved in a neutralized 5% formalin seawater solution.

1.2. Algal epiphyte load

Six uprights of the seagrass were haphazardly selected from each of the 5 samples taken from each of the 3 habitats at Jesser Point in both March 2010 (n = 90 uprights) and September 2010 (n = 90 uprights), as well as from the 10 samples collected from the exposed habitat at Maphelane in October 2010 (n = 60 uprights), totalling 240 individual seagrass uprights. Epiphytes from these uprights were removed by scrap- ing using a scalpel and forceps. The number of epiphytes and their cover was recorded per plant (those identified on stems and leaves noted separately) and the height of each plant was measured in cm. This was done to investigate the relationship between seagrass upright height, age of the plant, and the epiphyte load. Cover was estimated using a scale of 1 to 5 (1 = present, 2 = rare, 3 = common, 4 = abundant, 5 = dominant), a variation of the Braun-Blanquet cover-abundance scale (Wikum and Shanholtzer, 1978). The Braun-Blanquet scale was used because it is not affected by the amount of seagrass in a sample. Abundances were determined by wet weight recorded to the nearest 0.1 g where feasible, or by cover of a stem or leaf per taxon.

1.3. Statistical analyses

All data are expressed as means ± SD. Statistical analyses using one-way ANOVA and a post-hoc Tukey HSD test were used to com- pare means. Differences amongst treatments were considered statis- tically significant at p b 0.05. Statistical analyses were conducted using Statistica 10 software.

1.4. Histological analyses

Coralline algal histological methods follow Maneveldt and Van der Merwe (2012) and are summarized as follows. Depending on the thickness of the coralline epiphytes, formalin preserved specimens were first decalcified in either 1% (thin material) or 10% (thick mate- rial) 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. There- after, 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 were 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 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 h so that sections could adhere. 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).

Herbarium codes are those used in Index Herbariorum, previously in print (Holmgren et al., 1990) and now electronically online (Thiers, 2012, continuously updated).

2. Results

2.1. Epiphyte load

Three species of non-geniculate coralline red algae were identified growing epiphytically on T. leptocaule M.C. Duarte, Bandeira and Romeiras. H. farinosum and *Pneophyllum* amplexifrons were common in samples from both Jesser Point (Sodwana Bay) and Maphelane. Ninety percent of seagrass plants from Sodwana Bay and 98% of plants from Maphelane had H. farinosum growing on them, while 88% and 73% of plants had P. amplexifrons growing on them, respectively. The third species, Synarthrophyton patena, was less common and was only observed on the upper stems of a few plants from the Sodwana Bay and Maphelane collections. *Pneophyllum* amplexifrons and H. farinosum were the most abundant non-geniculate coralline algae found as epiphytes (Table 1). Cover of these species, however, varied between habitats and times of the year, though not significantly so (P. amplexifrons: $F_{(6,33)} = 2.31$, $p = 0.06$; H. farinosum: $F_{(6,33)} = 2.44$, $p = 0.05$), and was generally greater at Jesser Point, Sodwana Bay. At Jesser Point, P. amplexifrons cover was observed to be generally greatest in pool habitats. At Jesser Point, H. farinosum's cover was greatest in subtidal habitats during March, but greatest in exposed habitats during September of 2010.

Pneophyllum amplexifrons displayed an average wet weight of 0.6 ± 1.18 g per seagrass upright. The wet weight of H. farinosum was typically b 0.1 g and therefore cover scores were allocated as opposed to a measured wet weight.

As with abundance, the epiphyte load (in wet weight) differed between non-geniculate coralline algal species, between collection times, and between habitats (Table 2). Wet weights of P. amplexifrons sampled from the collections in different habitats from Jesser Point in March and September 2010 were significantly higher than those from Maphelane in October 2010 ($F_{(6,233)} = 3.816$, $p = 0.001$).

Pneophyllum amplexifrons' average wet weight per seagrass upright was significantly higher in the collections from Jesser Point March pools (1.05 ± 1.49 g) compared to the collections from Maphelane October exposed habitats (0.16 ± 0.42 g) ($p = 0.008$). Collections from Jesser Point September pools (1.12 ± 1.82 g) also had significantly higher P. amplexifrons wet weight compared to the collections from Maphelane October exposed habitats (0.16 ± 0.42 g) ($p = 0.003$). The wet weight of *Pneophyllum* amplexifrons was also found to increase with an increasing seagrass upright length ($N = 240$, $r = 0.63$, p b 0.05) (Fig. 1).

2.2. Observations

2.2.1. *Hydrolithon*. farinosum (J.V. Lamouroux) D. Penrose & Y.M. Chamberlain

BASIONYM: Melobesia farinosa J.V.Lamouroux, 1816: 315.

SYNONYMS: Fosliella farinosa (J.V. Lamouroux) M.A.Howe, 1920; and

Melobesia granulata (Meneghini) Zanardini, 1843.
LECTOTYPE: Epiphytic on Sargassum acinarium (Linnaeus) Setchell (formerly Sargassum linifolium C. Agardh. CN Herb. Lamouroux) (Chamberlain, 1994: 123). See also Penrose and Chamberlain (1993:296) for more information on the lectotype.

TYPE LOCALITY: Mediterranean, unspecified locality (Chamberlain, 1994: 123).

DISTRIBUTION: *Hydrolithon* farinosum is widely reported and has been recorded from all continents and in most oceans, with the exception of Antarctica. See Guiry and Guiry (2012) for distribution records. The species has been recorded in other Western Indian Ocean regions and elsewhere in East Africa, including Kenya (Penrose and Chamberlain, 1993; Silva et al., 1996; Bolton et al., 2007), Tanzania (Silva et al., 1996), Madagascar (Silva et al., 1996), Mauritius (Silva et al., 1996) and South Africa (Penrose and Chamberlain, 1993; Maneveldt et al., 2008).

In South Africa, from Maphelane (approximately 100 km south of Sodwana Bay) (this study) to Lala Neck (north of Sodwana Bay), KwaZulu-Natal (Maneveldt et al., 2008).

