A global revision of the nongeniculate coralline algal genera Porolithon Foslie (defunct) and Hydrolithon Foslie (Corallinales, Rhodophyta)

Volume 1.

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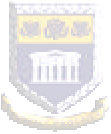
I declare that

“A global revision of the nongeniculate coralline algal genera Porolithon Foslie (defunct) and Hydrolithon Foslie (Corallinales, Rhodophyta)”

is my own work and that all sources I have used or quoted have been indicated and acknowledged by means of complete references



This thesis is dedicated to my family.

To Jill, my loving and faithful wife, and my children Amber and Joshua.

Thank you for your continued support and patience during the completion of this thesis.

I am eternally grateful to the Almighty for His grace and favour.

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GENERAL INTRODUCTION

Non-geniculate coralline algae are widespread in all of the world's oceans, where they often cover close to 100% of rocky substrata (Lee 1967; Adey 1978; Littler 1973; Adey & MacIntyre 1973; Adey et al. 1982; Steneck 1986; Keats & Maneveldt 1994; Littler & Littler 2000, 2003). Despite their ubiquity, they are a poorly known group of marine organisms (Keats & Chamberlain 1993, 1994a, b). Much of this lack of knowledge stems from a legacy of poor quality taxonomic work (Woelkerling & Lamy 1998) and it is not surprising that the non-geniculate coralline algae have been considered to constitute a 'difficult' taxonomic group (see Taylor 1942, 1945, 1950, 1960; Woelkerling 1988; Woelkerling & Lamy 1998).

Such difficulties have, however, been created by taxonomists rather than by any intrinsic characteristics of the group itself (van Steenis 1957; Woelkerling & Lamy 1998). According to Chamberlain (1991) it was a widely accepted practice to describe taxa largely or even solely on differences in growth forms. Foslie, for example, described some 192 taxa in this manner, quite often using specific vegetative features to delineate taxa, and basing his descriptions on single specimens or collections (Woelkerling 1984). With many researchers following suit (eg. Lemoine) this lead to a substantial increase in the number of described taxa, many of which were poorly delimited (Woelkerling 1984; Chamberlain 1991; Chamberlain et al. 1991). This problem was confounded by the fact that characters used then to delineate genera, are simply no longer reliable (e.g. Woelkerling 1985; Penrose & Woelkerling 1988; Penrose & Chamberlain 1993).

In their (Foslie, Lemoine and others) defense, however, it should be noted that these pioneering researchers had to their disposal, comparatively primitive collecting and examination equipment and where not confronted with the vast array of taxonomic criteria that present-day coralline taxonomists are faced with. Also, the number of species names that continue to include Foslie and Lemoine as authorities suggest that, for their time, their studies were quite remarkable. Additionally, Lemoine was originally interested in fossils and it is significant that fossil corallines continue to be a widespread focus of study (e.g. Johnson 1963; Braga 1993).

This said, many agree (e.g. Keats 1997; Keats et al. 1997) that to make studies on non-geniculate coralline algae useful in the long term, we have to describe as many species characters in sufficient detail so that future researchers will be able to assess species without having to resort to an analysis of type specimens. Similarly, we have to make use of standardised terminologies for describing species to facilitate re-evaluations (e.g. Adey & Adey 1973; Chamberlain 1990; Woelkerling et al. 1993). Modern taxonomic accounts from many parts of the world are already making use of just such criteria (e.g. Townsend 1979; Woelkerling & Irvine 1986; Woelkerling & Ducker 1987; May & Woelkerling 1988; Woelkerling & Foster 1989; Chamberlain 1990; Penrose 1991, 1992; Penrose & Woelkerling 1991, 1992; Woelkerling & Harvey 1992; Chamberlain 1993; Keats & Chamberlain 1993; Penrose & Chamberlain 1993; Verheij 1993; Woelkerling et al. 1993; Woelkerling & Harvey 1993; Chamberlain 1994; Chamberlain & Keats 1994; Chamberlain & Norris 1994; Keats & Chamberlain 1994a, b; Verheij 1994; Wilks & Woelkerling 1994; Townsend et al. 1994, 1995; Chamberlain et al. 1995; Keats & Chamberlain 1995; Keats 1997; Keats et al. 1997; Keats et al. 2000) and although new records and new species are constantly being described, this will no doubt also greatly reduce the number of real species as many will prove to be synonymous (see Chamberlain 1991). The coralline algal biodiversity of southern Australia, for example, has apparently been overestimated by some 80% (Woelkerling 1997).

Of particular importance in the ecology of coral reefs on a worldwide basis are various species of non-geniculate coralline algae that have been ascribed to the now defunct genus Porolithon Foslie (Lee 1967; Adey 1978; Littler 1973). In their earlier work, Penrose and Woelkerling (1988) subsumed this genus in Spongites. Later the type of the genus Porolithon was placed into Hydrolithon (Penrose & Woelkerling 1992).

There are many historical inconsistencies in the taxonomic treatment of the Mastophoroid genera Porolithon, Hydrolithon and Spongites that along with the genus Pseudolithophyllum, have been termed the Spongites-complex (Penrose & Woelkerling 1988). The above genera were separated from one another based primarily on their vegetative anatomy. Hydrolithon (Adey 1970) encompassed species lacking secondary pit connections, bore solitary trichocytes (= heterocysts of Adey 1970; see Table 1 for a selection of comparable thallus terminologies used by various authors) and had a dimerous medulla (= single layered hypothallium of Adey 1970; = unistratose basal region of Penrose & Woelkerling 1988). Porolithon (Adey 1970) encompassed species having trichocytes arranged in horizontal pustulous fields and a monomerous, plumose (noncoaxial) medulla (= multilayered hypothallium of Adey 1970; = multistratose, noncoaxial basal regions of Penrose & Woelkerling 1988). Spongites (Woelkerling 1985) encompassed species having trichocytes that were solitary or arranged in vertical series and had a monomerous, plumose medulla (= multistratose, noncoaxial basal regions of Penrose & Woelkerling 1988). These genera had thus been delineated from one another on 1) differences in the occurrence and arrangement of trichocytes, and 2) the number of layers in the medullary (basal) region. Woelkerling (1985) and Penrose & Woelkerling (1988) have given a thorough account of the inconsistencies when using these two characters and have concluded that neither is a reliable vegetative character since species from all three genera may possess all the above mentioned characters. Penrose & Woelkerling (1988) then subsumed both Hydrolithon and Porolithon in Spongites (the oldest available name for the complex) but did note that Spongites (sensu lato) encompassed a broad range of taxa. They further stated that some species might in due course be separated into distinct genera based on reproductive characters. In all essence, the genera Hydrolithon and Porolithon no longer existed.

During their course of study on the southern Australian taxa of Spongites (sensu lato), it became apparent to Penrose & Woelkerling (1992) that two distinct patterns of tetrasporangial conceptacle development occurred. Their conclusion was that Spongites and Hydrolithon were in fact distinct genera. In Hydrolithon, the pore canals of the tetrasporangial conceptacles were lined by a ring of conspicuous, elongate cells that arose from filaments interspersed among the sporangial initials. These cells do not protrude into the pore canal and are oriented more-or-less perpendicularly to the roof surface. In Spongites, cells that arise from the peripheral roof filaments line the pore canals of the tetrasporangial conceptacles. These cells protrude into the pore canal and are oriented more-or-less parallel to the roof surface.

Penrose & Woelkerling (1992) still, however, considered Hydrolithon and Porolithon to be congeneric and since Hydrolithon was described first, Porolithon was considered to be a heterotypic synonym and thus subsumed into Hydrolithon. Foslie's (1897, 1900a, b, 1901, 1904, 1906, 1907, 1909; see also Foslie & Howe 1906) Porolithons were originally described were under the genus Lithophyllum Philippi. Foslie (1909) established the genus Porolithon to encompass those taxa that lacked secondary pit connections, possessed a monomerous medulla, and the thallus bearing trichocytes in horizontal pustulous fields. In their 1992 reappraisal however, Porolithon onkodes, the type species of the former Porolithon, was the only species examined which was formally transferred to Hydrolithon. Only a few of the remaining taxa ascribed to Porolithon have received varying degrees of taxonomic review in light of these changes (see Verheij & Prud'homme van Reine 1993; Silva et al. 1996; Afonso-Carrillo & Sansón 1999); the majority have undergone none. The genus Hydrolithon on the other hand, has undergone a greater degree of taxonomic scrutiny than the now defunct genus Porolithon (e.g. Keats & Chamberlain 1994a; Iryu & Matsuda 1996; Penrose 1996).

As noted above the aforementioned genera have all undergone one or more changes in circumscription with their characteristics differing quite markedly through the years. The following features have been considered diagnostic for the genera Lithophyllum, Spongites, Hydrolithon, and Porolithon.

Lithophyllum Philippi 1837: 387 (sensu lato Adey 1970; see also Johansen 1981)

1. Plants crustose or branching, sometimes free;
2. medulla dimerous to monomerous (= hypothallium single to multi-layered) – if monomerous, it is coaxial;
3. cells of contiguous filaments interconnected by secondary pit connections (cell fusions apparently absent or comparatively rare);
4. cortical (= perithallial) cells strongly to weakly layered;
5. epithallial cells single to multi-layered;
6. uniporate sporangial conceptacles lacking apical plugs.

Spongites Kützing 1841: 30 (sensu lato Woelkerling 1985; see also Penrose & Woelkerling 1988)

1. Thallus non-geniculate;

2. uniporate tetra/bisporangial conceptacles lacking apical plugs;
3. cells of contiguous filaments interconnected by cell fusions (secondary pit connections unknown);
4. thallus composed of numerous layers of cells normally over 200 µm thick, non-coaxial;
5. trichocytes, when present, solitary or in a vertical series.

Hydrolithon Foslie 1909: 55 (sensu lato Adey 1970)

1. Plants crustose or branching;
2. medulla dimerous, cells essentially isodiametric;
3. cortical filaments sometimes layered but generally irregular due to a wide range of cell dimensions;
4. cells of contiguous filaments interconnected by cell fusions (secondary pit connections unknown);
5. trichocytes occurring singularly;
6. single epithallial layer;
7. uniporate sporangial conceptacles lacking apical plugs.

Porolithon Foslie 1909: 57 (sensu lato Adey 1970; see also Johansen 1981)

1. Massive crustose or branching plants;
2. thallus over 200 µm thick, trichocytes in horizontal rows;
3. medulla monomerous, non-coaxial;
4. cortical filaments strongly layered;

5. cells of contiguous filaments interconnected by cell fusions (secondary pit connections unknown);
6. epithallial layer single to several cells thick;
7. uniporate tetrasporangial conceptacles lacking apical plugs.

Lithophyllum Philippi 1837: 387 (sensu stricto Woelkerling 1988; see also Chamberlain et al. 1991)

1. thallus non-geniculate, non-endophytic, and lacking haustoria;
2. thallus dimerous, possessing a basal layer of cells that are predominately non-palisade;
3. thallus lacking areas that are bistratose (consisting of basal cell and epithallial cell);
4. cells of contiguous vegetative filaments normally joined by secondary pit connections (cell fusions apparently absent or comparatively rare);
5. tetrasporangia/bisporangia lacking apical plugs and borne within uniporate conceptacles;
6. spermatangial systems confined to the floor of the male conceptacle.

Lithophyllum is distinguished from *Titanoderma* (Chamberlain 1991) on the basis of:

1. the possession of a basal layer consisting predominately of non-palisade cells, and
2. no areas of bistratose thallus are present, as the thallus begins to thicken immediately behind the primary meristematic cell.

Spongites Kützing 1841: 30 (sensu stricto Penrose & Woelkerling 1992)

1. Thallus non-geniculate, non-endophytic, and lacking haustoria;
2. thallus lacking a basal layer of palisade cells throughout;

3. cells of contiguous filaments interconnected by cell fusions (secondary pit connections unknown);
4. tetrasporangia/bisporangia lacking apical plugs and borne within uniporate conceptacles;
5. pore canals of tetrasporangial conceptacles lined by cells that arise from peripheral roof filaments, protrude into the pore canal, and are oriented more-or-less parallel to the roof surface;
6. male conceptacles containing simple spermatangia that are restricted to the conceptacle floor;
7. carposporophytes with gonimoblast filaments borne only from the margin of the fusion cell.

Hydrolithon Foslie 1909: 55 (*sensu stricto* Penrose & Woelkerling 1992)

1. Thallus non-geniculate, non-endophytic, and lacking haustoria;
2. thallus lacking a basal layer of palisade cells throughout;
3. cells of contiguous filaments interconnected by cell fusions (secondary pit connections unknown);
4. tetrasporangia/bisporangia lacking apical plugs and borne within uniporate conceptacles;
5. pore canals of tetrasporangial conceptacles lined by a ring of conspicuous, elongate cells that arise from filaments interspersed among sporangial initials; these cells do not protrude into the pore canal, and are oriented more-or-less perpendicularly to the roof surface;
6. male conceptacles containing simple spermatangia that are restricted to the conceptacle floor;
7. carposporophytes with gonimoblast filaments borne only from the margin of the fusion cell.

With all this in mind, it seems likely that some of the species within the "*Porolithon*" may be conspecific. For example, Lemoine (1911) suggested that *Lithophyllum antillarum* and *L.*

craspedium are probably conspecific. Furthermore, Afonso-Carrillo et al. (1993) published a description of a species that they called *Spongites africanum* (Foslie) Afonso-Carrillo Chacana *et* Sanson. From their description, it seems likely that this species is conspecific with *Hydrolithon onkodes*; it certainly does not pertain to *Spongites* as presently circumscribed. The possibility that these and other species once ascribed to *Porolithon* may be conspecific has not been examined in a modern context.

The purpose of this thesis is therefore three-fold: 1) to provide a revision and characterization of the species of nongeniculate coralline algae previously ascribed to the now defunct genus *Porolithon*; 2) to provide a modern account of selected taxa (excluding taxa conforming to the *Fosliella*-state of *Hydrolithon* – see Penrose & Chamberlain 1993) from the genus *Hydrolithon* and descriptions of taxa found to conform to the generic delimitation of *Hydrolithon*; and 3) to use a phenetic cluster analysis to determine the taxonomic relationships between the various taxa ascribed to the genera *Porolithon* (defunct) and *Hydrolithon*.

NAME OF JOURNAL

Phycologia

Paper 1.

MANEVELDT G.W. 2005. *A revision and characterization of the species of nongeniculate coralline algae previously ascribed to the now defunct genus Porolithon (Corallinales, Rhodophyta)*. PhD Dissertation, Paper 1. Unpublished, University of the Western Cape, Bellville. 220 pp., 114 pl.

Paper 2.

MANEVELDT G.W. 2005. *A modern account of selected taxa from the genus Hydrolithon (Corallinales, Rhodophyta) and descriptions of taxa found to conform to the generic delimitation of Hydrolithon*. PhD Dissertation, Paper 2. Unpublished, University of the Western Cape, Bellville. 182 pp., 73 pl.