REPRESENTATIVE SPECIMENS EXAMINED: In total, 40 samples were examined. South Africa. KwaZulu-Natal: Jesser Point, Sodwana Bay (27°32′ 23″S 32°40′49″E), epiphytic on T. leptocaule (01.iii.2010, C.M. Browne & J.J. Bolton, UCT ME1, ME2, ME3, ME4, ME5); (02.iii.2010, C.M. Browne & J.J. Bolton, UCT MS1, MS2, MS3, MS4, MS5); (03.iii.2010, C.M. Browne & J.J. Bolton, UCT MP1, MP2, MP3, MP4, MP5); (06.ix.2010, C.M. Browne & J.J. Bolton, UCT SP1, SP2, SP3, SP4, SP5); (08.ix.2010, C.M. Browne & J.J. Bolton, UCT SE1, SE2, SE3, SE4, SE5); (09.ix.2010, C.M. Browne & J.J. Bolton, UCT SS1, SS2, SS3, SS4, SS5); Maphelane (28˚24′27‴S 32°25′36‴E), epiphytic on T. leptocaule (10.x.2010, C.J. Ward & A. Connell, UCT OM1.1, OM1.2, OM1.3, OM1.4, OM1.5, OM2.1, OM2.2, OM2.3, OM2.4, OM2.5) (Fig. 2).

DESCRIPTION: H. farinosum is characterised by the following com- bination of features: 1) tetra/bisporangia simultaneously cleaved, zonately arranged, and borne in uniporate conceptacles that lack apical pore plugs (Fig. 6); 2) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions (Fig. 4); secondary pit connec- tions absent or comparatively rare; 3) all plants non-geniculate; 4) thallus non-endophytic and lacking haustoria (Figs. 3 and 4); 5) epithallial cells present on vegetative thallus filaments (Fig. 4); 6) growth form not arbo- rescent (tree-like) (Fig. 2); 7) thallus lacking a basal layer of predomi- nantly palisade cells throughout (Figs. 3 & 4); 8) pore canals of tetra/ bisporangial conceptacles lined by a ring of conspicuously enlarged cells (Fig. 6) that arise from filaments interspersed among and peripheral to the developing sporangia (Fig. 5); these cells do not protrude into the pore canal, but are oriented more or less perpendicular to the conceptacle roof surface; 9) spermatangial (male) conceptacles containing simple (unbranched) spermatangial systems that are confined to the conceptacle floor (Fig. 7); and 10) gonimoblast filaments borne only from the margins of the central fusion cell i.e. they are arranged peripherally in the carposporangial conceptacle (Fig. 8).

Character 1 places the taxon within the order Corallinales and family Corallinaceae, characters 2 and 3 within the subfamily Mastophoroideae, and the remaining 7 characters collectively within the genus Hydrolithon (Maneveldt et al., 2012). Within the genus Hydrolithon, South African plants ascribed to H. farinosum are characterised by being: 1) thin (up to 150 μm thick, reproductively mature thalli no more than 5 cells thick) (Fig. 3); 2) epiphytic (Fig. 2); and 3) possessing a dimerous internal construction (Figs. 3 and 4) (Maneveldt et al., 2008). All of these characters were clearly evident in this study's samples for this taxon. This study is the first to report on the species occurring epiphytically on the seagrass T. leptocaule from South Africa (Figs. 3–8).

2.2.2. P. amplexifrons (Harvey) Y.M. Chamberlain & R.E. Norris

BASIONYM: Melobesia amplexifrons Harvey, 1849: 110.

SYNONYMS: Lithophyllum amplexifrons (Harvey) Heydrich, 1897; LithophyllumpseudolichenoidesHeydrich, 1902; andLithothamnion pseudolichenoides (Heydrich) Lemoine, 1910.

LECTOTYPE: Epiphytic on Gelidium pteridifolium. TCD (unnumbered). See Chamberlain and Norris (1994: 10) for more information on the lectotype. Isolectotype material also exists at TCD and BM (Woelkerling and Campbell, 1992, Fig. 63B).

TYPE LOCALITY: Port Natal (i.e. Durban, KwaZulu-Natal), South Africa (Chamberlain and Norris, 1994: 10).

DISTRIBUTION: P. amplexifrons has been widely reported from Japan (Yoshida et al., 1990; Yoshida, 1998), South-west Asia in India (Silva et al., 1996; Sahoo et al., 2001), tropical east Atlantic (John et al., 2004; Prud'homme Van Reine et al., 2005), Chile and Fuegia (Papenfuss, 1964; Ramírez and Santelices, 1991), and the Western Indian Ocean in Madagascar (Chamberlain and Norris, 1994; Silva et al., 1996), Mozambique (Chamberlain and Norris, 1994), and South Africa (Chamberlain and Norris, 1994).

In South Africa, from Palm Beach (south of Port Shepstone, KwaZulu-Natal) northward into southern Mozambique (Bandeira, 2002; Maneveldt et al., 2008). The species is abundant intertidally in rock pools, growing epiphytically on leaves and stems of the seagrass T. leptocaule (Fig. 9), and also on other intertidal fringe algae such as G. pteridifolium, Chamaedoris delphinii and Halimeda sp. (Chamberlain and Norris, 1994: 10).

REPRESENTATIVE SPECIMENS EXAMINED: In total, 40 samples were examined. South Africa. KwaZulu-Natal: Jesser Point, Sodwana Bay (27°32′ 23″S 32°40′49″E), epiphytic on T. leptocaule (01.iii.2010, C.M. Browne & J.J. Bolton, UCT ME1, ME2, ME3, ME4, ME5); (02.iii.2010, C.M. Browne & J.J. Bolton, UCT MS1, MS2, MS3, MS4, MS5); (03.iii.2010, C.M. Browne & J.J. Bolton, UCT MP1, MP2, MP3, MP4, MP5); (06.ix.2010, C.M. Browne & J.J. Bolton, UCT SP1, SP2, SP3, SP4, SP5); (08.ix.2010, C.M. Browne & J.J. Bolton, UCT SE1, SE2, SE3, SE4, SE5); (09.ix.2010, C.M. Browne & J.J. Bolton, UCT SS1, SS2, SS3, SS4, SS5); Maphelane (28˚24′27″S 32°25′36″E), epiphytic on T. leptocaule (10.x.2010, C.J. Ward & A. Connell, UCT OM1.1, OM1.2, OM1.3, OM1.4, OM1.5, OM2.1, OM2.2, OM2.3, OM2.4, OM2.5).

DESCRIPTION: *Pneophyllum* amplexifrons is characterised by the following combi- nation of features: 1) tetra/bisporangia simultaneously cleaved, zonately arranged, and borne in uniporate conceptacles that lack apical pore plugs (Fig. 14); 2) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions (Figs. 11 & 12), secondary pit connections absent or comparatively rare; 3) all plants non-geniculate (Fig. 9); 4) thallus non-endophytic and lacking haustoria (Figs. 10 & 12); 5) epithallial cells present on vegetative thallus filaments; 6) growth form not arbores- cent (tree-like); 7) thallus primarily dimerous (Figs. 11 & 13), but may be secondarily monomerous (Fig. 11), and lacking a basal layer of predomi- nantly palisade cells throughout (Figs. 11–13, 16); 8) pore canals of tetra/ bisporangial conceptacles lined by cells that arise from filaments inter- spersed among and peripheral to the developing sporangia (Fig. 13); these cells protrude into the pore canal as papillae and are orientated more or less parallel, or at a steep angle to the conceptacle roof surface (Fig. 15); 9) spermatangial (male) conceptacles containing simple (un- branched) spermatangial systems that are confined to the conceptacle floor (Fig. 16); and 10) gonimoblast filaments borne only from the mar- gins of the central fusion cell i.e. they are arranged peripherally in the carposporangial conceptacle.

Character 1 places the taxon within the order Corallinales and family Corallinaceae, characters 2 and 3 within the subfamily Mastophoroideae, and the remaining characters collectively within the genus Pneophyllum (Maneveldt et al., 2012). Within the genus Pneophyllum, South African plants ascribed to P. amplexifrons are characterised by plants that form thick, trumpet-shaped adjoining thalli encircling seagrasses and green algal stalks (Maneveldt et al., 2008). Except for character 10 above (no female plants were ob- served in this study) all of these characters were clearly evident in this study's samples for this taxon. This study is the first to report on the species occurring epiphytically on the seagrass T. leptocaule from South Africa (Figs. 10–16). In addition, individual plants of P. amplexifrons often overlap or fuse at their rims to create dumb-bell shapes (Fig. 9). The thallus surface is sometimes noticeably ribbed.

2.2.3.S. patena (D.J. Hooker & Harvey) R.A. Townsend
BASIONYM: Melobesia patena J.D. Hooker & Harvey in Harvey, (1849: 111), Fig. 40.

SYNONYMS: Lithophyllum patena (J.D. Hooker & Harvey) Rosanoff, 1866; Lithothamnion patena (J.D. Hooker & Harvey) Heydrich, 1897; Polyporolithon patena (J.D. Hooker & Harvey) L.R. Mason, 1953; Mesophyllum patena (J.D. Hooker & Harvey) R.W. Ricker, 1987. See Guiry and Guiry (2012) for an extensive list.

LECTOTYPE: Colenso 1331; TCD (Womersley, 1996: 209). Notes: Designated by Chapman and Parkinson (1974, pl. 72).

TYPE LOCALITY: Flat Point (near Castlepoint), New Zealand (Townsend, 1979).

DISTRIBUTION: S. patena appears to be a temperate species and seems largely restricted to the Southern hemisphere. The species has been reported from the Falkland Islands (May and Woelkerling, 1988), Chile (May and Woelkerling, 1988; Ramírez and Santelices, 1991), Australia (May and Woelkerling, 1988;

Womersley, 1996), New Zealand (Adams, 1994), and South Africa (May and Woelkerling, 1988; Silva et al., 1996; Wiencke and Clayton, 2002; Maneveldt et al., 2008). *Synarthrophyton*. patena occurs epiphytically on a variety of green, brown and red algae, and on seagrasses, tunicates, molluscs and sponges; found in intertidal pools and subtidally to depths of 37 m (Womersley, 1996).

In South Africa from Robben Island (Table Bay, off the Cape Peninsula) to Sodwana Bay (KwaZulu-Natal) (Maneveldt et al., 2008). REPRESENTATIVE SPECIMENS EXAMINED: In total, 7 samples were examined. South Africa. KwaZulu-Natal: Jesser Point, Sodwana Bay (27°32′23″S 32°40′49″E), epiphytic on T. leptocaule (03.iii.2010, C.M. Browne & J.J. Bolton, UCT MP1); Maphelane (28˚24′27″S 32°25′36″E), epiphytic on T. leptocaule (10.x.2010, C.J. Ward & A. Connell, UCT OM1.2, OM1.3, OM1.4, OM2.2, OM2.3, OM2.4).

DESCRIPTION: S. patena is characterised by the following combina- tion of features: 1) tetra/bisporangia simultaneously cleaved, zonately arranged, and borne in multiporate conceptacles that have apical pore plugs (Fig. 20); 2) all plants non-geniculate (Fig. 17); 3) cells of contig- uous (adjacent) vegetative filaments joined primarily by cell fusions (Figs. 18 and 19), secondary pit connections absent or comparatively rare; 4) tetra/bisporangial conceptacle pore plate of cellular construc- tion (Fig. 20); 5) thallus non-endophytic and lacking haustoria (Fig. 17); 6) growth form not arborescent (tree-like); 7) thallus con- struction monomerous throughout (Fig. 18); 8) outermost walls of ter- minal epithelial cells are rounded or flattened, but without flared corners (Figs. 18, 19); and 9) subepithelial initials as long as, or longer than their immediate inward derivatives (Figs. 18 and 19).

Characters 1 and 2 place the taxon within the order Corallinales and family Hapalidiaceae, characters 3 and 4 within the subfamily Melobesioideae and the remaining characters variously with- in the genera Clathromorphum, Mesophyllum and Synarthrophyton (Maneveldt et al., 2012). Spermatangial (male) conceptacles are re- quired to separate the three genera. This study did not find male plants. However, South African plants ascribed to S. patena are characterised by being: 1) epiphytic on a host of fleshy and turf algae (Figs. 17–20), but not on geniculate corallines; and 2) discoid in appearance with concep- tacle roofs raised and dome-like (rather than flush to somewhat sunk- en) (Maneveldt et al., 2008). These latter characters were clearly evident in this study's samples for this taxon.

3. **Discussion**

The results of the present study show that at least three species of non-geniculate coralline red algae (H. farinosum, P. amplexifrons, S. patena) are present as epiphytes on the seagrass T. leptocaule from intertidal and shallow subtidal locations on the north eastern coast of South Africa. This supports the findings of several authors (e.g. Humm, 1964; Bramwell and Woelkerling, 1984; Jones and Woelkerling, 1984; Harlin et al., 1985; Pardi et al., 2006; Balata et al., 2007; Piazzi et al., 2007) who have reported species of Hydrolithon and Pneophyllum to be common epiphytes on seagrasses in many parts of the world.