Paper 3.

MANEVELDT G.W. 2005. *A phenetic character analysis of selected taxa belonging to the genus Hydrolithon (Corallinales, Rhodophyta).* PhD Dissertation, Paper 3. Unpublished, University of the Western Cape, Bellville. 70 pp.

Paper 1.

A revision and characterization of the species of nongeniculate coralline algae previously ascribed to the now defunct genus *Porolithon* Foslie (Corallinales, Rhodophyta)

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ABSTRACT

In 1909 Foslie established the genus Porolithon to encompass 11 species that lacked secondary pit connections, possessed a monomerous thallus, have uniporate sporangial conceptacles with a central columella, and more importantly, bore trichocytes in horizontal fields. Following Foslie, an additional 10 species had been ascribed to Porolithon. Through a series of previous taxonomic reviews, Porolithon was considered to be a heterotypic synonym and subsumed into Hydrolithon. Porolithon onkodes, the type species of Porolithon was, however, the only species examined that was formally transferred to Hydrolithon based on modern research. Only a few of the remaining taxa ascribed to Porolithon have received varying degrees of taxonomic review in light of these changes; the majority have undergone none. The current research has attempted to reassess all 21 species ascribed to Porolithon in a modern-day revision to determine their present-day status. The following taxa conformed well to the present-day diagnosis of the genus Hydrolithon; H. boergesenii, H. craspedium, H. gardineri, H. improcerum, H. onkodes, and H. reinboldii. Although successfully transferred by a host of authors, some of these taxa were transferred without any taxonomic study. Lithophyllum africanum, on the other hand, underwent a detailed taxonomic revision and subsequent transfer by Afonso-Carrillo et al. (1993) to the genus Spongites. Afonso-Carrillo later questioned this transfer and suggested that Lithophyllum africanum probably belongs to Hydrolithon as delimited by Penrose & Woelkerling (1988). This transfer was never effected. The results of this study supports Afonso-Carrillo et al's (1993) original diagnosis as the taxon conforms to the genus Spongites (sensu strictu). This research also showed that nine taxa were conspecific with H. craspedium (Porolithon castellum), H. gardineri (Lithophyllum aequinoctiale, Lithophyllum coarctatum, Lithophyllum praetextatum and Porolithon marshallense) and H. onkodes (Lithophyllum antillarum, Lithophyllum pachydermum, Lithophyllum sandvicense, and Porolithon cocosicum). Lithophyllum

oligocarpum conforms to the genus Spongites and should therefore be referred to as Spongites oligocarpus (Foslie) Maneveldt & Keats comb. nov. For various reasons we were unable to obtain four type specimens (P. colliculosum, P. orbiculatum, P. somaliae and P. sonorense) and have commented as much as possible on these taxa based on previous research.

INTRODUCTION

Non-geniculate coralline algae that have been ascribed to the now defunct genus Porolithon Foslie are important in the ecology of coral reefs (Lee 1967; Adey 1978; Littler 1973; Adey et al. 1982; Littler & Littler 2000, 2003). Foslie (1909) established the genus Porolithon to encompass those taxa that lack secondary pit connections, possess a monomerous thallus, have uniporate sporangial conceptacles with a central columella, and most importantly, the thallus bearing trichocytes in horizontal fields. Adey et al. (1982) added to the diagnosis by commenting on the pustulate ('pustulous') nature of the tightly packed trichocyte fields, making reference to the blister-like appearance of the slightly raised trichocyte fields. Foslie however, never designated the type specimen for Porolithon and it was not until two years later that Lemoine (1911: 66) designated the lectotype specimen of Porolithon onkodes (Heydrich) Foslie. Still later, Kylin (1956: 207) designated another specimen of Porolithon onkodes (Heydrich) Foslie as a lectotype specimen. However, the specimens depicted in the Heydrich (1897) protologue have apparently been destroyed (Woelkerling 1993: 164) and subsequently Adey et al. (1982: 9) designated a Heydrich specimen in TRH as the new type (lectotype) specimen of Porolithon onkodes (Heydrich) Foslie. To date, Walter Adey's (1970) "A Revision of the Foslie Crustose Coralline Herbarium" and William Woelkerling's (1984) "M.H. Foslie and the Corallinaceae: an Analysis and Indexes", have been the only publications to cite fully the complete list of the Foslie Porolithon species (see Table 1). Foslie's (1897, 1900a, c, 1901a, 1904, 1906a, 1907a, 1909; see also Foslie & Howe 1906) original 11 species though were previously classified under the genus Lithophyllum Philippi (Adey 1970). Through the years, an additional 10 taxa have been ascribed to Porolithon (see Table 1).

Woelkerling (1985) and Penrose & Woelkerling (1988) concluded that the characters used to delineate the type of Porolithon were not reliable, as the types of the genera Spongites and Hydrolithon also possessed these characters. Penrose & Woelkerling (1988) then subsumed both Hydrolithon and Porolithon in Spongites (the oldest available name for the complex) but did note that Spongites (sensu lato) encompassed a broad range of taxa. During their course of study on the southern Australian taxa of Spongites (sensu lato), it became apparent to Penrose & Woelkerling (1992) that two distinct patterns of tetrasporangial conceptacle development occurred. Their conclusion was that Spongites and Hydrolithon were distinct genera.

Based on this new evidence, Penrose & Woelkerling (1992) still considered Hydrolithon and Porolithon to be congeneric and since Hydrolithon was described first, Porolithon was considered to be a heterotypic synonym and thus subsumed into Hydrolithon. In their 1992 reappraisal however, Porolithon onkodes, the type species of the former Porolithon, was the only species examined which was formally transferred to Hydrolithon. Only a few of the remaining taxa ascribed to Porolithon have received varying degrees of taxonomic review in light of these changes; the majority have undergone none. Some have even been transferred without any study e.g. H. craspedium (P. Silva in Silva et al. 1996). It seems likely that some of the species within the “Porolithon” may even be conspecific (eg. Lemoine 1911). Furthermore, a number of more recent publications still separate Porolithon from Hydrolithon (e.g. Naim 1993; Verheij 1993; Littler and Littler 2003). The purpose of this paper is therefore to revisit those taxa originally ascribed to the now defunct genus Porolithon and to determine their current generic status and investigate the possibility that some may be conspecific.

MATERIALS AND METHODS

Type specimens were obtained from **BM**, **PC**, **TRH**, and **UC** (Table 2). Type material was first fixed in 1 part liquid detergent: 4 parts commercial formalin in distilled water (10% ~ 4% formaldehyde) for at least 48 hours prior to examination. This method was found useful for rehydrating most of the material. For representative material, 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.

For scanning electron microscopy (SEM), air-dried material was fractured using either finger nails, forceps, diagonal cutters, or a small hammer & cold chisel. Wherever possible a fracture 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 gold for 4-6 min in an Edwards S150B sputter coater, and examined with a Hitachi X650 scanning electron microscope, equipped with a Mamiya 6X7 camera at an accelerating voltage of 20 or 25 kV.

Formalin-preserved specimens were decalcified in 10% nitric acid. After decalcification all specimens were immersed in 70%, 90% and 100% ethanol solutions respectively for a minimum of 30 minutes each. Specimens were then immersed in Leica Historesin filtration medium (50ml basic resin [liquid] and 1 packet [0.5g] activator) until completely infiltrated. Infiltration is complete when the specimen appears slightly translucent and sinks to the bottom of the infiltration vessel. A hardening solution was added to the infiltration medium (15 ml infiltration solution + 1 ml hardener) and the specimens orientated in this final solution until set. Gelling of the hardener usually occurred within about 15mins; some specimens were placed in an oven to allow more rapid hardening. All specimens were sectioned at 12 –15 μm thickness using a Bright 5030 microtome. Each individual section was removed from the microtome blade using a fine sable hair brush, and transferred to a slide covered with distilled water. All slides were then placed on a slide warmer until dry. Slides were then stained with toluidine blue (0.25 g borax/100ml and 0.06g toluidine blue/100ml), left to dry and later covered with cover slips using DPX Mountant for microscopy (BDH Laboratory Supplies, England). Photographs were taken from prepared slides using an Olympus microscope equipped with a digital camera. In some instances, when good sections were not obtained, drawings were made directly from prepared slides using a Zeiss microscope equipped with a drawing tube.

Conceptacle outside diameter and pore diameter was measured directly from the SEM. All other measurements were made using a calibrated eyepiece micrometer. In cell measurements for monomerous thalli, length denotes the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. For dimerous thalli, the dimensions of the cells of basal filaments are given as follows: height denotes the dimension at right angles to the substratum (technically diameter as defined for monomerous thalli), while width denotes the dimension between successive primary pit connections parallel to the substratum (technically length as defined for monomerous thalli). Conceptacle measurements follow the system of Adey & Adey (1973). Thallus terminology follows Chamberlain (1990). Growth-forms terminology follows Woelkerling et al. 1993 unless otherwise stated. Typification data follow Woelkerling (1993) unless otherwise stated.

Preparation of the plates (digitisation) was made using the graphics software package Adobe® Photoshop® and were constructed at 300dpi. The plates are arranged in alphabetical order of the species basionym.

Herbarium material is decreasing due to sampling for study. Therefore, although many species are well known (e.g. <u>H. onkodes</u>), I have illustrated all material in detail for all specimens studied to provide a detailed record and reduce the need to refer to dwindling type material. Also, many previous publications that have reported studies of type material have not presented detailed analyses of the types.

OBSERVATIONS

The defunct genus Porolithon

Porolithon Foslie (1909: 57) (see also Lemoine 1911: 61; Taylor 1950: 124; Kylin 1956: 207; Adey 1970: 10; Adey et al. 1982: 7), emend Penrose and Woelkerling (1992: 83)
Lithophyllum Philippi subgenus Porolithon Foslie, 1906b: 24

Foslie (1906b: 24) originally described Porolithon as a subgenus of Lithophyllum Philippi comprising the six taxa; Lithothamnion onkodes Heydrich (as Lithophyllum onkodes), Lithophyllum pachydermum Foslie, Lithophyllum oligocarpum Foslie, Lithophyllum africanum Foslie, Lithophyllum antillarum Foslie & Howe (as Lithophyllum Antillarum) and Lithophyllum craspedium Foslie. Later Foslie (1909: 57) raised Porolithon to genus status and included an additional five taxa namely; P. gardineri (Foslie) Foslie (as Porolithon Gardineri), P. sandvicense (Foslie) Foslie, P. coarctatum (Foslie) Foslie, P. preatextatum (Foslie) Foslie, and P. aequinoctiale (Foslie) Foslie. Foslie however, never designated the type specimen for Porolithon and it was not until two years later that Lemoine (1911: 66) designated the lectotype specimen of Porolithon onkodes (Heydrich) Foslie. Still later, Kylin (1956: 207) designated another specimen of Porolithon onkodes (Heydrich) Foslie as a lectotype specimen. However, the specimens depicted in the Heydrich (1897) protologue have apparently been destroyed (Woelkerling 1993: 164) and subsequently Adey et al. (1982: 9) designated a Heydrich specimen in TRH as the new type (lectotype) specimen of Porolithon onkodes (Heydrich) Foslie.

Heterotypic synonyms

Hydrolithon Foslie (1909: 55) (see Penrose & Woelkerling 1988: 173-174)

Spongites Kützing (1841: 30) (see Penrose & Woelkerling 1988: 173-174)

Description

Massive crustose or branching plants; plants monomerous, with plumose (noncoaxial) medullary filaments, with cells of medullary filaments elongated parallel to substrate; cells of cortical filaments strongly layered; some but not all cells of contiguous vegetative filaments normally joined by cell fusions; trichocytes ('heterocysts' of Adey 1970) arranged in tightly packed, raised, blister-like, horizontal pustulate ('pustulous' of Adey et al. 1982) fields; epithallium single celled to frequently several cells thick; asexual sporangia not capped with pore plugs (caps of Adey 1970); sporangial conceptacles uniporate.

Type species

Basionym

Lithothamnion onkodes Heydrich 1897: 6-7

Pl. 85-89, Figs 1-19.

Current Placement/Name

Hydrolithon onkodes (Heydrich) Penrose & Woelkerling 1992: 83

Pl. 90-95, Figs 1-23.

Lectotype

TRH. Tami Island, north-west edge of Huon Gulf, Papua New Guinea; Heydrich no. 97 (designated by Adey et al. 1982: 9). Previous references to typification were by Penrose & Woelkerling 1988: 162 (as *Porolithon*), Penrose & Woelkerling 1992: 83, Verheij 1993: 47, Woelkerling 1993: 164, Keats & Chamberlain 1994: 8, Barry & Woelkerling 1995: 140, Penrose 1996: 263 (as Hydrolithon).

Isolectotype

Isolectotype material exists in PC. The PC material was also examined during this study and was found to either be misidentified, or contaminated as the fragments sent on loan belong to a species of Neogoniolithon (the fragment possessed very large [~ 1000 µm] uniporate sporangial conceptacles that displayed peripheral roof development, numerous long vertical chains of trichocytes and coaxial medullary filaments).

Synonyms

Homotypic synonyms:

Goniolithon onkodes (Heydrich) Foslie 1898: 8. (see also Foslie 1899: 5)

Lithophyllum onkodes (Heydrich) Heydrich 1901: 533 (see also Foslie 1903: 468; De Toni 1905: 1787-1788; Foslie 1907c: 105; Reinbold 1907: 579; Pilger 1908: 44-45; Foslie 1909: 38-40; Schröder 1912: 302; Printz 1929: 36; Adey & Lebednik 1967: 46).

Porolithon onkodes (Heydrich) Foslie 1909: 57 (see also Lemoine 1911: 160; De Toni 1924: 689; Jadin 1935: 171; Børgesen 1943: 16; Taylor 1950: 124; Kylin 1956: 207; Baissac et al. 1962: 269; Adey 1970: 10; Isaac 1971: 17; Rhyne 1971: 62; Subbaramaiah 1974: 59; Hackett 1977; Tsuda & Wray 1977: 111; Pichon 1978: 209; Zhang & Zhou 1978: 17; Chelazzi & Vannini 1980: 582; Lawson 1980: 59; Adey et al. 1982: 7; Segonzac 1983: Table 1, 1984: 100; Payri 1985: 640; Sartoni 1986: 371; Baba 1987: 314; Krishnamurthy & Jayagopal 1987: 83-85; Penrose & Woelkerling 1988: 162; Tsuda 1991: 56; Naim 1993: 141; Littler & Littler 2003: 50).

Spongites onkodes (Heydrich) Penrose & Woelkerling 1988: 173 (see also Dreckmann 1991; 35; Coppejans & Prud'homme van Reine 1992: 185).