Hydrolithon. farinosum and P. amplexifrons have only ever been reported to be epiphytic). For example, in Australia H. farinosum is found over a wide ecological range from the intertidal to deep sublittoral (Penrose and Chamberlain, 1993) where it is commonly found on various algae and on the seagrass Amphibolis antarctica (Womersley, 1996; Ringeltaube and Harvey, 2000). In Florida (USA) H. farinosum has been reported as epiphytic on the seagrasses Thalassia testudinum and Syringodium filiforme (Won et al., 2010). Similarly, H. farinosum is described as a common seagrass epiphyte along the Atlantic and Caribbean coast of Mexico (Mendoza-Gonzalez et al., 2009), as well as in Mozambique (Perry and Beavington-Penney, 2005).

Like *H. farinosum*, *P. amplexifrons* has only ever been reported to be epiphytic (Chamberlain and Norris, 1994; Bandeira, 2002; De Clerck *et al.* 2005). Despite the species' apparently widespread distribution, limited data on its ecology exists. Thus far, ecological data for only southern Africa exists (Chamberlain and Norris, 1994; Bandeira, 2002; De Clerck *et al.*, 2005). Interestingly, the genus *Pneophyllum* has only ever been reported to be epiphytic in South Africa (Chamberlain 426 and Norris, 1994; Maneveldt *et al.*, 2008) and in other regions of the world where it has been comparatively well studied (e.g. Australia [Womersley, 1996; Morcom *et al.*, 1997]; New Zealand [Harvey *et al.* 2005; Farr 429 *et al.* 2009]).

While S. patena has only been recorded as an epiphyte in South Africa (Maneveldt et al., 2008), in Australia the species has a range of habitats, growing on seagrasses, tunicates, mollusks and sponges, and found in intertidal pools and subtidally to depths of 37 m (Womersley, 1996; Harvey et al., 2003). May and Woelkerling (1988) were the first to report the species in southern Australia growing epiphytically only on members of the red algal genus Ballia (Ceramiaceae). Later, Harvey et al. (1994) reported the species growing epiphytically on a number of other sea- weeds. Still later Harvey et al. (2005) found only one collection of S patena to be epilithic and most occurrences to be either epiphytic or epizoic (on sponges). Apart from Australia and South Africa, little has been reported on the ecology of S. patena.

Interestingly, P. amplexifrons and S. patena, appear to be restricted to the seagrass stems, and H. farinosum to the leaves. Distribution of these epiphytes on the seagrass could be explained by the longevity of the components of the seagrass. The leaves are regularly shed (on average every 60 days (Hemminga et al., 1999)) and tend to be colonised only by the very thin, fast growing corallines. Since the seagrass stems are longer living, this allows more time for the colonisation of the thicker S. patena and P. amplexifrons.

Not all three species were observed on every seagrass plant examined. P. amplexifrons and H. farinosum were most abundant and ecologically important. It was frequently observed that other epiphytes grew directly on these corallines rather than on the seagrass itself. *Jania* spp. (geniculate corallines) were often bserved to grow out from the collars of *P. amplexifrons*. Similarly, small ctocarpoid brown algae and other small seaweed taxa (e.g. *Asterocladon rhodochortonoides* (Børgesen) Uwai, Nagasato, Motomura & Kogame; *Colaconema gracile* (Børgesen) Ateweberhan & Prud'homme van Reine; *Platysiphonia delicata* (Clemente) Cremades in Cremades & Ferez Cirera) grew epiphytically on *H. farinosum*. The coralline algae appear to offer a rougher surface that seems more susceptible to attachment by other epiphytic seaweeds, compared to the seagrass surface. These non-geniculate coralline epi- phytes therefore provide additional secondary substrates that support a greater diversity within the seagrass bed ecosystem. The distribution of the coralline epiphytes on the leaves and stems of the seagrass is different. The stems and leaves of *T. leptocaule* provide structurally and temporally different microhabitats. The lignified stems survive for several years unlike the leaves, which are shed on average every 60 days (Hemminga *et al*., 1999). Stems therefore, provide more stable substrata.

The non-geniculate coralline red algae observed in this study appear to be primary colonisers of both the leaves and stems of T. leptocaule, just as they are on other seagrass species (e.g. Humm, 1964; Borowitzka et al., 1990). Our observa- tions suggest that the coralline epiphytes are acting, at least in part, as pioneer plants, possibly providing a suitable substratum for other non-coralline epiphytes as a number of smaller epiphytes were observed growing on these coralline epiphytes on T. leptocaule.

Our data further showed that *P. amplexifrons*' biomass increased proportionally with seagrass stem length. Borowitzka *et al.* (1990) found there was a clear relationship between the number of epiphyte species and heights of plants on *Amphibolis* in Australia. It might be assumed that plant height is a function of plant age. Older plants thus support a higher number and abundance of epiphytes. This is expected, as over time, there should be increased recruitment of epiphytes, with the epiphytes themselves increasing in biomass with time. Older, taller seagrass uprights support higher epiphyte loads as they have survived longer, allowing for greater epiphyte settlement. Older seagrasses also have developed thicker stems with more branching and leaves. This also allows for more substrate onto which epiphytes may attach. In conclusion, this study lends to further understanding of non-geniculate coralline red algal epiphytes, and provides baseline information of those non-geniculate corallines epiphytic on South African *T. ciliatum*. This information would be useful for facilitating the monitoring of change within the region sampled, as well as for comparison with other seagrass communities.

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Figure Captions

Figure 1: Relationship between *Pneophyllum amplexifrons* wet weight (g) and seagrass upright height (cm).

Figure 2: *Hydrolithon farinosum* (note the numerous raised conceptacles) occurring epiphytically on a leaf of *T. leptocaule*. Scale bar = 10 mm.

Figures 3-8: Vegetative and reproductive anatomy of *H. farinosum* growing on *T. leptocaule*.

Figure 3: Cross section through a leaf of *T. leptocaule* (white double arrowheads) showing the general habit of *H. farinosum* (black arrows). Scale bar = 120 µm.

Figure 4: Vertical section of the dimerous thallus of *H. farinosum* showing a single basal layer of non-palisade cells (black arrow), a thallus comprised of no more than five cell layers (E), and a single layer of rounded epithelial cells (white arrowheads). Note the cell fusions between cells of continuous filaments (arrow heads). Scale bar = 75 µm.

Figure 5: Vertical section through an immature tetrasporangial conceptacle of *H. farinosum* showing the development of the conceptacle roof from filaments interspersed among (black arrowheads) and peripheral (white arrowheads) to the sporangial initials (t). Scale bar = 30 µm.

Figure 6: Vertical section through a mature uniporate (p) tetrasporangial conceptacle of *H. farinosum* showing the absence of an apical pore plug. Note the conspicuously enlarged cells (arrowheads) lining the pore canal and the single, large tetrasporangium (t). Scale = 25 µm.

Figure 7: Vertical section through a spermatangial 722 (male) conceptacle of *H. farinosum* showing simple spermatangia (S) distributed across the conceptacle floor. Scale bar = 30 µm.

Figure 8: Vertical section through a carposporangial conceptacle of *H. farinosum* showing peripherally arranged gonimoblast filaments terminating in large carpospores (C). Note the unfertilised remains of the carpogonial branches at the centre of the chamber floor (arrowhead). Scale bar = 30 µm.

Figure 9: External appearance of *P. amplexifrons* growing on *T. leptocaule*. Note the trumpet or dumbell-shaped appearance of the coralline as it encircles the seagrass stem. Scale bar = 20 mm.

Figures 10-16: Vegetative and reproductive anatomy of P. *amplexifrons* growing on *T.leptocaule*.

Figure 10: Cross section through a leaf of *T. leptocaule* (white double arrowheads), showing the general habit of *P. amplexifrons* (black arrows). Scale bar = 200 µm.

Figure 11: Vertical section of the thallus of *P. amplexifrons* showing a dimerous thallus construction with single basal layer of non-palisade cells (black arrowhead) and erect filaments (E). Note the cell fusions (f) between cells of contiguous vegetative filaments. Scale bar = 50 µm.

Figure 12: Vertical section of the thallus of P. *amplexifrons* showing a secondarily monomerous medulla with downward curving filaments (black arrowhead). Note the cell fusions (white arrowheads) between cells of continuous vegetative filaments. Scale bar = 50 µm.

Figure 13: Vertical section through an immature 746 tetrasporangial conceptacle of *P. amplexifrons* showing the development of the conceptacle roof from filaments interspersed among (black arrowheads) and peripheral (white arrowheads) to the sporangial initials (t). Note the developing single pore (p). Scale bar = 40 µm.

Figure 14: Vertical section through a mature uniporate tetrasporangial conceptacle of *P. amplexifrons* showing tetrasporangia (t) developing peripherally around a central columella (C). Scale bar = 100 µm.

Figure 15: Vertical section through the pore canal (P) of a tetrasporangial conceptacle of *P.amplexifrons* showing the absence of an apical pore plug and papillate cells (arrowheads) lining the pore canal. Scale bar = 30 µm.

Figure 16: Vertical section through a spermatangial (male) conceptacle of *P. amplexifrons* showing simple spermatangial systems (S) distributed across the conceptacle floor. Scale bar = 50 µm.

Figures 17-20: Vegetative and reproductive anatomy of *S. patena* growing on *T. leptocaule*.

Figure 17: Cross section through a stem of *T. leptocaule* (white double arrowheads), showing the general habit of *S. patena* (black arrow). Note the raised, domed multiporate conceptacle (white arrowhead). Scale bar = 300 µm.

Figure 18: Vertical section of the thallus of *S. patena* showing a monomerous construction in which medullary (M) filaments give rise to cortical (C) filaments. Note too the cell fusions (f) between cells of contiguous vegetative filaments, the single layer of epithallial cells (black arrow) and the layer of subepithallial initials (white arrowhead). Scale bar = 30 µm.

Figure 19: Magnified view of the outer thallus of 769 *S. patena* showing a single layer of rounded epithallial cells (black arrow), the subepithallial initials (white arrowhead) and cell fusions (f) between cells of contiguous vegetative filaments. Scale bar =20 µm.

Figure 20: Vertical section through a multiporate tetrasporangial conceptacle of *S. patena* showing incompletely formed apical pore plugs (white arrowheads) situated apically above zonately arranged tetrasporangia (t). Scale bar = 50 µm.

Table 1: Abundance (scale 1-5) (mean ± SD) per 777 habitat of the two most abundant non geniculate coralline algal species recorded as epiphytes on *T. leptocaule* from collections made from Jesser Point (Sodwana Bay, March and September 2010) and from Maphelane (October 2010). Comparative values with the same superscript are not statistically different.

Collection	**Jesser Point: March 2010**			**Jesser Point: September 2010**			**Maphelane: October 2010**
Habitat	**Pools**	**Exposed**	**Subtidal**	**Pools**	**Exposed**	**Subtidal**	**Exposed**
P. amplexifons	3.40 $\pm1.52^{a}$	2.40 $\pm0.55^{a}$	3.20 $\pm0.84^{a}$	3.80 $\pm2.17^{a}$	4.00 $\pm0.71^{a}$	3.60 $\pm1.14^{a}$	1.80 $\pm1.69^{a}$
H. farinosum	2.00 $\pm1.73^{b}$	1.80 $\pm1.92^{b}$	3.40 $\pm0.55^{b}$	3.40 $\pm2.07^{b}$	4.20 $\pm0.84^{b}$	3.60 $\pm1.14^{b}$	1.90 $\pm1.52^{b}$

Table 2: Abundance (in wet weight (g)) (mean ± SD) per seagrass upright of the most abundant non-geniculate coralline algal species, *P. amplexifrons*, recorded as epiphytic on *T. leptocaule* from collections made from Jesser Point (Sodwana Bay, March and September 2010) and from Maphelane (October 2010). Comparative values with the same superscript are not statistically different.