Etymology

'*onkodes*', *onco* = swollen, puffed out, bulky (Stearn 1973). Heydrich (1897) did not explain the origin of the epithet. It possibly makes reference to the granular texture of the thallus surface owing to the presence of abundant pustulate trichocyte fields. This may have given the surface a swollen, puffed out appearance. Alternatively, Heydrich (1897) may simply have referred to the growth form of the coralline growing over lumpy coral.

Description of Type

Habit and Vegetative Structure

The following description is based on the lectotype material housed at TRH (Pl. 85, Fig. 1). The type fragments are adherent, measuring up to at least 2450 µm thick. Thalli are flat and smooth, lack protuberances and have adherent margins that are entire to lobed, but lack orbital ridges. The cell surface (SEM) is both of the *Phymatolithon*- and *Leptophytum*-type (Pl. 86, Fig. 2). The surface texture is matt and granular due to the presence of abundant tightly packed, pustulate trichocyte fields (Pl. 86, Figs 3 & 5).

The thallus is monomerous, and dorsiventrally organised (Pl. 86, Fig. 4). The medullary filaments comprise no more than 30% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 86, Figs 4 & 7; Pl. 88, Fig. 15), with cells that are squat to rectangular and measure 6-32 µm long X 6-19 µm in diameter. Cell fusions are abundant (Pl. 86, Figs 6 & 7; Pl. 88, Fig. 15). Secondary pit connections have not been seen.

The cortical filaments comprise the bulk of the thallus thickness (Pl. 86, Fig. 4). Cells of cortical filaments are squat to rectangular and measure 5-15 µm long X 5-16 µm in diameter. Cell fusions are abundant (Pl. 86, Fig. 6). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 87, Figs 8-10; Pl. 88, Fig. 14). Subepithallial initials are squat to square (Pl. 86, Fig. 6; Pl. 88, Fig. 13), and measure 6-12 µm long X 6-12 µm in diameter. Epithallial cells (Pl. 86, Fig. 6; Pl. 88, Fig. 13) are elliptical and measure 3-6 µm long X 6-12 µm in diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 5 when shedding). Fields of squarish to rectangular trichocytes (Pl. 86, Figs 3 & 5; Pl. 87, Fig. 8; Pl. 88, Fig. 12) commonly occur at the thallus surface in tightly packed pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are **not** separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 15-43 µm long X 11-21 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 87, Figs 8-10; Pl. 88, Fig. 14).

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are more-or-less flush with the thallus surface (Pl. 89, Fig.17), measuring 205-400 µm in external diameter. Their chambers (Pl. 87, Fig. 10; Pl. 89, Figs 16 & 17) are elliptical to bean-shaped, and measure 190-270 µm in diameter X 65-125 µm high, with the roof 43-74 µm (7-12 cells; incl. epithallial cell) thick (Pl. 89, Figs 17 & 18). The conceptacle floor is located c. 18-19 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia (Pl. 89, Figs 17 & 18). A ring of enlarged, domed cells lines the base of the pore canal (Pl. 87, Fig. 11; Pl. 89, Fig 19). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. There is a small central columella present (giving the conceptacle chamber its bean-shape), and the zonately divided tetrasporangia are located peripheral to it. Sporangia measure 69-77 µm long X 31-38 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 87, Fig. 10; Pl. 89, Fig. 16), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Description of representative specimens

Representative specimens examined

Comoros: Chimoni (D Keats, 27.xi.1992, UWC: 92/542); Treasure Cove, Le Galawa (D Keats, 3.xii.1992, UWC: 92/581).

Fiji: Makaluva Island, Suva Lagoon, Suva (D Keats & G Yeo, 24.iv.1994, UWC: 94/1002); Usborne Passage, Great Astrolabe Reef (D Keats, 2.vi.1994, UWC: 94/1030); Herald Passage, Great Astrolabe Reef (D Keats, 10.vi.1994, UWC: 94/1074); Beqa Lagoon (D Keats, 16.vii.1994, UWC: 94/1128); Suva Barrier Reef (D Keats, 11.viii.1994, UWC: 94/1157; D Keats, 21.ix.1994, UWC: 94/1207); East of Dravuni, Great Astrolabe Reef (D Keats, 23.viii.1994, UWC: 94/1175, UWC: 94/1179); Fish Patch, Suva Barrier Reef (D Keats, 13.x.1994, UWC: 94/1253; D Keats, 9.xi.1994, UWC: 94/1269; D Keats, 22.xi.1995, UWC: 95/1509; D Keats, 13.xi.1999, UWC: 99/FJ-04).

South Africa: Kwazulu-Natal, Sodwana Bay: Two mile Reef (D Keats, 21.i.1991, UWC: COR/122; D Keats, 24.i.1991, UWC: COR/159; D Keats, 3.vii.1991, UWC: COR/324; D Keats, 3.vii.1991, UWC: COR/326; D Keats & YM Chamberlain, 5.xi.1991, UWC: 91/134, 7.xi.1991, UWC: 91/169); Five Mile Reef (D Keats, 24.i.1991, UWC: COR/158; D. Keats, 2.vii.1991, UWC: COR/314; D Keats, 2.vii.1991, UWC: COR/320).

Taiwan: Hou Wan Bay, southern Taiwan (D Keats, GW Maneveldt, J Lewis & Jacson, 18.ix. 1998, UWC: 98/335; UWC: 98/340); Long Dong (D Keats, GW Maneveldt, J Lewis & Jacson, W Wei Lung, 25.ix.1998, UWC: 98/413).

Tanzania: Bawi Island, Zanzibar (D Keats, GW Maneveldt & J Kangwe, 2.vii.1999, UWC: 99/114).

Habitat and Phenology

Hydrolithon onkodes is one of the most common corallines in the shallower areas of Indo-Pacific coral reefs (<15m), where it occurs on dead coral skeletons and other hard substrata (Keats, pers.comm.). It commonly occurs within a mixture of species belonging to the genera Hydrolithon, Neogoniolithon, Pneophyllum, Lithophyllum, and Titanoderma within which H. onkodes is sometimes as abundant as all the other species taken together. It is frequently the dominant coralline on the intertidal areas of reefs. The surface is usually grazed by sea urchins, chitons, limpets, and commonly shows deep bites from parrotfish feeding. The thallus regenerates readily to repair this damage. Conceptacles of all reproductive types were observed throughout the year. This species is found throughout the tropical Indo-Pacific region.

Distribution

Antilles (Lemoine 1911, 1964), Australia (Penrose & Woelkerling 1992; Verheij 1993, 1994; Silva et al. 1996; Penrose 1996; Ringeltaube & Harvey 2000), Azores (Lemoine 1964), Borneo (Adey et al. 1982), Easter Island (Lemoine 1920; Adey et al. 1982), Canary Islands (Lemoine 1964; Penrose 1996; Haroun et al. 2002), Cape Verde Islands (Lemoine 1964), Caroline Islands (Abbot 1961), Chagos Archipeligo (Egmont Atoll and Salmon Atoll) (Lemoine 1911; Lee 1967; Silva et al. 1996), Chile (Penrose 1996), China (Zhang & Zhou

1978; Penrose 1996), Comores (Segonzac 1984; Silva et al. 1996; This study), Costa Rica (Pacific) (Dawson 1960b; Penrose 1996), Cuba (Penrose 1996), Diego Garcia Atoll (Silva et al. 1996), Djibouti (Segonzac 1984; Silva et al. 1996), Ellice Islands (Lemoine 1911; Penrose 1996), Fiji (Keats 1995; Littler & Littler 2003; This study), French Polynesia (Payri et al. 2000; Littler & Littler 2003), Gambia (Northern) (Lawson et al. 1995), Ghana (Lawson & John 1982, 1987), Guam (Gordon et al. 1976; Adey et al. 1982), Gulf of Guinea (Lemoine 1964), Hawaiian Islands (Littler & Doty 1975; Adey et al. 1982; Penrose 1996), India (Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Indonesia (Sulawesi, Sumatra and Sumba) (Foslie 1904; Verheij 1993, 1994; Silva et al. 1996), Japan (Baba 1987; Iryu & Matsuda 1988; Matsuda 1989; Yoshida 1998), Kenya (Silva et al. 1996; Penrose 1996), Laccadive Islands (Foslie 1903; Lemoine 1911; Adey et al. 1982; Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Madagascar (Silva et al. 1996), Maldives (Foslie 1903; Lemoine 1911; Adey et al. 1982; Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Marshall Islands (Bikini Atoll, Rongelap Atoll) (Taylor 1950; Lee 1967; Adey et al. 1982; Penrose 1996), Mauritius (Lemoine 1911; Segonzac 1984; Ballesteros & Afonso-Carrillo 1995; Silva et al. 1996), Mexico (Pacific) (Dreckmann 1991; Fragoso & Rodríguez 2002), Papua New Guinea (Heydrich 1897; Lemoine 1911; Adey et al. 1982; Krishnamurthy & Jayagopal 1987; Penrose 1996), Philippines (Penrose 1996), Red Sea (Lemoine 1966; Adey et al. 1982; Penrose 1996; Littler & Littler 2003), Réunion (Segonzac 1984; Silva et al. 1996), São Tomé (Lawson & John 1982, 1987), Seychelles (Foslie 1907a; Lee 1967; Segonzac 1984; Silva et al. 1996), Solomon Islands (Adey et al. 1982; Penrose 1996), Somalia (Silva et al. 1996), South Africa (Keats & Chamberlain 1994; Silva et al. 1996; This study), Sri Lanka (Segonzac 1984; Silva et al. 1996; Penrose 1996), Sulu Archipelago (Adey et al. 1982), Tahiti (Penrose 1996, see also Payri et al. 2000), Taiwan (This study), Tanzania (Zanzibar) (Silva et al. 1996; This study), Tuvalu (Funafuti Atoll) (Foslie 1899, 1900b;

Lemoine 1911; Krishnamurthy & Jayagopal 1987; Adey et al. 1982), Yemen (Northern) (Segonzac 1984).

Habit and Vegetative Structure

Plants are generally adherent (Pl. 90, Fig. 1A), measuring up to at least 100 mm in diameter and 1-10 mm thick. Thalli are generally smooth but tend to become warty to lumpy when conforming to an irregular substratum (Pl. 90, Fig. 1B). Thalli generally lack protuberances, and have adherent margins that are entire to lobed, but lack orbital ridges. The thallus surface is frequently grazed by sea urchins or deeply bitten by parrotfish. The cell surface (SEM) is of the Phymatolithon-type (Pl. 91, Fig. 2). Thalli are pale greyish pink in well-lit situations. The surface texture is matt, and granular due to the presence of abundant tightly packed, pustulate trichocyte fields (Pl. 91, Figs 3 & 5) that are easily visible with a hand lens.

A three-dimensional honey-combed form occurs in some shallow South Pacific coral reef areas in which upright lobes are produced (Pl. 90, Fig. 1C). At the bases of these upright lobes are found the tubular burrows of the chiton Cryptoplax larvaeformis Blaineville (see also Littler & Littler 2003). This form is evidently caused by growth in response to the grazing activities of this chiton (Littler & Littler 2003).

The thallus is monomerous, and dorsiventrally organised (Pl. 91, Figs 4 & 7; Pl. 93, Fig. 14). The medullary filaments comprise 7-33% of thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 91, Figs 4 & 7; Pl. 93, Fig. 14), with cells measuring 7-35 µm long X 5-19 µm in diameter. Cell fusions are abundant (Pl. 91, Fig. 7). Secondary pit connections have not been seen.

The cortical filaments comprise the bulk of the thallus thickness (Pl. 91, Fig. 4), with cells becoming progressively shorter and thinner toward the thallus surface. Cells of cortical filaments measure 5-16 µm long X 5-16 µm in diameter. Cell fusions are abundant. Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 91, Figs 4 & 6). Subepithallial initials are squat to squarish (Pl. 91, Fig. 6; Pl. 93, Fig. 12), and measure 6-14 µm length X 6-12 µm in diameter. Epithallial cells (Pl. 91, Fig. 6; Pl. 93, Fig. 12) are elliptical and measure 3-7 µm long X 6-12 µm diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 5 when shedding). Fields of squarish to rectangular trichocytes (Pl. 91, Figs 3 & 5; Pl. 92, Fig. 9; Pl. 93, Fig. 13) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are **not** separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 15-37 µm long X 6-24 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 91, Figs 4 & 6).

Reproduction

Gametangial plants may be monoecious (Pl. 94, Figs 17 & 18) or dioecious. Spermatangial conceptacles are small (Pl. 94, Figs 17 & 18), measuring about 175-275 µm in external diameter. Spermatangial conceptacle roofs are usually more-or-less flush with the surrounding thallus surface, but are sometimes slightly raised, and they usually possess a small spout. The conceptacle chamber is wide and shallow to elliptical, measuring 80-125 µm in diameter X 25-50 µm high, with the roof 19-37 µm thick. Spermatangial conceptacles are often seen buried in the thallus (Pl. 94, Figs 17 & 18). Simple spermatangial systems are borne only on the floor of the conceptacle chamber (Pl. 94, Fig. 19).

Carpogonial conceptacles are small and inconspicuous (Pl. 95, Fig. 20) measuring only 110-175 µm in external diameter. Carpogonial conceptacle roofs are more-or-less flush with the surrounding thallus surface. Their chambers are flask-shaped, and measure 56-99 µm in diameter X 19-31 µm high. Chambers are usually found near the thallus surface but sometimes sunken to 62 µm deep, with a long pore canal leading to the surface. Three-celled carpogonial branches occur centrally on the chamber floor (Pl. 95, Fig. 21). Completely immersed conceptacles containing carpogonia are commonly observed in thallus sections. Carposporangia develop in carpogonial conceptacles after presumed karyogamy.

Carposporangial conceptacles are relatively large, measuring 250-400 µm in external diameter (Pl. 94, Fig. 18; Pl. 95, Fig. 22). Chambers of carposporangial conceptacles are elliptical to bean-shaped, and measure 150-225 µm in diameter X 50-100 µm high with the roof 43-50 µm thick. The pore canal (Pl. 95, Fig. 22) is lined with small filaments. The continuous central fusion cell is narrow and thick, with gonimoblast filaments borne peripherally (Pl. 94, Fig. 18; Pl. 95, Figs 22 & 23). Gonimoblast filaments are 9-11 (mostly 11) cells long (Pl. 95, Fig. 23) including a terminal carpospore that measures 37-62 µm long X 43-55 µm in diameter. Mature carpospores almost fill the conceptacle chamber.

Tetrasporangial conceptacles are more-or-less flush with the thallus surface, to slightly raised above it (Pl. 92, Figs 9 & 10) and measure 190-500 µm in external diameter. Their chambers are elliptical to bean-shaped, and measure 175-350 µm in diameter X 65-140 µm high, with the roof 25-56 µm (7-11 cells) thick. The conceptacle floor is located 12-19 cells below the surrounding thallus surface. The roof is formed from filaments interspersed among the sporangia and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 93, Fig. 16). The pore-canal filaments are usually oriented more-or-less vertically, and do not tilt markedly into the pore. There is a central columella present (giving the conceptacle chamber its bean-shape), and the zonately divided tetrasporangia are located peripheral to it (Pl. 93, Fig. 15). Sporangia measure 25-87 µm long X 10-37 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 93,

Fig. 15), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Key features

Hydrolithon onkodes is characterised by the following **combination** of characters: 1) thallus thick, adherent, generally lacking protuberances but may be warty to lumpy; 2) thallus monomerous; 3) medullary filaments plumose; 4) tetrasporangial conceptacles that are only slightly raised or flush with the thallus surface; 5) Plants commonly with up to 5 layers of epithallial cells; 6) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 7) within fields, trichocytes are not separated by the cells of normal cortical filaments; 8) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 9) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 10) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 11) the tetrasporangial conceptacle roof is commonly 7-11 cells thick; 12) the sporangial conceptacle floor is commonly 12-19 cells below the surrounding thallus surface.

Remarks

Hydrolithon onkodes is a well-known species throughout the tropical and sub-tropical Indo-Pacific region (Adey et al. 1982; Gordon et al. 1976; Keats & Chamberlain 1993; Littler and Doty 1975; Littler & Littler 2003). Its taxonomy has been well documented (Keats & Chamberlain 1993; Penrose & Woelkerling 1988, 1992). Penrose & Woelkerling (1988) transferred Porolithon onkodes (Heydrich) Foslie to Spongites because it could not be distinguished at the generic level on the basis of previously used vegetative characters. Later, they recognised Hydrolithon on the basis of the sporangial roof development and pore structure described above, and moved Spongites onkodes (Heydrich) Penrose and Woelkerling to Hydrolithon (Penrose & Woelkerling 1992).

Descriptions of taxa in alphabetical order of their basionym

Basionym

Goniolithon boergesenii Foslie 1901a: 19

Pl. 1-5, Figs 1-18.

Current Placement/Name

Hydrolithon boergesenii (Foslie) Foslie 1909: 56

Lectotype

TRH. St. Croix, US Virgin Islands; unnumbered (designated by Adey in Adey & Lebednik 1967:31). Previous references to typification were by Adey & Lebednik 1967: 31 (as Goniolithon) and Adey 1970: 11 (as Hydrolithon).

Synonyms

Homotypic synonyms:

Porolithon boergesenii (Foslie) Lemoine in Børgesen 1917: 178 (see also Steentoft 1967: 131; Masaki 1968: 42-43).

Spongites boergesenii (Foslie) Deckmann ("borgensenii") 1991: 35.

Etymology

'boergesenii', named after Norwegian phycologist F. Børgesen.

Description of Type

Habit and Vegetative Structure

The following description is based on the lectotype material housed at TRH (Pl. 1, Fig. 1). The two existing type fragments are adherent measuring up to 640 µm thick. Thalli are warty, lumpy to smooth, lacking any real protuberances. Margins are free, entire to lobed, but lack orbital ridges. The cell surface (SEM) may be of the Phymatolithon-type, Leptophytum-type and often also neither of the two types (Pl. 2, Figs 2-4). The surface texture is matt.

The thallus is dimerous (Pl. 2, Fig. 6; Pl. 4, Figs 11, 13 & 14). The single basal layer of cells are non-palisade and book-shaped (Pl. 4, Figs 13 & 14), with cells that measure 12-37 µm long X 6-14 µm in diameter (palisade view) X 12-29 µm in diameter (in box-view). Cell fusions are abundant (Pl. 4, Fig. 14). Secondary pit connections have not been seen.

The erect filaments form the bulk of the thallus and often form extensive connections due to broad cell fusions (Pl. 4, Fig. 11). Cells of the erect filament are typically square to rectangular, and spherical to rectangular and measure 20-25 µm long X 9-19 µm in diameter. Cell fusions are abundant (Pl. 2, Figs 5 & 6; Pl. 4, Fig. 11). Secondary pit connections were not seen. Buried trichocytes frequently occur in the cortex (Pl. 4, Fig. 16). Subepithallial initials are square to rectangular (Pl. 2, Fig. 5; Pl. 4, Figs 11 & 12), and measure 7-15 µm long X 6-15 µm in diameter. Epithallial cells (Pl. 2, Fig. 5; Pl. 4, Figs 11 & 12) are squat to elliptical and measure 4-7 µm long X 7-14 µm in diameter, and occur as only 1 cell layer. Trichocytes are square to rectangular and commonly occur singly or in groups of no more than 2-3 (Pl. 2, Figs 2 & 4; Pl. 4, Fig. 15). Trichocytes (except groups) are separated from one another by the cells of one or generally more, normal erect filaments and trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes measure 22-38 µm long X 19-31 µm in diameter. Trichocytes are often overgrown and buried within the thallus (Pl. 4, Fig. 16).

Reproduction

Type fragments lacked gametangial material.

Sporangial conceptacles are flush to only slightly raised above the rest of the thallus measuring 240-480 µm in external diameter (Pl. 3, Figs 7-9; Pl. 5, Fig. 17). Their chambers (Pl. 3, Fig. 9; Pl. 5, Fig. 17) are elliptical, and measure 225-255 µm in diameter X 110-160 µm high, with the roof 34-56 µm (4-5 cells – mostly 4; incl. epithallial cell) thick. The conceptacle floor is located c. 12 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 3, Fig. 10; Pl. 5, Fig 18). The pore is slightly sunken (Pl. 3, Figs 9 & 10; Pl. 5, Fig. 18) and the pore canal also narrows dorsally, and is lined by a single elongate cell (oriented more-or-less vertically) plus an epithallial cell that tilts slightly into the pore, giving it its tapered appearance. The pore-canal is typically funnel-shaped measuring c. 15 µm at its apex and 31-47 µm at its base. There were no signs of a central columella. Tetra/bisporangia were also not seen. Sporangial conceptacles often become buried in the thallus; infilled conceptacles have not been observed.

Distribution

Tropical and subtropical western Atlantic (Antilles, Bahamas, southern and western Caribbean, Florida, Gulf of Mexico, US Virgin Islands) (Foslie 1901a; Lawson & John 1987; Wynne 1998; Littler & Littler 2000), Mexico (Pacific) (Dreckmann 1991), Japan (Masaki 1968; Baba 1987; Yoshida 1998), São Tomé (Steentoft 1967; Lawson & John 1987).

Key features

Hydrolithon boergesenii is characterised by the following **combination** of characters: 1) thallus thick, adherent, warty, lumpy to smooth, generally lacking protuberances; 2) thallus dimerous; 3) has a single basal layer of non palisade cells; 4) sporangial conceptacles that are only slightly raised above the thallus surface; 5) trichocytes present, both at the surface and immersed in the thallus, occurring singly, but also in groups of 2-3; 6) trichocytes are quite often separated by the cells of normal erect filaments; 7) the sporangial conceptacle pore is sunken; 8) the base of sporangial conceptacle pore canals consistently lined by a ring of conspicuous, enlarged, domed cells; 9) the enlarged cell in the sporangial pore canal is subtended by a single epithallial cell that tilts slightly into the pore and gives it a tapered appearance in vertical section; 10) the sporangial conceptacle pore canal is more-or-less funnel shaped; 11) the sporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 12) the sporangial pore canal not lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 13) the tetrasporangial conceptacle roof is commonly 4 cells thick; 14) the sporangial conceptacle floor is commonly up to 12 cells below the surrounding thallus surface.

Remarks

Goniolithon boergesenii is a poorly known species having being reported only from the western tropical and subtropical Atlantic, São Tomé and Japan. The most recent taxonomic review for this species was by Masaki (1968) who retained this taxon within Porolithon. Goniolithon boergesenii is remarkably similar to H. reinboldii differing only in its gross morphology and the absence of the strongly horizontally arranged erect filaments that also characterize the latter species. Based on characters 7, 8 and 9 above, the current research supports Foslie (1909), Adey (1970) and Penrose & Woelkerling (1992) in placing Goniolithon boergesenii in the genus Hydrolithon.

Basionym

Goniolithon improcerum Foslie & Howe in Foslie 1907b: 24

Pl. 6-9, Figs 1-17.

Current Placement/Name

Hydrolithon improcerum (Foslie & Howe) Foslie 1909; 55 (see also Townsend & Adey 1990: 99; Penrose 1996: 258)

Holotype

TRH. Montego Bay, Jamaica; Howe no. 4760b. Previous references to typification were by Adey & Lebednik 1967: 31 (as Goniolithon), Adey 1970: 11 (as Hydrolithon), and Townsend & Adey 1990: 99 (as *Goniolithon*). Isotype material also exists in NY.

Synonyms

Homotypic synonyms:

Porolithon improcerum (Foslie & Howe) Howe 1920: 587 (see also Lemoine 1917: 135; Taylor 1960: 401).

Etymology

"*improcerum*", *im(brex)* = roof, tile + *procerus* = very tall, high (Stearn 1973). Foslie & Howe (in Foslie 1907b) did not explain the origin of the epithet, but it presumably makes reference to the thick layering of the thallus formed by the applanate, tile-like branching.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype material housed at TRH (Pl. 6, Fig. 1). The type fragments are extremely thin and adherent ranging from only 2 (typical) – 4 (when producing regenerated margins) cells thick. Individual thalli measure c. 60 µm thick but frequently occur as applanate branches that overgrow one another measuring up to 500 µm thick (Pl. 7, Figs 2 & 3). Thalli are flat and smooth, lacking protuberances (Pl. 6, Fig. 1), and have adherent margins that lack orbital ridges. The cell surface (SEM) is neither of the Phymatolithon- nor the Leptophytum-type (Pl. 7, Figs 3-5). The surface texture is matt and numerous small trichocyte fields occur (Pl. 7, Figs 6 & 7).

The thallus is dimerous (Pl. 9, Figs 12 & 13) with a bistratose margin (Pl. 9, Fig. 15). The single basal layer comprises cells that are non-palisade and roughly squarish, with cells that measure 9-21 µm long X 9-22 µm in diameter. Cell fusions are abundant (Pl. 9, Fig. 14). Secondary pit connections have not been seen.

The erect filaments typically comprise only an epithallial cell resting above the basal cell (i.e. 1 cell layer thick) (Pl. 9, Fig. 15). Only when new margins are about to be produced, do the erect filaments increase in cell number to 3 cells resting above a single basal cell (incl. the epithallial cell) (Pl. 9, Figs 12-14). When this does happen, cells of the erect filaments become rectangular to elongate (columnar) and measure 12-50 µm long X 7-16 µm in diameter. Cell fusions are abundant (Pl. 9, Fig. 14). Secondary pit connections were not seen. In bistratose sections, the basal cells behave as subepithallial initials and are roughly squarish, and measure 9-21 µm long X 9-22 µm in diameter. When new margins are being generated, subepithallial initials are distinct from the basal cells and are roughly square to rectangular (columnar), measuring 9-43 µm long X 6-22 µm in diameter. Epithallial cells (Pl. 9, Figs 13-15) are squat to elliptical and measure 4-9 µm long X 6-14 µm in diameter. Epithallial cells occur as single layers and stain darker than the rest of the thallus. Small groups of trichocytes occur in horizontal rows (Pl. 7, Figs 6 & 7; Pl. 9, Fig. 12). Trichocytes also occur singly (Pl. 9, Fig. 12 & 13). Trichocytes are rectangular and may be 2-3X the diameter of normal erect filament cells. The cells of normal erect filaments do not separate trichocytes in groups. Individual trichocyte chains typically comprise only 2 cells; a megacell and a support cell (which is also the basal cell of the thallus) (Pl. 9, Figs 12 & 13). Trichocytes end abruptly at their dorsal ends and the remains of the hair that stains darkly is clearly visible (Pl. 9, Fig 12). Trichocytes appear to form only once the thallus has started overgrowing itself (in the bistratose form, it is too thin to bear the trichocytes) and commonly occur in the applanate discs that are visible at the thallus surface (Pl. 7, Figs 6 & 7). Individual trichocytes measure 19-37 µm long X 12-34 µm in diameter. Trichocytes are often overgrown, along with the rest of the thallus that becomes overlain, and become buried within the thallus in small horizontal rows (Pl. 9, Fig. 12).

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are raised above the thallus surface (Pl. 9 Fig. 16), but often appear flush (Pl. 8, Figs. 8-11) due to the regeneration of margins surrounding these conceptacles. Tetrasporangial conceptacles measure 200-375 µm in external diameter. Their chambers (Pl. 9 Fig. 16) are elliptical, and measure 130-250 µm in diameter X 54-105 µm high, with the roof 27-37 µm (2-4 cells; mostly 2, incl. epithallial cell) thick. The conceptacle floor is usually flush with the thallus surface to 2 cells below the surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 9, Fig. 17). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. A central columella was not visible although zonately divided tetrasporangia were seen to be located more-or-less peripherally in the conceptacle chamber

(Pl. 9, Fig. 16). Tetrasporangia measure 56-134 µm long X 16-69 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried through overlaying of the thalli and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Distribution

Australia (southern) (Penrose 1996), Bahamas (Howe 1920; Townsend & Adey 1990; Penrose 1996), Caribbean (Jamaica, Panama, US Virgin Islands) (Townsend & Adey 1990; Penrose 1996), Comores (Silva et al. 1996), Jamaica (Foslie 1907b; Penrose 1996), Mauritius (Silva et al. 1996), New Zealand (Harvey et al. 2005), Tasmania (Penrose 1996).

Key features

Hydrolithon improcerum is characterised by the following **combination** of characters: 1) thallus extremely thin, adherent, lacking protuberances; 2) thallus dimerous; 3) has a single basal layer of non palisade cells, and bistratose margin and thallus, except where localized development of erect filaments occur and where conceptacle initiation is taking place; 4) plants commonly composed of applanate branches that overgrow one another; 5) sporangial conceptacles that are raised above the thallus surface; 6) trichocytes present, occurring singly and in numerous small horizontally oriented rows; 7) within groups, trichocytes are generally not separated by the cells of normal erect filaments; 8) the base of sporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 9) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 10) the tetrasporangial pore canal not lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 11) the tetrasporangial conceptacle roof is more commonly 2-4 cells thick; 12) the sporangial conceptacle floor is commonly 0-2 cells below the surrounding thallus surface.

Remarks

Townsend & Adey (1990) provided the most detailed account of Hydrolithon improcerum. The authors pointed out that not only did Hydrolithon improcerum exhibit a number of morphological and anatomical features described in other genera, it also possessed some unique features that may set this species aside in a new genus. However, in light of the work then underway, particularly in the subfamily Mastophoroideae (e.g. Campbell & Woelkerling 1990; Penrose & Woekerling 1992), Townsend & Adey (1990) chose not to place Goniolithon improcerum in any genus arguing that further investigation of the Corallinaceae was necessary before the relationship of this species could be accurately determined. Since then the Corallinaceae has undergone much taxonomic review (e.g. Penrose & Woelkerling 1992; Chamberlain 1994; Chamberlain & Irvine 1994; Woelkerling 1996a, b) and much of the concerns expressed by Townsend & Adey (1990) appear to have been addressed.