Collection	**Jesser Point: March 2010**			**Jesser Point: September 2010**			**Maphelane: October 2010**
Habitat	**Pools**	**Exposed**	**Subtidal**	**Pools**	**Exposed**	**Subtidal**	**Exposed**
P. amplexifons	1.05 $\pm1.49^{a}$	0.54 $\pm0.90^{ab}$	0.88 $\pm1.57^{ab}$	1.12 $\pm1.82^{a}$	0.39 $\pm0.60^{ab}$	0.51 $\pm0.92^{ab}$	0.16 $\pm0.42^{b}$

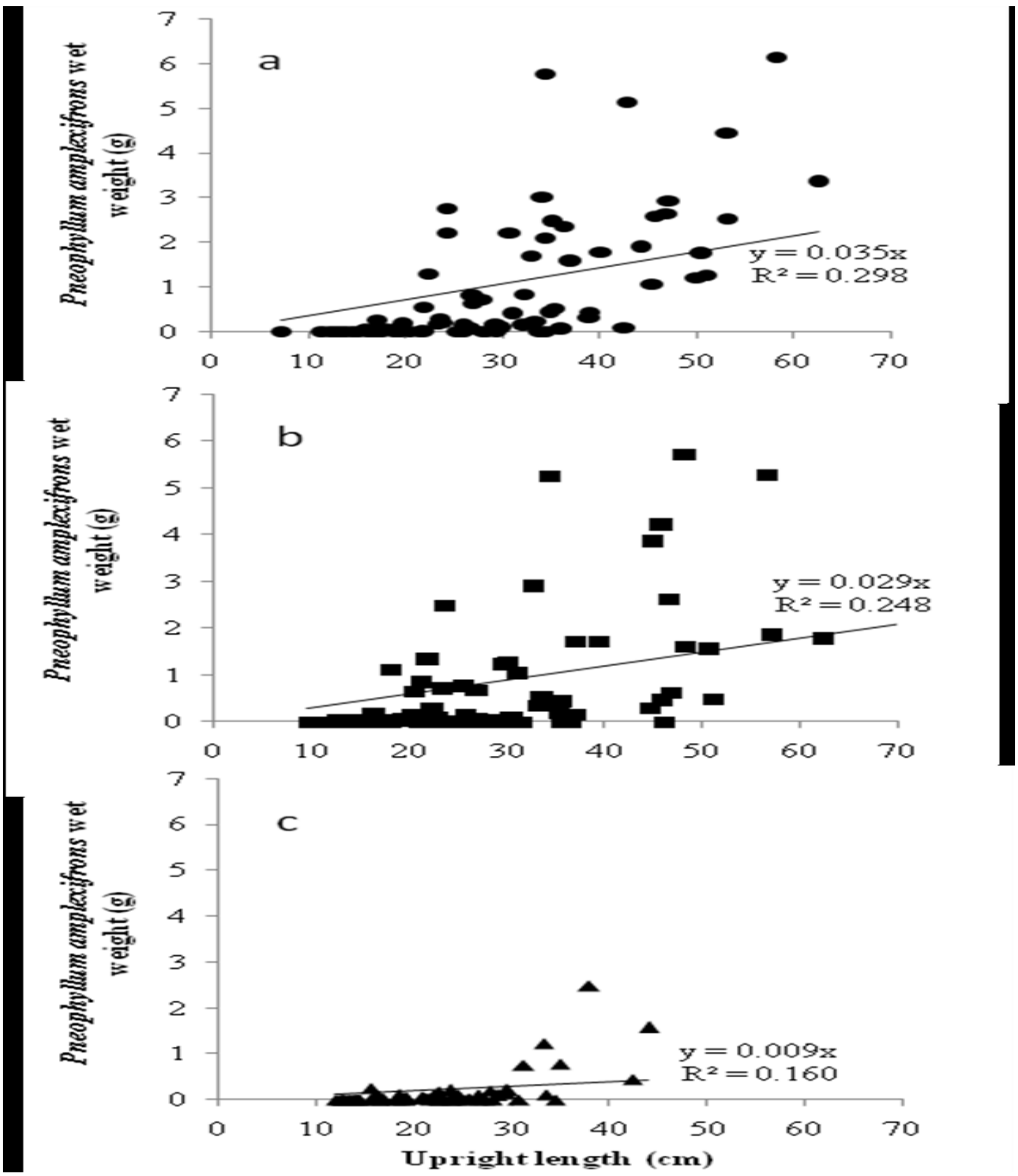
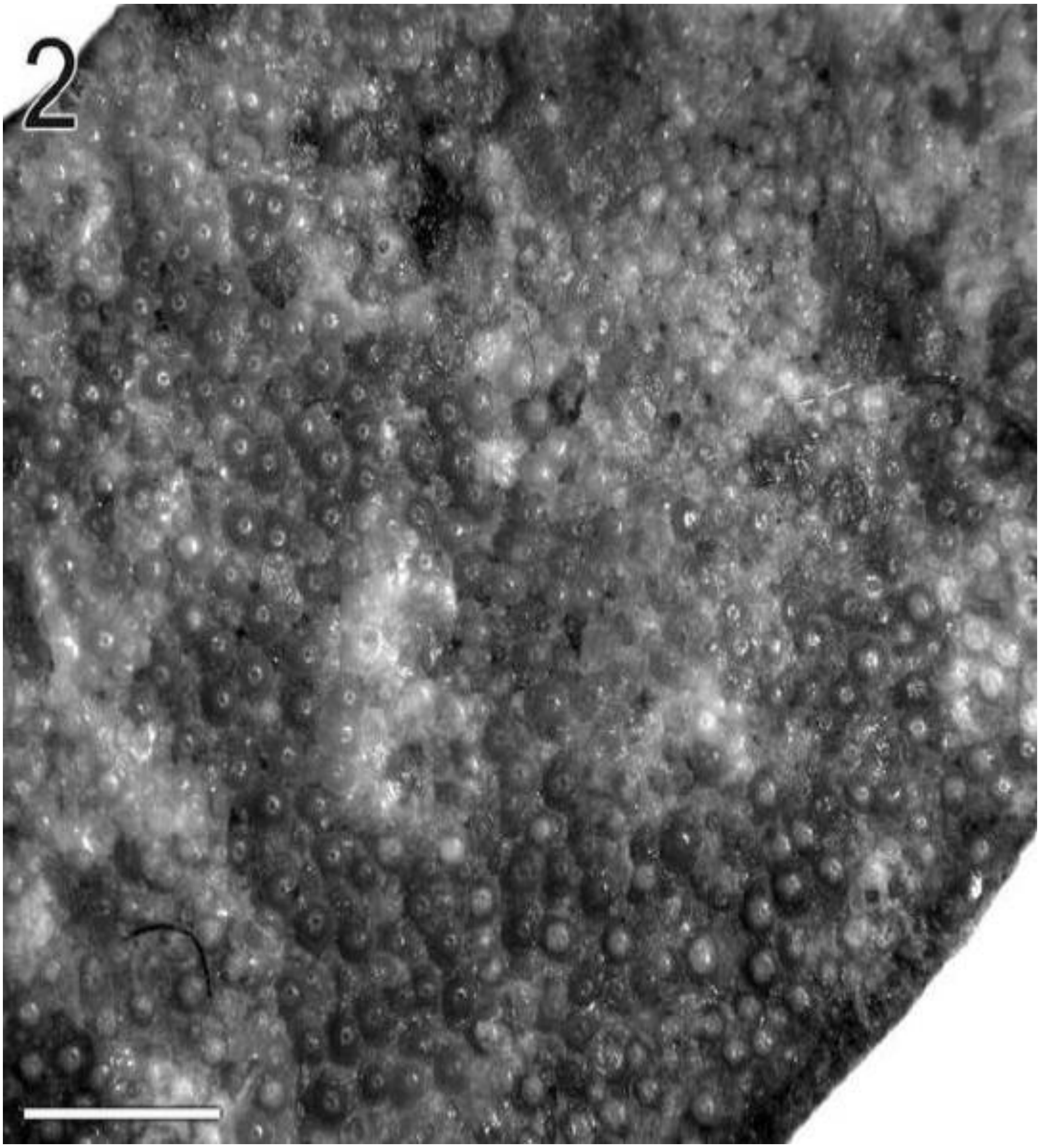