Based on modern research, Hydrolithon improcerum is very similar in anatomical structure to taxa from the genera Mastophora Decaisne 1842: 365 and Lithoporella (Foslie) Foslie 1909: 58 (see Turner & Woelkerling 1982; Townsend & Adey 1990). Hydrolithon improcerum differs from the general characters that diagnose Mastophora, in its tetrasporangial conceptacle roof development and by having non-palisade basal cells. It differs from the general characters that diagnose Lithoporella largely only in having non-palisade basal cells and sporangia located peripherally in the sporangial conceptacle along with the presence of a central columella (see Townsend & Adey 1990; Penrose 1996; Woelkerling 1996c). Hydrolithon improcerum has a remarkably similar tetrasporangial conceptacle roof structure to taxa from the genus Lithoporella and it has been suggested to be closely related to *L. melobesioides* (Penrose 1996). While there still remains debate about the importance of palisade vs. non-palisade basal layers as key characters (see Campbell & Woelkerling 1990; Chamberlain et al. 1991; Chamberlain & Irvine 1994), the presence or absence of a central columella and the distribution of the sporangia within the sporangial conceptacle chamber has been accepted as distinguishing characters (see Penrose 1996). Until more clarity is obtained regarding these characters, based on characters 7, 8 and 9 above, this research supports Foslie (1909) in placing *Goniolithon improcerum* in the genus *Hydrolithon*.

Basionym

Lithophyllum aequinoctiale Foslie 1909: 46 (see also Steentoft 1967: 128).

Pl. 10-13, Figs 1-15.

Current Placement/Name

Status and disposition uncertain.

Holotype

TRH. Rotas Island, São Tomé; no 33. Previous references to typification were by Adey & Lebednik 1967: 48 (as Lithophyllum) and Adey 1970: 10 (as Porolithon). The holotype is the only collection of this species identified by Foslie.

Synonyms

Homotypic synonyms:

Porolithon aequinoctiale (Foslie) Foslie 1909: 57 (see also Taylor 1950: Pl. 68; Adey 1970: 10; Tsuda & Wray 1977: 111; Lawson & John 1987: 215; Lawson et al. 1995: 111-112).

Etymology

"aequinoctiale", aequinoctialis = of the equinox or equator (Stearn 1973). Foslie (1909) did not explain the origin of the epithet, but it presumably makes reference to the type locality São Tomé located on the equator.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype material housed at TRH (Pl. 10, Fig. 1). The type material consists of two fruticose fragments with numerous terete, loosely dichotomously branched, predominantly unfused protuberances. For this study, however, only a single terete protuberance measuring 2.5 mm in diameter X 3.5 mm in length was obtained. This single fragment did, however, possess an adherent margin that lacked orbital ridges (Pl. 11, Fig. 3). The cell surface (SEM) is of the Phymatolithon-type; remnants of the primary pit connections are often still visible (Pl. 11, Fig. 2). The surface texture is matt.

The thallus is monomerous and dorsiventrally organised (Pl. 11, Figs 3 & 4), measuring up to 264 µm thick. The medullary filaments comprise roughly 20% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 11, Figs 3, 4 & 8), with cells that are square to rectangular and measure 6-12 µm long X 5-12 µm in diameter. Cell fusions are abundant. Secondary pit connections have not been seen.

The cortical filaments comprise the bulk of the thallus thickness (Pl. 11, Figs 3 & 4). Cells of cortical filaments are square to rectangular and measure 5-14 µm long X 5-11 µm in diameter. Cell fusions are abundant (Pl. 11, Fig. 6; 13, Fig. 11). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 13, Fig. 13). Subepithallial initials are squat to rectangular (Pl. 11, Fig. 6; Pl. 13, Fig. 11), and measure 6-14 µm long X 5-9 µm in diameter. Epithallial cells (Pl. 11, Fig. 6; Pl. 13, Fig. 11) are squat to elliptical and measure 3-5 µm long X 5-10 µm in diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 4 when shedding). Fields of squarish to slightly rectangular trichocytes (Pl. 11, Fig. 7; Pl. 13, Fig. 12) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 15-25 µm long X 6-25 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 13, Fig. 13).

Reproduction

The type fragment consists of only Spermatangial material and it is presumed that the species is dioecious. Spermatangial conceptacle roofs are more-or-less flush to only slight raised above the surrounding thallus surface (Pl. 12, Figs 9 & 10), measuring 180-300 µm in external diameter. The conceptacle chamber is wide and shallow (triangular to boat-shaped) (Pl. 13, Fig. 14), measuring 150-240 µm in diameter X 35-50 µm high, with thick roofs of 100-200 µm. Simple spermatangial systems are borne only on the floor of the conceptacle chamber (Pl. 13, Figs 14 & 15). Spermatangial conceptacles become buried in the thallus (Pl. 13, Fig. 14), and often contain apparently viable gametes; infilled conceptacles have not been observed.

Tetrasporangial plants have not been seen!

Distribution

Caroline Islands (Abbot 1961), Gambia (Northern) (Lawson et al. 1995), Marshall Islands (Lee 1967), São Tomé (Foslie 1909; Steentoft 1967; Lawson & John 1982, 1987).

Key features

Lithophyllum aequinoctiale is characterised by the following **combination** of characters: 1) thallus thin, adherent, producing narrow terete, loosely dichotomously branched, predominantly unfused protuberances; 2) thallus monomerous; 3) medullary filaments predominantly plumose in crustose part of thallus; 4) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 5) within fields, trichocytes are not separated by the cells of normal cortical filaments; 6) Spermatangial conceptacles flush to only slightly raised, bearing simple spermatangial restricted to the conceptacle floor; 7) Spermatangial conceptacle roofs are thick.

Remarks

Based on features 4 and 5 above, Lithophyllum aequinoctiale in all probability should be placed in Hydrolithon if we are to consider trichocyte arrangements as diagnostic (see Adey 1970). Penrose & Woelkerling (1988) did, however, show that horizontal fields of trichocytes, said to be diagnostic of Hydrolithon (as Porolithon, Adey 1970), were found to be very common in a number of taxa belonging to the genus Spongites. This feature on its own is therefore not sufficient to warrant such a move. The type specimen lacks tetrasporangial material with which to make a more confirmed judgment. Lithophyllum aequinoctiale is, however, very similar in external morphology to Hydrolithon gardineri. If this taxon does prove to be a Hydrolithon, I suspect that it is conspecific with Hydrolithon gardineri. This taxon requires substantially more investigation before a final conclusion can be reached.

Basionym

Lithophyllum africanum Foslie 1900c: 3

Pl. 14-17, Figs 1-22.

Current Placement/Name

Spongites africanum (Foslie) Afonso-Carrillo, Chacana & Sansón 1993

Holotype

TRH. Cape Verde Islands, Africa; Henriques no. 23. Previous references to typification were by Adey & Lebednik 1967: 47 (as Lithophyllum) and Adey 1970: 10 (as Porolithon). See also Woelkerling & Lamy (1998). Isotype material also exists in PC (Woelkerling & Lamy (1998).

Synonyms

Homotypic synonyms:

Lithophyllum africanum Foslie f. intermedia Foslie: 1900c: 3 (see also Foslie 1909: 42; Printz 1929: Pl. 68; Steentoft 1967: 128; Woelkerling 1993: 127; Woelkerling & Lamy 1998: 300).

Lithophyllum africanum Foslie f. truncata Foslie: 1900c: 3 (see also see also Foslie 1909: 42; Printz 1929: Pl. 68; Woelkerling 1993: 226).

Lithophyllum africanum (Foslie) Lemoine 1911: 146.

Porolithon africanum (Foslie) Foslie 1909: 57 (see also Lemoine 1911: 146; Adey 1970: 10; Lawson & John 1982: 244, 1987: 215).

Heterotypic synonyms:

Lithothamnion ponderosum Foslie 1897: 15 (see also Foslie 1909: 42; Steentoft 1967: 128; John et al. 1994: 62 [as *Lithophyllum incrustans*]; Woelkerling et al 1998: 139).

Lithothamnion proboscideum Foslie 1897: 14 (see also Woelkerling 1993: 176; Woelkerling et al. 1998: 139).

Lithophyllum proboscideum (Foslie) Foslie 1900d: 18 (see also Mason 1953: 342; Dawson 1960a: 47; Adey & Lebednik 1967: 44; Adey 1970: 5; Johansen 1976: 395; John et al. 1994: 64).

Etymology

"*africanum*", Foslie (1900c) did not explain the origin of the epithet, but it presumably makes reference to the type locality along the West coast of Africa.

Description of Type

Habit and Vegetative Structure

The following description is based on the lectotype material housed at TRH. A single terete protuberance measuring 6 mm in diameter X 8 mm in length was obtained for analysis. The thallus is adherent, measuring up to at least 1150 µm thick. The thallus is flat and smooth and has an adherent margin that is entire to lobed, but lacking an orbital ridge. The cell surface (SEM) is of the *Leptophytum*-type (Pl. 14, Figs 1 & 2). The surface texture is matt and granular due to the presence of abundant tightly packed, pustulate trichocyte fields (Pl. 14, Fig. 3).

The thallus is monomerous and dorsiventrally organised (Pl. 14, Fig. 5). The medullary filaments comprise 52-67% of the thallus thickness with a core that is predominantly coaxial (Pl. 14, Fig. 5). Cells of medullary filaments are square to rectangular and measure 5-34 µm long X 5-12 µm in diameter. Cell fusions are abundant (Pl. 14, Fig. 7). Secondary pit connections have not been seen.

The cortical filaments comprise a small portion of the thallus thickness, never accounting for more than half of the thallus. Cells of cortical filaments are square to rectangular and measure 4-15 µm long X 3-11 µm in diameter. Cell fusions are abundant (Pl. 14, Fig. 6; Pl. 16, Fig. 15). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 16, Fig. 17). Subepithallial initials are square to rectangular (Pl. 14, Fig. 6; Pl. 16, Fig. 15), and measure 4-19 µm long X 4-10 µm in diameter. Fusions between adjacent subepithallial initials are common (Pl. 14, Fig. 6; Pl. 16, Fig. 15). Epithallial cells (Pl. 14, Fig. 6; Pl. 16, Fig. 15) are squat to elliptical and measure 3-10 µm long X 5-12 µm in diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 4 when shedding). Fields of squarish to elongate trichocytes (Pl. 14, Fig. 4; Pl. 16, Fig. 16) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 16-43 µm long X 9-19 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 15, Fig. 12; Pl. 16, Fig. 17).

Reproduction

Type fragment lacked gametangial material.

Tetrasporangial conceptacles are flush to only slightly raised above the rest of the thallus and measure 300-650 µm in external diameter (Pl. 15, Figs 9, 10 & 14; Pl. 17, Fig. 18). Their chambers are elliptical to bean-shaped (Pl. 15, Figs 13 & 14; Pl. 17, Figs 18 & 19), and measure 175-315 µm in diameter X 65-125 µm high, with the roof 43-62 µm (7-11 cells; incl. epithallial cell) thick. The conceptacle floor is located c. 21 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from peripheral roof filaments (Pl. 17, Figs 21 & 22). These cells protrude into the pore canal as papillae, and are oriented more-or-less parallel to the roof surface (Pl. 17, Fig. 20). The pore canal is typically funnel-shaped measuring c. 31 µm at its apex to c. 62 µm at its base. There is a central columella present (giving the conceptacle chamber its bean-shape) (Pl. 15, Fig. 13), and the zonately divided tetrasporangia are located peripheral to it. Sporangia measure 41-99 µm long X 19-56 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 15, Figs 12 & 13; Pl. 17, Fig. 19), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Distribution

Annobon (Pagalú) (Steentoft 1967), Bioko (Lawson & John 1987; Woelkerling et al. 1998), Cameroun (Lawson & John 1982, 1987), California to Mexico (Foslie 1897; Mason 1953; Dawson 1960a; Johansen 1976), Canaries (Lemoine 1911, 1964), Cape Verde Islands (Foslie 1900c; Lemoine 1911, 1964; Adey & Lebednik 1967; Steentoft 1967; Afonso-Carrillo et al. 1993), Gambia (Northern) (Woelkerling et al. 1998), Gulf of Guinea (Lemoine 1964), Mauritanie (Lemoine 1964; Woelkerling et al. 1998), Morocco (Lemoine 1964; Benhissoune et al. 2002), São Tomé (Adey & Lebednik 1967; Steentoft 1967), Senegal (Foslie 1900c; Foslie 1909; Steentoft 1967; Afonso-Carrillo et al. 1993).

Key features

Lithophyllum africanum is characterised by the following **combination** of characters: 1) thallus thick, adherent, possessing terete, often fused protuberances; 2) thallus monomerous; 3) medullary filaments comprise the greater portion of the thallus thickness, with a predominantly coaxial core; 4) tetrasporangial conceptacles that are flush to only slightly raised above the rest of the thallus surface; 5) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 6) within fields, trichocytes are not separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals not lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments peripheral to the conceptacle chamber and not from filaments interspersed among the sporangia; 9) the tetrasporangial pore canal is lined by narrow filaments that tilt into the pore canal, are orientated more-or-less parallel to the roof surface, and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is commonly 7-11 cells thick; 11) the sporangial conceptacle floor is commonly up to 21 cells below the surrounding thallus surface.

Remarks

Based on characters 7, 8 and 9 above, Lithophyllum africanum belongs within the genus Spongites. This move had already been proposed by Afonso-Carrillo et al. (1993) who formally transferred Lithophyllum africanum to Spongites as delimited by Penrose & Woelkerling (1988). This early concept of Spongites (sensu lato Woekerling 1985: 146; Penrose & Woelkerling 1988: 174), however, encompassed the genus Hydrolithon. Based on the studies of Penrose & Woelkerling (1988) who subsumed Hydrolithon into Spongites, Afonso-Carrillo (pers. comm. in Woelkerling et al. 1998: 123) then suggested that Lithophyllum africanum probably belongs to Hydrolithon as delimited by Penrose (1996). This transfer was, however, never affected.

In their study of Lithophyllum africanum, Afonso-Carrillo et al. (1993) never managed to obtain any tetrasporangial material from the type specimen, although they did make mention of one empty uniporate conceptacle. Their tetrasporangial data was thus based entirely on their material collected from the Cape Verde Islands. This study has revealed fertile tetrasporangial material in the type collection and both the type and the Cape Verde Island (Afonso-Carrillo et al. 1993) material conform to the concept of *Spongites* (*sensu stricto*) as delimited by Penrose & Woelkerling (1992). *Spongites africanum*, therefore, remains in *Spongites*. This study therefore supports the transfer of *Lithophyllum africanum* by Afonso-Carrillo et al. (1993) to *Spongites* as 5 of the 7 criteria diagnostic of *Spongites* (*sensu stricto* Penrose & Woelkerling 1992) are evident in this taxon.

It should be noted, however, that S. africanum is remarkably similar to Pneophyllum *conicum* Keats, Chamberlain & Baba (1997) (see Table 3). The genera *Spongites* and *Pneophyllum* are distinguished primarily on the development of the sporangial conceptacle roof. In *Spongites*, the sporangial conceptacle roof is formed from peripheral roof filaments only, while in *Pneophyllum*, the conceptacle roof is formed from both peripheral roof filaments as well as filaments interspersed among the sporangia. In *Pneophyllum*, however, the conceptacle roof development is only evident in developing young (immature) sporangial conceptacles; it is seldom evident in the mature conceptacles, and therefore appears like that of *Spongites*. As only mature sporangial conceptacles were seen in *S. africanum* during this study and by Afonso-Carrillo et al. (1993), the *Pneophyllum*-type sporangial conceptacle roof development cannot be ruled out as a possibility. Spongites africanum and P. conicum (see Keats et al. 1997) differ largely with respect to their gross morphologies, the number of epithallial cell layers, and the absence and presence respectively of a single elongated cell in the sporangial conceptacle wall (Table 3). These differences are quite consistent and until such time as representative material of *S. africanum* (particularly of plants bearing young, developing [immature] sporangial conceptacles) are found to fully evaluate the taxonomic placement of this species, this taxon appears to conform to the generic description of the genus Spongites.

This species does, however, display a very interesting feature. It was reported that Hydrolithon (as Porolithon, see Adey 1970) is characterised by among other features, the existence of horizontal fields of pustulate trichocytes that are not separated by normal cortical cells. Spongites africanum possess these same pustulate trichocytes in horizontal fields. This is not surprising as Penrose & Woelkerling (1988) had reported a number of southern Australian taxa, belonging to the genus Spongites, possessing trichocyte fields in horizontal fields and so too have Keats et al. (1997) shown them to occur in P. conicum. A number of earlier reports (see Lemoine 1917; Cabioch 1972) had already highlighted the variability in trichocyte arrangements in taxa ascribed to the defunct genus Porolithon. It will thus become necessary to review our concept of trichocyte arrangements as a diagnostic feature.

Basionym

Lithophyllum antillarum Foslie et Howe 1906: 579

Pl. 18-22, Figs 1-23; Pl.23-27, Figs 1-22.

Current Placement/Name

Status and disposition uncertain.

Holotype

NY. Culebra, Puerto Rico; Howe no. 4373. Previous references to typification were by Adey & Lebednik 1967: 47 (as *Lithophyllum*) and Adey 1970: 10 (as *Porolithon*), Tittley et al. 1984: 8, Woelkerling 1993: 28 and Woelkerling & Lamy 1998: 300.

Isotypes

NY, PC, & TRH. Culebra, Puerto Rico, Howe no. 4373; BM, algal collection box 899.

Synonyms

Homotypic synonyms:

Porolithon antillarum (Foslie et Howe) Foslie 1909: 57 (see also Adey 1970: 10).

Etymology

"*antillarum*", *antill* referring to the Antilles, the group of islands in the Caribbean Sea + *arum* = of (Stearn 1973). Foslie & Howe (1906) did not explain the origin of the epithet, but it presumably makes reference to the type locality within the Antilles.

Description of Type

Habit and Vegetative Structure

The following description is based on isotype material housed at BM (Pl. 18, Fig. 1) and TRH (Pl. 23, Fig. 1). The isotype fragments are all relatively large, upright, honey-combed (lobed) in form, measuring up to 105 mm in height X 114 mm in diameter (Pl. 18, Fig. 1; Pl. 23, Fig. 1). Grazing scars are very obvious features of the surfaces of the fragments. The type fragments are adherent, measuring up to at least 900 µm thick. Encrusting portions of the thalli are generally flat, lacking protuberances, and have adherent to free margins that are entire to lobed, but lacking orbital ridges (Pl. 19, Fig. 4; Pl. 21, Fig. 14). The lobed portions of the thallus measure up to 7 mm thick, up to 26 mm in width and up to 38 mm in height. The cell surface (SEM) is of the Phymatolithon-type (Pl. 19, Fig. 2; Pl. 24, Fig. 2). The surface is course and granular due to the presence of abundant grazing scars (Pl. 20, Figs 9-11; Pl. 25, Figs 9 & 10) and tightly packed, pustulate trichocyte fields (Pl. 19, Fig. 3; Pl. 24, Fig. 3).

The thallus is monomerous and dorsiventrally organised (Pl. 19, Figs 4, 6 & 7; Pl. 21, Fig. 18; Pl. 24, Figs 5, 6 & 8; Pl. 26, Fig. 17). The medullary filaments comprise roughly 17-44% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 19, Figs 4 & 6-8; Pl. 21, Figs 18 & 19; Pl. 24, Figs 5 & 8; Pl. 26, Fig. 17). Cells of medullary filaments are square to rectangular and measure 5-50 µm long X 4-15 µm in diameter. When a thallus bearing an extremely thin medullary region is sectioned parallel to the growing edge, a falsely dimerous thallus is often observed (Pl. 26, Figs 13, & 18). In the protuberances, the medullary filaments are generally coaxial. Cell fusions are abundant (Pl. 19, Figs 7 & 8; Pl. 21, Figs 18 & 19; Pl. 26, Fig. 17). Secondary pit connections have not been seen.

The cortex is relatively thick (up to 83% of the thallus, Pl. 19, Figs 4 & 6; Pl. 24, Fig. 5; Pl. 26, Fig. 13), being present throughout the thallus. Cells of cortical filaments are square to rectangular and measure 5-17 µm long X 5-12 µm in diameter. Cell fusions are abundant

(Pl. 19, Fig. 5; Pl. 24, Fig. 7). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 19, Fig. 5; Pl. 21, Fig. 17; Pl. 24, Fig. 5; Pl. 26, Fig. 15). Subepithallial initials are square to rectangular (Pl. 19, Fig. 5; Pl. 21, Fig. 16; Pl. 26, Fig. 16), and measure 4-19 µm long X 6-12 µm in diameter. Epithallial cells (Pl. 19, Fig. 5; Pl. 21, Fig. 16; Pl. 26, Fig. 16) are squat to elliptical and measure 3-7 µm long X 6-12 µm in diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 5 when shedding). Fields of squarish to rectangular trichocytes (Pl. 19, Fig. 5; Pl. 21, Fig. 15; Pl. 24, Fig. 4; Pl. 26, Fig. 14) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 14-41 µm long X 6-21 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 19, Fig. 5; Pl. 21, Fig. 17; Pl. 24, Fig. 5; Pl. 26, Fig. 15).

Reproduction

Gametangial plants appear to be dioecious. Spermatangial and carpogonial plants were not seen. Carposporangial conceptacles are flush to slightly raised above the thallus surface, are large and measure 335-600 µm in external diameter (Pl. 20, Figs 9-11; Pl. 22, Fig. 21). Chambers of carposporangial conceptacles are bean-shaped, and measure 160-240 µm in diameter X 40-100 µm high with the roof 43-55 µm thick. The pore canal (Pl. 20, Figs 12 & 13) is lined with small papillate filaments. The continuous central fusion cell is narrow and thick, with gonimoblast filaments borne peripherally. Intact gonimoblast filaments were not found. Carpospores measures 15-30 µm long X 35-42 µm in diameter. Mature carpospores almost fill the conceptacle chamber.

Tetrasporangial conceptacles are more-or-less flush to only slightly raised above the rest of the thallus and measure 300-500 µm in external diameter (Pl. 25, Figs 9-11; Pl. 27, Fig. 19). Their chambers (Pl. 25, Fig. 11; Pl. 27, Figs 19 & 20) are elliptical to bean-shaped, and measure 187-375 µm in diameter X 50-180 µm high, with the roof 43-74 µm (5-11 cells; incl. epithallial cell) thick. The conceptacle floor is located 13-19 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 22, Fig. 23; Pl. 27, Fig. 21). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. Through secondary overgrowth, however, buried conceptacles may bear papillate cells along their pore canals (Pl. 27. Fig.22). There is a small central columella present (giving the conceptacle chamber its bean-shape) (Pl. 27, Fig. 20), and the zonately divided tetrasporangia are located peripheral to it. Tetrasporangia measure 37-155 µm long X 15-93 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 22, Fig. 22; Pl. 27, Fig. 20), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Distribution

Puerto Rico (Foslie & Howe 1906).

Key features

Lithophyllum antillarum is characterised by the following **combination** of characters: 1) thallus thick, adherent, lacking conventional protuberances, but bearing lobed branches that form a honey-combed structure; 2) thallus monomerous; 3) medullary filaments plumose; 4) tetrasporangial conceptacles that are only slightly raised or flush with the thallus surface; 5) Plants commonly with up to 5 layers of epithallial cells; 6) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 7) within fields, trichocytes are not separated by the cells of normal cortical filaments; 8) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 9) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 10) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 11) the tetrasporangial conceptacle roof is commonly 5-11 cells thick; 12) the sporangial conceptacle floor is commonly 13-19 cells below the surrounding thallus surface.

Remarks

Lithophyllum antillarum is a poorly known species and despite the large collection made by Howe in 1906 (Woelkerling 1993), it is based on a collection of plants made from a single locality in Culebra, Puerto Rico. Since then, I have been unable to find any new records of this species in the literature. Nonetheless, the review of this species has led me to conclude that Lithophyllum antillarum is the honey-combed form of Hydrolithon onkodes which is commonly found in the South Pacific. In their recent book, Littler & Littler (2003) documents this very same honey-combed structure in Hydrolithon onkodes (as Porolithon onkodes). The grazing activity of the chiton, Cryptoplax larvaeformis Blainville & Burrow that lives at the bases of the lobes, is apparently responsible for the three-dimensional honey-combed structure in the South Pacific Hydrolithon onkodes (Littler & Littler 2003). Similarly, on some Caribbean reefs, Porolithon pachydermum has been reported to have the same castle-like, three-dimensional honey-combed structure. At the bases of the coralline are found the tubular burrows of the chiton, Choneplax lata Guilding (Littler et al. 1995; Littler & Littler 2000). This form too is evidently caused by growth in response to the grazing activities of this chiton (Littler et al. 1995). Not withstanding the gross morphology, this species matches perfectly the description of Hydrolithon onkodes and I therefore propose that Lithophyllum antillarum is conspecific with Hydrolithon onkodes. Lithophyllum antillarum is thus a heterotypic synonym for Hydrolithon onkodes.

Basionym

Lithophyllum coarctatum Foslie 1907a: 31

Pl. 28-32, Figs 1-19

Current Placement/Name

Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine 1993: 451 (see also Verheij 1994: 106-107)

Pl. 51-55, Figs 1-18.

Holotype

TRH. Cocos Keeling Islands; unnumbered. Previous references to typification were by Adey & Lebednik 1967: 48 (as Lithophyllum) and Adey 1970: 10 (as Porolithon). The holotype is the only collection of this species identified by Foslie.

Synonyms

Homotypic synonyms:

Porolithon coarctatum (Foslie) Foslie 1909: 57 (see also De Toni 1924: 692; Adey 1970: 10; Verheij 1993: 46, 1994: 106).

Heterotypic synonyms:

Lithophyllum gardineri Foslie 1907a: 30-31 ("forma typica") (see also Foslie 1907c: 106-107, 1907d 190-191; Gardiner 1907: Fig 30; Foslie 1909: 44-45; Printz 1929: 34; Adey & Lebednik 1967: 48; Woelkerling 1993: 102-103; Verheij 1993: 46, 1994: 106 [Verheij (1993, 1994) considered Lithophyllum gardineri, L. gardineri forma obpyramidatum and Lithophyllum coarctatum conspecific]; Silva et al. 1996: 237).

Lithophyllum gardineri Foslie forma obpyramidatum Foslie 1907a: 30-31 ("obpyramidata") (see also Foslie 1907c: 106-107, 1907d 190-191; Printz 1929: 34; Woelkerling 1993: 103, 160; Verheij 1993: 46, 1994: 106; Silva et al. 1996: 237; Woelkerling & Lamy 1998: 313).

Porolithon gardineri (Foslie) Foslie 1909: 57 (see also De Toni 1924: 691; Adey 1970: 10; Hackett 1977: 21; Adey et al. 1982: 10; Kalugina-Gutnik et al. 1992: 17; Woelkerling 1993: 102-103; Verheij 1993: 46, 1994: 106; Silva et al. 1996: 237; Littler & Littler 2003: 48).

Porolithon marshallense W.R. Taylor ("*marshallensis*") 1950: 128-129 (Taylor considered *Lithophyllum gardineri* forma *obpyramidatum* conspecific with *Porolithon marshallense*).

Spongites gardineri (as *Spongines gadineri*) Titlyanova et al. 1992: 43.

Etymology

"*coarctatum*", *coarctatus* = pressed together, close-set, narrowed (Stearn 1973). Foslie (1907a) did not explain the origin of the epithet, but it presumably makes reference to the tightly packed nature of the fruticose thallus.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype material housed at TRH (Pl. 28, Fig. 1). The type consists of a single fruticose fragment bearing numerous tightly packed, terete, finely dichotomously branched, unfused protuberances measuring up to 3 mm in diameter and up to 16 mm in length. The rest of the thallus is adherent measuring up to 350 µm in thickness. No margins were observed from the type specimen. The cell surface (SEM) is mostly of the *Leptophytum*-types (Pl. 29, Figs 2 & 3). The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate trichocyte fields (Pl. 29, Figs 4 & 5).

The thallus is monomerous and dorsiventrally organised (Pl. 31, Fig. 15). The medullary filaments comprise 21-50% of the thallus thickness. The medullary filaments in crustose areas is predominantly plumose (non-coaxial) and composed of cells that are square to rectangular and measure 6-31 µm long X 6-19 µm in diameter. In the protuberances, the medullary filaments are coaxial (Pl. 31, Fig. 14). Cell fusions are abundant. Secondary pit connections have not been seen.

The cortical filaments comprise up to 79% of the thallus thickness in crustose parts with cells that are square to rectangular, and measure 5-20 µm long X 4-12 µm in diameter. Cell fusions are abundant (Pl. 29, Figs 5 & 7). Secondary pit connections have not been seen. Buried trichocyte fields occur frequently in the cortex (Pl. 29, Figs 6 & 7). Subepithallial initials are square to rectangular (Pl. 29, Fig. 7; Pl. 31, Fig. 13), and measure 6-14 µm long X 5-11 µm in diameter. Epithallial cells (Pl. 29, Fig. 7; Pl. 31, Fig. 13) are squat to elliptical and measure 3-6 µm long X 5-14 µm in diameter, and occur in 1-3 (mostly 2-3 but up to 4 when shedding) cell layers. Fields of squarish to elongate trichocytes (Pl. 29, Fig. 5; Pl. 31, Fig. 16) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are <u>not</u> separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 19-43 µm long X 9-25 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 29, Figs 6 & 7).