Figure 1: Relationship between *P. amplexifrons* wet weight 791 (g) and seagrass upright length (cm) collected from a) Jesser Point (March 2010); b) Jesser Point (September 2010); and c) Maphelane (October 2010).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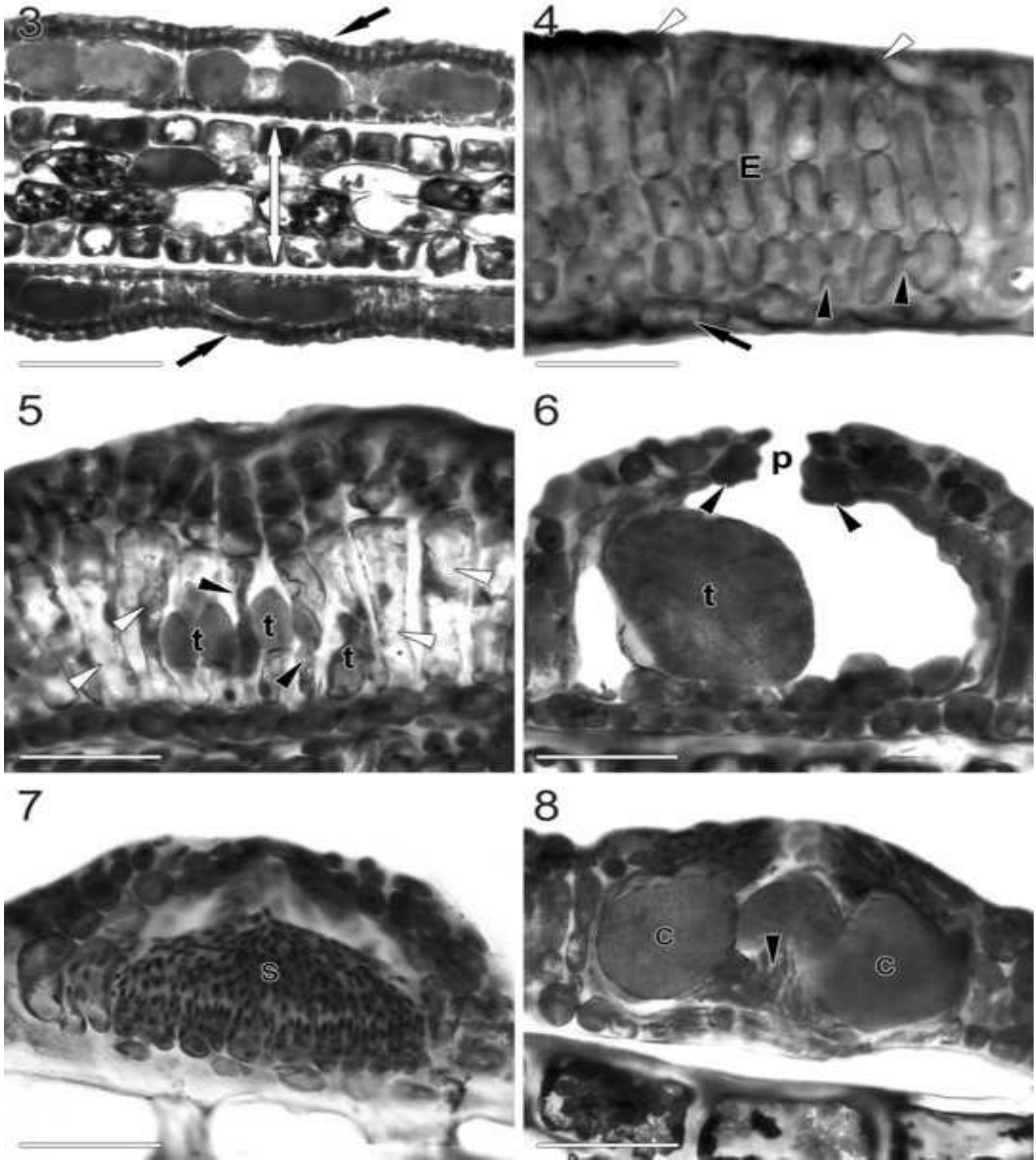
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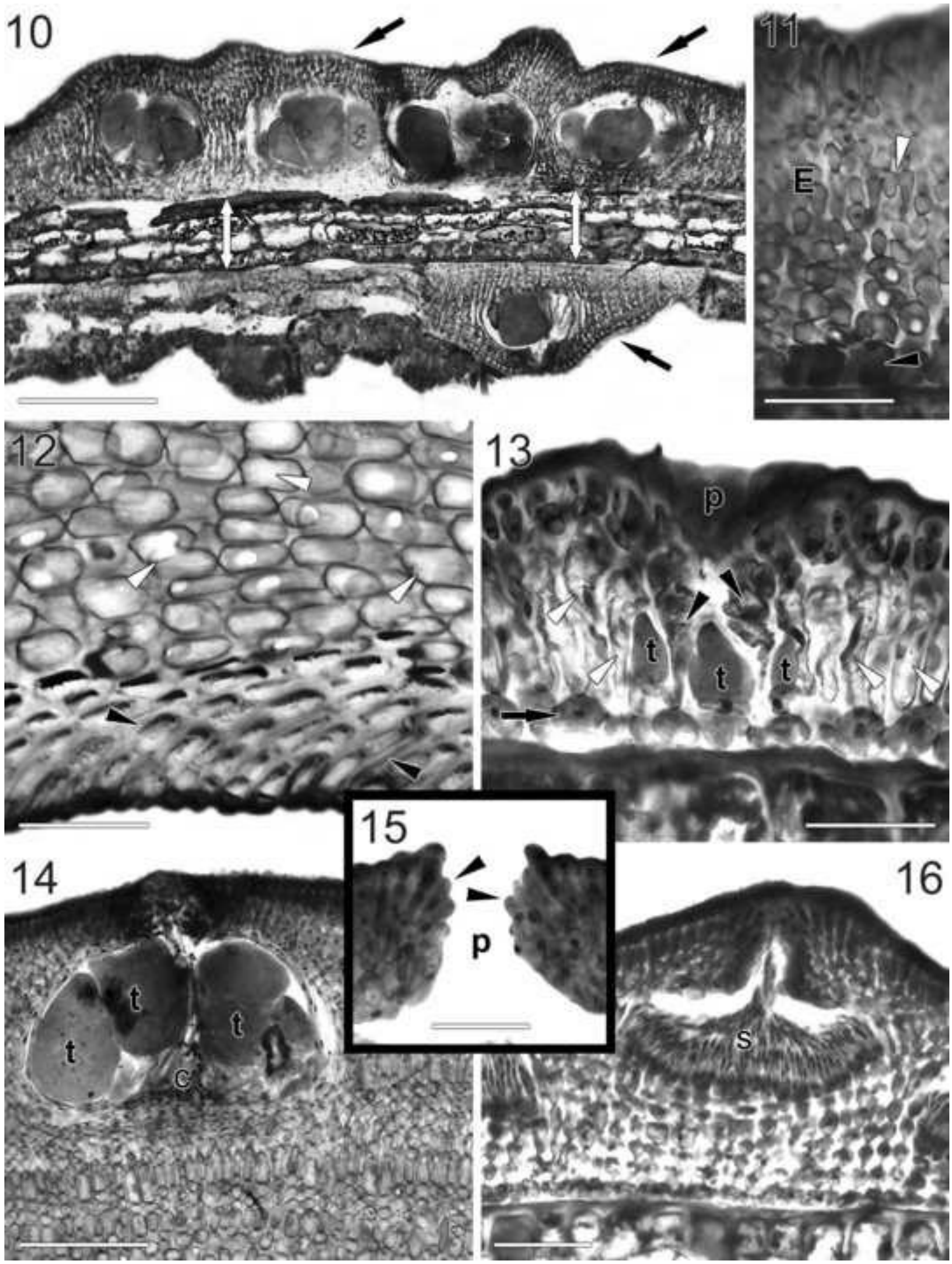