Protuberances are composed of a thick central core of medullary filaments with vertically oriented cells arranged in a coaxial manner (Pl. 31, Fig. 14). From this central core arise the cortical filaments composed of cells that are oriented perpendicularly to the long axis of the protuberance. The protuberances branch dichotomously and are predominantly unfused (Pl. 28, Fig. 1).

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are slightly raised above the rest of the thallus surface (Pl. 30, Figs 8-11; Pl. 32, Fig. 17), measuring 240-450 µm in external diameter. Their chambers (Pl. 30, Figs 10 & 11; Pl. 32, Figs 17 & 18) are elliptical, and measure 190-225 µm in diameter X 85-115 µm high, with the roof 29-43 µm (4-8 [mostly 5-6] cells; incl. epithallial cell) thick (Pl. 30, Fig. 12). The conceptacle floor is located 9-13 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 30, Fig. 12; Pl. 32, Fig. 19). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. A central columella has not been observed for this specimen. Zonately divided tetrasporangia, located peripherally in the tetrasporangial conceptacles, have however, been observed. Sporangia measure 50-93 µm long X 16-62 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 30, Fig. 11; Pl. 32, Fig. 18), and often contain apparently viable sporangia (Pl. 32, Fig. insert). Completely infilled conceptacles have not been observed although a degree of infilling has been observed (Pl. 30, Fig. 11).

Distribution

Cocos (Keeling) Islands (Foslie 1907a), Indonesia (SW Sulawesi) (Verheij 1993, 1994), Marshall Islands (Taylor 1950; Lee 1967), Seychelles (Verheij 1993, 1994; Titlyanova et al. 1992).

Key features

Lithophyllum coarctatum is characterised by the following **combination** of characters: 1) thallus thin, adherent, producing narrow terete, dichotomously branched, predominantly unfused protuberances; 2) thallus monomerous; 3) medullary filaments predominantly plumose in crustose part of thallus; 4) tetrasporangial conceptacles that are only slightly raised above the thallus surface; 5) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 6) within fields, trichocytes are not separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 9) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is commonly 5-6 cells thick; 11) the sporangial conceptacle floor is commonly 9-13 cells below the surrounding thallus surface.

Remarks

The most recent reference to the type of Lithophyllum coarctatum was by Verheij (1993, 1994). In his study of the nongeniculate coralline algae of the Spermonde Archipelago, Sulawesi, Indonesia, Verheij (1993, 1994) proposed that Lithophyllum coarctatum, L. gardineri and L. gardeneri forma obpyramidatum were all conspecific, and therefore synonymous with Hydrolithon gardineri as described by Verheij & Prud'homme van Reine (in Verheij 1993, 1994). Although no central columella (a character considered by Verheij [1993: 47, 1994: 107] as diagnostic of Hydrolithon gardineri), has been observed for Lithophyllum coarctatum, this species still conforms well to the description of Hydrolithon gardineri. The current research, therefore, supports the synonymy of Lithophyllum coarctatum with Hydrolithon gardineri (see Lithophyllum gardineri in this paper).

Basionym

Lithophyllum craspedium Foslie 1900a : 26

Pl. 33-36, Figs 1-21

Current Placement/Name

Hydrolithon craspedium (Foslie) P. Silva in Silva et al. 1996: 235

Pl. 37-41, Figs 1-19.

Holotype

TRH. Onoataa, Gilbert Islands (Kiribati); British Museum no. A27. Previous references to typification were by Adey & lebednik 1967: 47 (as Lithophyllum), Adey 1970: 10 (as *Porolithon*), and Tittley et al. 1984: 8 (as *Lithophyllum*). The BM also contains a portion of the holotype material; this material was not examined during this study.

Synonyms

Homotypic synonyms:

Porolithon craspedium (Foslie) Foslie 1909: 57 (see also Lemoine 1911, 163; Taylor 1950: 127; Adey 1970: 10; Hackett 1977: 21; Tsuda & Wray 1977: 111; Pichon 1978: 357, 419; Lawson 1980: 58; Krisnamurthy & Jayagopal 1987: 81; Littler & Littler 2003: 48).

Etymology

'*craspedium*', *cras(sus)* = thick + *ped* = foot (or *ped(alis)* = a foot long) (Stearn 1973). Foslie (1900a) did not explain the origin of the epithet, but it presumably makes reference to the thick, mountain-like, and probably in Foslie's opinion, foot-long protuberances that characterise this species.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype material housed at TRH. The thallus is massive and mountain-like, bearing broad individual to fused vertical columns (Keats pers. comm.). Only tiny fertile fragments were sent on loan for observation during this study. The type fragments are adherent, measuring up to 675 µm in crustose areas. Thalli are generally smooth and young plants have free margins that are entire to lobed, but lack orbital ridges. The cell surface (SEM) is somewhat between the Leptophytum- and Phymatolithon-type (Pl. 33, Fig. 1). The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate trichocyte fields (Pl. 33, Figs 2 & 3).

The thallus is monomerous, and dorsiventrally organised in crustose areas (Pl. 33, Figs 5 & 7; Pl. 35, Figs 13 & 16). The medullary filaments comprise 11-43% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 33, Figs 5 & 7; Pl. 35, Figs 13 & 16). Cells of medullary filaments are square to rectangular and measure 10-32 µm long X 6-19 µm in diameter. Cell fusions are abundant (Pl. 33, Fig. 7; Pl. 35, Fig. 16). Secondary pit connections have not been seen.

The cortical filaments comprise the bulk of the thallus thickness (up to 89%) (Pl. 33, Fig. 5; Pl. 35, Fig. 13). Cells of cortical filaments are square to rectangular and measure 6-17 µm long X 5-12 µm in diameter. Cell fusions are abundant (Pl. 33, Fig. 6; Pl. 35, Fig. 14). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 33, Fig. 4; Pl. 35, Fig. 15). Subepithallial initials are squat to square (Pl. 33, Fig. 6; Pl. 35, Fig. 14), and measure 6-10 µm long X 6-12 µm in diameter. Epithallial cells (Pl. 33, Fig. 6; Pl. 35, Fig. 14) are squat to elliptical to domed and measure 3-7 µm long X 6-12 µm in diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 4 when shedding). Fields of squarish to elongate trichocytes commonly occur at the thallus surface in tightly packed, pustulate horizontal fields (Pl. 33, Figs 2 & 3). These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 19-31 µm long X 7-19 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 33, Fig. 4; Pl. 35, Fig. 15).

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are more-or-less flush to only slight raised above the rest of the thallus, measuring 350-550 µm in external diameter (Pl. 34, Figs 8-10; Pl. 36, Figs 17 & 18). Their chambers (Pl. 34, Figs 10 & 11; Pl. 36, Figs 17 & 18) are elliptical to bean-shaped, and measure 185-250 µm in diameter X 75-125 µm high, with the roof 37-62 µm (6-9 cells; incl. epithallial cell) thick (Pl. 34, Fig. 12; Pl. 36, Fig. 19). The conceptacle floor is flush with the thallus surface to 15 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 34, Fig. 12; Pl. 36, Figs 20 & 21). This ring of enlarged cells is substantially smaller than those commonly found in other species of Hydrolithon. While the ring of enlarged cells is typically 2/3 the length of the conceptacle pore in most species of Hydrolithon, it is generally only 1/3 the length of the conceptacle pore in Lithophyllum craspedium. Above the enlarged cells, the tetrasporangial pore canal is often lined by narrow filaments that may or may not tilt slightly into the pore canal and create the appearance of papillae (Pl. 34, Fig. 12; Pl. 36, Figs 19-21). There is a small central columella present (only ever seen in SEM) (giving the conceptacle chamber its bean-shape), and the zonately divided tetrasporangia are located peripheral to it. Sporangia measure 37-68 µm long X 12-41 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 36, Fig. 17), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Description of representative specimens

Representative specimens examined

Fiji: Dravuni, Great Astrolabe Reef (D Keats, 9.vi.1994, UWC: 94/1112; 8.ix.1994, UWC: 941176).

Kiribati: Tamana Atoll (G Yeo, ?.ix.1994, UWC: 94/1280).

Habitat and Phenology

Hydrolithon craspedium is common on the shallower areas of windward reefs (5-20 m) (tropical Indo-Pacific region) that have not been recently affected by cyclone damage (Keats pers. comm.).

Distribution

Chagos Archipelago (Foslie 1907c, d; Lemoine 1911; Silva et al. 1996), Fiji (Littler & Littler 2003; This study), India (Krusadi Island) (Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Kiribati (Gilbert Islands, Tamana Atoll) (Foslie 1900a; Lemoine 1911; This study), Laccadive Islands (Foslie 1907c, d; Lemoine 1911), Madagascar (Silva et al. 1996), Maldives (Male Atoll) (Foslie 1907c, d; Lemoine 1911; Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Marshall Islands (Rongelap Atoll) (Taylor 1950; Lee 1967), Seychelles (Coetivy

Reef) (Foslie 1907c, d; Silva et al. 1996), Somalia (Silva et al. 1996), Tahiti (Lemoine 1911), Tuvalu (Funafuti Atoll) (Foslie 1900b; Lemoine 1911; Krishnamurthy & Jayagopal 1987).

Habit and Vegetative Structure

Plants are generally adherent on dead coral skeletons and other hard substrata, measuring up to at least 100 mm in diameter. Thalli are massive and mountain-like, (Pl. 37, Fig. 1) bearing broad individual to fused vertical columns that measure up to 500 mm tall. Thalli thicken up early in development, and become distinct from the closely related H. onkodes and H. gardineri even while still less than one cm in diameter (Pl. 37, Fig 1B). Crustose areas are narrow or absent in older thallli. Thalli are strongly adherent, with a thick adherent margin. Newly formed margins produce free, scrolled ends (Pl. 38, Fig. 5) that quickly become insignificant as the margin thickens. The thick margin is entire to slightly lobed, and lacks orbital ridges. The surface is usually smooth, and the colour pale greyish pink with a faint bluish cast in well lit situations. The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate trichocyte fields that are easily visible with a hand lens (Pl. 38, Fig. 3). The cell surface (SEM) is both of the Phymatolithon- and Leptophytum-types (Pl. 38, Fig. 2).

The thallus is monomerous, and dorsiventrally organised in crustose areas. The medullary filaments comprise 11-52% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 38, Fig. 7). Cells of medullary filaments are square to rectangular and measure 7-27 µm long X 6-19 µm in diameter. Cell fusions are abundant. Secondary pit connections have not been seen.

The cortical filaments comprise the bulk of the thallus thickness (up to 89%). Cells of cortical filaments are square to rectangular and measure 6-21 µm long X 6-10 µm in diameter. Cell fusions are abundant (Pl. 38, Fig. 6; Pl. 40, Fig. 14). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 38, Fig. 4; Pl. 39, Fig. 11). Subepithallial initials are squat to square (Pl. 38, Fig. 6; Pl. 40, Fig. 14), and measure 5-10 µm long X 7-11 µm in diameter. Epithallial cells (Pl. 38, Fig. 6; Pl. 40, Fig. 14) are squat to elliptical and measure 3-6 µm long X 7-11 µm in diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 4 when shedding). Fields of squarish to elongate trichocytes (Pl. 38, Fig. 4; Pl. 40, Fig. 13) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are <u>not</u> separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 12-20 µm long X 6-16 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 38, Fig. 4; Pl. 39, Fig. 11).

Reproduction

Gametangial plants have not been seen!

Tetrasporangial conceptacles are more-or-less flush to only slight raised above the rest of the thallus, measuring 275-500 µm in external diameter (Pl. 39, Figs 8-10; Pl. 41, Fig. 15). Their chambers are elliptical to bean-shaped (Pl. 39, Figs 10 & 11; Pl. 41, Figs 15 & 16), and measure 240-265 µm in diameter X 50-110 µm high, with the roof 37-62 µm (5-9 cells; incl. epithallial cell) thick (Pl. 41, Figs 17 & 18). The conceptacle floor is flush with the thallus surface to 19 cells below the surrounding thallus surface. The roof is formed from filaments interspersed among the sporangia and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 39, Fig. 12; Pl. 41, Figs 18 & 19). This ring of enlarged cells is substantially smaller than those commonly found in other species of <u>Hydrolithon</u>. While the ring of enlarged cells is typically 2/3 the length of the conceptacle pore in most species of

Hydrolithon, it is generally only 1/4-1/3 the length of the conceptacle pore in these representative specimens. Above the enlarged cells, the tetrasporangial pore canal is often lined by narrow filaments that may tilt slightly into the pore canal and create the appearance of papillae (Pl. 39, Fig. 12; Pl. 41, Fig. 18). There is a small central columella present (giving the conceptacle chamber its bean-shape) (Pl. 41, Fig. 16), and the zonately divided tetrasporangia are located peripheral to it. Sporangia measure 12-72 µm long X 9-57 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 39, Fig. 11; Pl. 41, Fig. 16), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Key features

Hydrolithon craspedium is characterised by the following **combination** of characters: 1) thallus massive, mountain-like, with broad, thick vertical columns when mature; 2) thallus monomerous; 3) medullary filaments plumose in crustose part of thallus; 4) tetrasporangial conceptacles that are flush with the thallus surface to slightly raised above it; 5) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 6) within fields, trichocytes are not separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of enlarged, domed cells; 8) these enlarged cells are smaller than in other Hydrolithon taxa and typically only 1/4 to 1/3 the length of the conceptacle pore; 9) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 10) above the enlarged cells, the tetrasporangial pore canal is lined by narrow filaments that may tilt slightly into the pore canal and create the appearance of papillae; 11) the tetrasporangial conceptacle roof is commonly 5-9 cells thick; 12) the sporangial conceptacle floor is commonly 0-19 cells below the surrounding thallus surface.

Remarks

Hydrolithon craspedium is a very visible feature in shallow subtidal areas and windward reef spurs and buttresses of many tropical Indo-Pacific reefs (Littler & Littler 2003). Its characteristic massive, mountain-like structure with broad, thick vertical columns makes it stand out against the rest of the reef. Even early in its development, while still less than one cm in diameter, the thallus thickens up and becomes quite distinct from the closely related H. onkodes and H. gardineri (Pl. 37, Fig. 1B).

Besides it gross morphology, Hydrolithon craspedium is quite unique in its tetrasporangial roof anatomy. Unlike most Hydrolithon, the ring of enlarged cells that typically lines the pore canal in tetrasporangial conceptacles is rarely visible. This is so because these cells are substantially smaller than in most Hydrolithon and when visible, are quite often less than 1/2 to 1/3 the length of the conceptacle pore canal. In most Hydrolithon taxa, these enlarged pore canal cells are roughly 2/3 to 3/4 the length of the conceptacle pore canal. Nonetheless, Hydrolithon craspedium conforms to the features that are considered diagnostic of Hydrolithon (sensu stricto Penrose & Woelkerling 1992).