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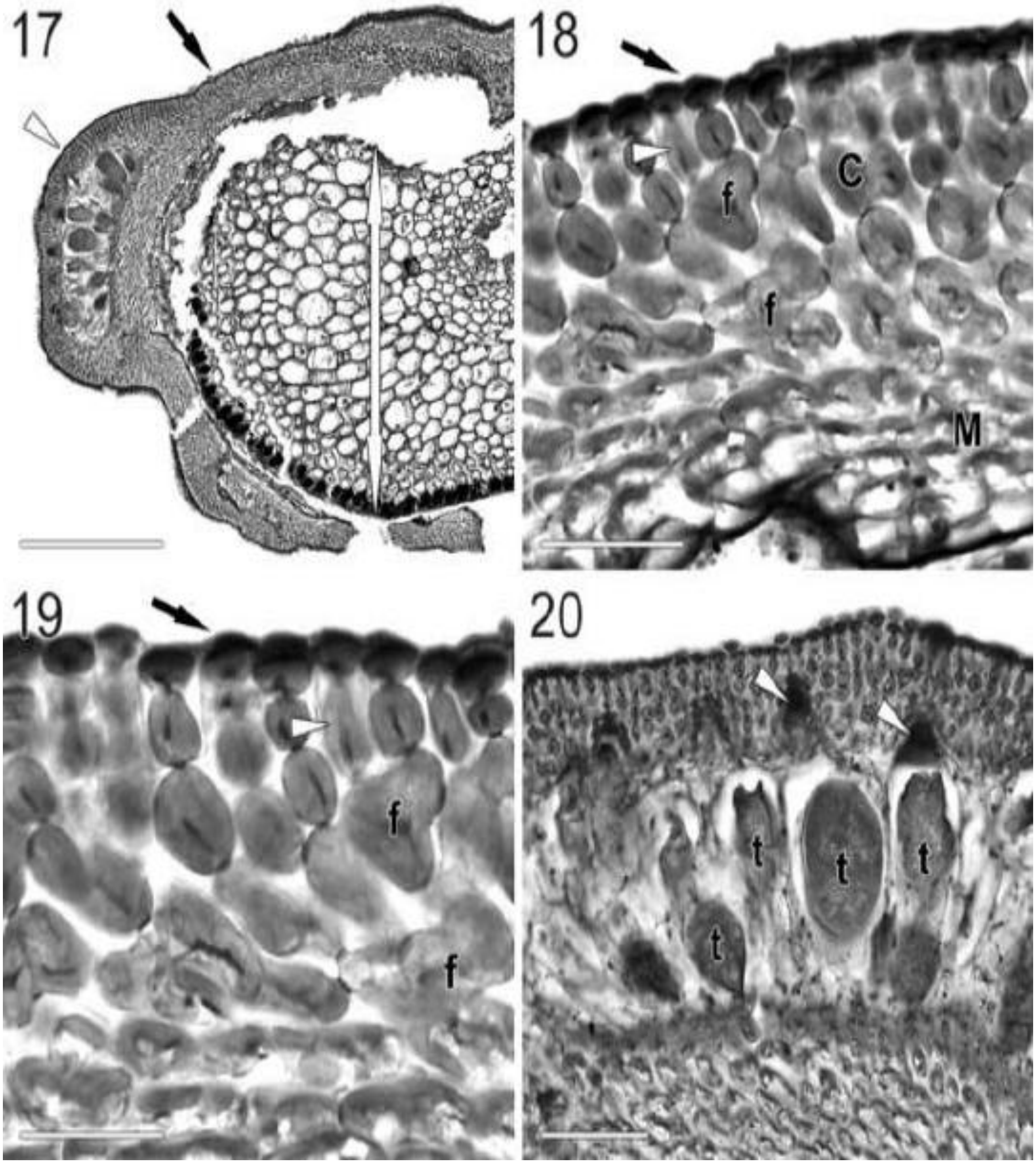
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