Basionym

Lithophyllum dentatum f. *sandvicensis* Foslie 1901a: 11

Pl. 42-45, Figs 1-23.

Current Placement/Name

Status and disposition uncertain.

Holotype

TRH. Hawaiian Islands; Farlow no. XXX. Previous references to typification were by Adey & Lebednik 1967: 48 (as *Lithophyllum sandvicense*) and Adey 1970: 11 (as *Porolithon* sanvicense). Foslie (1909: 45) raised Lithophyllum dentatum f. sandvicensis to the rank of species, as *Lithophyllum sandvicense*.

Synonyms

Homotypic synonyms:

Lithophyllum sandvicense Foslie 1909: 45 (see also Adey & Lebednik 1967).

Porolithon sandvicense (Foslie) Foslie 1909: 57 (see also Adey 1970: 10).

Etymology

"*dentatum*", *dentatus* = toothed (Stearn 1973); "*sandvicensis*", presumably after the South Sandwich Islands approximately 1000 km east of the Falkland Islands.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype material housed at TRH. The type is comprised of an upright, three dimensional, honey-combed (lobed) structure, measuring roughly 60 mm in height X 65 mm in diameter along its longest axis (see Printz 1929; Pl. 70, Fig. 6). The fertile fragment sent on lone appears to be from a single lobe. Grazing scars are a very obvious feature of the surfaces of the fragment. The type fragments appear adherent, the thallus measuring up to at least 225 µm thick. The thallus is generally smooth (Pl. 43, Fig. 7) and has adherent margins that are entire to lobed, but lacking orbital ridges (Pl. 44, Fig. 12). The cell surface (SEM) is of the Leptophytum-type (Pl. 42, Fig. 1). The surface is granular due to the presence of numerous tightly packed, pustulate trichocyte fields (Pl. 42, Fig. 2).

The thallus is monomerous, and dorsiventrally organised (Pl. 44, Figs 12 & 17). The medullary filaments comprise no more than 31% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 44, Figs 12, 16 & 17), with cells that are square to rectangular and measure 6-26 µm long X 4-15 µm in diameter. Cell fusions are abundant (Pl. 44, Figs 16 & 17). Secondary pit connections have not been seen.

The cortical filaments make up the bulk of the thallus thickness (up to 71%) (Pl. 44, Fig. 12) in crustose areas. Cells of cortical filaments are square to rectangular and measure 4-19 µm long X 5-13 µm in diameter. Cell fusions are abundant (Pl. 42, Fig. 5; Pl. 44, Fig. 14). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 42, Fig. 3; Pl. 44, Fig. 15). Subepithallial initials are generally square (Pl. 42, Fig. 5; Pl. 44, Fig. 14), and measure 6-11 µm long X 5-10 µm in diameter. Epithallial cells (Pl. 42, Fig. 5; Pl. 44, Fig. 14) are squat to elliptical and measure 3-6 µm long X 5-11 µm in diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 5 when shedding). Fields of squarish to rectangular trichocytes (Pl. 42, Fig. 3; Pl. 44, Fig. 13) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 14-31 µm long X 9-25 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 42, Fig. 3; Pl. 44, Fig. 15). Wedge-shaped individuals of another species of coralline have been observed in the thallus of Lithophyllum dentatum f. sandvicensis Foslie (Pl. 45, Fig. 18).

Reproduction

The type fragment lacked gametangial material.

Tetrasporangial conceptacles are more-or-less flush with the thallus surface to only slightly raised above it, measuring 250-400 µm in external diameter (Pl. 43, Figs 7-9; Pl. 45, Figs 19-21). Their chambers are elliptical to bean-shaped (Pl. 43, Figs 9 & 10; Pl. 45, Figs 19-21), and measure 135-225 µm in diameter X 70-100 µm high, with the roof 22-37 µm (4-12 cells; incl. epithallial cell) thick (Pl. 45, Fig. 22). The conceptacle floor is located up to 18 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 43, Fig. 11; Pl. 45, Fig. 22). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. There is a small central columella present (giving the conceptacle chamber its bean-shape) (Pl. 45, Fig. 20), and the zonately divided tetrasporangia are located peripheral to it. Sporangia measure 37-78 µm long X 12-31 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 45, Fig. 21), and often contain apparently viable sporangia; infilled conceptacles (Pl. 45, Fig. 23) have been observed although this is not common.

Distribution

Hawaiian Islands (Foslie 1901a).

Key features

Lithophyllum sandvicense is characterised by the following **combination** of characters: 1) thallus thin, adherent, lacking conventional protuberances, but bearing lobed branches that form a honey-combed structure; 2) thallus monomerous; 3) medullary filaments plumose; 4) tetrasporangial conceptacles that are only slightly raised or flush with the thallus surface; 5) Plants commonly with up to 5 layers of epithallial cells; 6) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 7) within fields, trichocytes are *not* separated by the cells of normal cortical filaments; 8) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 9) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and *not* peripheral to them; 10) the tetrasporangial pore canal *not* usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 11) the tetrasporangial conceptacle roof is commonly 4-12 cells thick; 12) the sporangial conceptacle floor is commonly up to 18 cells below the surrounding thallus surface.

Remarks

Lithophyllum sandvicense has not previously been studied in a modern context. Despite the fact that very little material was available for observation, the review of this species has led me to conclude that *Lithophyllum sandvicense*, like *L. antillarum*, is the honey-combed form of Hydrolithon onkodes which is commonly found in the South Pacific. In their recent book, Littler & Littler (2003) documents this very same honey-combed structure in Hydrolithon onkodes (as Porolithon onkodes). The grazing activity of the chiton, Cryptoplax larvaeformis that lives at the bases of the lobes, is apparently responsible for the three-dimensional honey-combed structure in the South Pacific Hydrolithon onkodes (Littler & Littler 2003).

Furthermore, a number of wedge-shaped individuals of another species of coralline have been observed to occur endophytically in the thallus of Lithophyllum dentatum f. sandvicensis Foslie (Pl. 45, Fig. 18). These wedge-shaped individuals appear to be Lithophyllum cuneatum Keats that are characteristically found to occur semi-endophytically on individuals of Hydrolithon onkodes (Keats 1995). Keats (1995) had found this wedge-shaped species to occur very commonly on individuals of Hydrolithon onkodes and only occasionally on species of Neogoniolithon. Whether this wedge-shaped coralline endophytic on Lithophyllum dentatum f. sandvicensis is indeed Lithophyllum cuneatum, could not be ascertained as there was insufficient material for a detailed analysis.

Not withstanding the gross morphology though and the potential semi-host-specific endophyte described above, this species matches perfectly the description of Hydrolithon onkodes and I therefore propose that Lithophyllum sandvicense, like L. antillarum, is conspecific with Hydrolithon onkodes. Lithophyllum sandvicense is thus also a heterotypic synonym for Hydrolithon onkodes.

Basionym

Lithophyllum gardineri Foslie 1907a: 30-31 ("forma *typica*") (see also Foslie 1907c: 106-107, 1907d: 190-191; Gardiner 1907: Fig 30; Foslie 1909: 44-45; Printz 1929: 34; Adey & Lebednik 1967: 48; Woelkerling 1993: 102-103)

Pl. 46-50, Figs 1-24.

Current Placement/Name

Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine 1993: 451 (forma gardineri) (see also Verheij 1993: 46-47, 1994: 106-107).

Pl. 51-55, Figs 1-19.

Lectotype

TRH. Coetivy Reef, Seychelles; unnumbered. Previous references to typification were by Adey & lebednik 1967: 48 (as *Lithophyllum*), Adey 1970: 10 (as *Porolithon*) and Adey et al. 1982: 10 (as *Porolithon*).

BM also contains lectotype fragments. The two BM fragments were analysed during this study.

Synonyms

Homotypic synonyms:

Porolithon gardineri (Foslie) Foslie 1909: 57 (see also De Toni 1924: 691; Taylor: 1950: 130; Adey 1970: 10; Hackett 1977: 21; Adey et al. 1982: 10; Kalugina-Gutnik et al. 1992: 17; Woelkerling 1993: 102-103; Verheij 1993: 46, 1994: 106).

Lithophyllum gardineri Foslie forma obpyramidatum Foslie 1907a: 30-31 ("obpyramidata") (see also Foslie 1907c: 106-107, 1907d: 190-191; Printz 1929: 34; Woelkerling 1993: 103, 160; Verheij 1993: 46, 1994: 106; Woelkerling & Lamy 1998: 313).

Spongites gardineri (as *Spongines gadineri*) Titlyanova et al. 1992: 43.

Heterotypic synonyms:

Lithophyllum coarctatum Foslie 1907a: 31-32 (see also Printz 1929: 32; Adey & Lebednik 1967: 48; Verheij 1993: 46, 1994: 106; Woelkerling 1993: 52-53).

Porolithon coarctatum (Foslie) Foslie 1909: 57 (see also De Toni 1924: 692; Adey 1970: 10; Verheij 1993: 46, 1994: 106).

Etymology

"*gardineri*" after Stanley Gardiner who collected the type material

Description of Type

Habit and Vegetative Structure

The following description is based on the type material housed at BM (Pl. 46, Fig. 1). The BM type consists of two similar sized fragments. The one fragments is roughly 45 mm high X 40 mm in diameter bearing distinctly terete, somewhat loosely dichotomously branched, unfused protuberances measuring 28 mm in length X 13 mm in diameter. The other fragment is roughly 30 mm high X 50 mm is diameter and is generally smooth to only slightly lumpy bearing very shallow terete protuberances. This latter fragment appears to be a crustose portion of the larger fragment.

The thallus in the crustose areas is adherent, measuring up to 725 µm thick, is generally flat and smooth. The margins are free and entire to lobed, but lack orbital ridges (Pl. 48, Figs 9 & 10). The cell surface (SEM) is both of the *Phymatolithon*- and

Leptophytum-types (Pl. 46, Fig. 2). The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate trichocyte fields (Pl. 46, Fig. 3).

The thallus is monomerous, and dorsiventrally organised (Pl. 47, Figs 4 & 7; Pl. 48, Figs 9 & 10; Pl. 49, Figs 15 & 20). In crustose areas, the medullary filaments comprise up to 38% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 47, Figs 4, 7 & 8; Pl. 48, Figs 9 & 10; Pl. 49, Figs 20 & 21) with cells that are square to rectangular and measure 4-22 µm long X 6-20 µm in diameter. Cell fusions are abundant. Secondary pit connections have not been seen. Downward curving filaments are present, and are terminated by an epithallial cell (Pl. 47, Fig. 7). The thallus in protuberances is coaxial (Pl. 49, Fig. 19).

The cortical filaments comprise up to 76% of thallus thickness in crustose parts and are composed of cells that are square to elongate, and measure 6-16 µm long X 4-11 µm in diameter (Pl. 47, Fig. 4; Pl. 49, Fig. 15). Cell fusions are abundant (Pl. 47, Fig. 6). Secondary pit connections have not been seen. Buried trichocyte fields occur frequently in the cortex (Pl. 49, Fig. 17). Subepithallial initials are square to rectangular (Pl. 47, Fig. 6; Pl. 49, Fig. 18), and measure 6-12 µm long X 5-10 µm in diameter. Epithallial cells (Pl. 47, Fig. 6; Pl. 49, Fig. 18) are squat to elliptical and measure 3-5 µm long X 5-9 µm in diameter, and occur in 1-3 (mostly 2-3 but up to 4 when shedding) cell layers. Fields of squarish to elongate trichocytes (Pl. 47, Fig. 5; Pl. 49, Fig. 16) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes taper slightly at their dorsal ends and measure 14-29 µm long X 7-16 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 49, Fig. 17).

Protuberances are composed of a thick central core of medullary filaments with vertically oriented cells arranged in a coaxial manner (Pl. 49, Fig. 19). From this central core arise the cortical filaments composed of cells that are oriented perpendicularly to the long axis of the protuberance. The protuberances branch dichotomously and are predominantly unfused.

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are slightly raised above the rest of the thallus surface measuring 300-675 µm in external diameter (Pl. 48, Figs 11 & 13; Pl. 50, Figs 22 & 23). Their chambers are elliptical (Pl. 48, Figs 12 & 13; Pl. 50, Figs 22 & 23), and measure 160-290 µm in diameter X 75-120 µm high, with the roof 31-41 µm (4-7 [mostly 5-6] cells; incl. epithallial cell) thick (Pl. 48, Fig. 14; Pl. 50, Fig. 23). The conceptacle floor is located 12-17 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 48, Fig. 14; Pl. 50, Fig. 24). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. A central columella has not been observed for this specimen. Zonately divided tetrasporangia, located peripherally in the tetrasporangial conceptacles, have however, been observed. Sporangia measure 31-81 µm long X 15-41 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 48, Fig. 12; Pl. 50, Fig. 22), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Description of representative specimens

Representative specimens examined

Fiji: Herald Passage, Great Astrolabe Reef (*D Keats*, 10.vi.1994, UWC: 94/1079), Dravuni, Great Astrolabe Reef (*D Keats*, 8.ix.1994, UWC: 94/1178), Alacrity Rocks, Great Astrolabe Reef (*D Keats*, 9.ix.1994, UWC: 94/1189).

Habitat and Phenology

Hydrolithon gardineri is relatively common, but nowhere very abundant, in the shallower areas of coral reefs (<15 m) on both windward and leeward reefs in Fiji (Keats pers. comm.). Massively abundant on the algal ridges of Rangiroa Atoll in French Polynesia (Keats pers. comm.).

Distribution

Aldabra Islands (Silva et al. 1996), Caroline Islands (Abbot 1961), Chagos Archipelago (Silva et al. 1996), Cocos (Keeling) Islands (Silva et al. 1996), Fiji (Littler & Littler 2003; This study), French Polynesia (Payri et al. 2000), Hawaiian Islands (Littler 1971; Littler & Doty 1975; Adey et al. 1982), Indonesia (SW Sulawesi) (Coppejans & Prud'homme van Reine 1992, Verheij 1993, 1994), Maldives (Silva et al. 1996), Marshall Islands (Taylor 1950; Lee 1967; Adey et al. 1982), Samoa (Lee 1967), Seychelles (Foslie 1907a; Verheij 1993, 1994; Silva et al. 1996; Titlyanova et al. 1992).

Habit and Vegetative Structure

Plants are generally adherent on dead coral skeletons and other hard substrata, measuring up to at least 30 mm in diameter. Thalli are centrally adherent, with a thin free margin in older plants. Thalli are dominated by narrow, terete to somewhat scrolled, dichotomously branched and generally unfused protuberances that measure 2-24 mm long X

1-4 mm in diameter (sometimes up to 10 mm when two or more protuberances are fused) (Pl. 51, Fig. 1). Protuberances characteristically taper toward their distal ends and are bluntly tipped. Crustose areas are moderately thick and measure 300-900 µm. The margins are free, entire to slightly lobed, and lacks orbital ridges. According to Keats (pers. comm.) the free margin and incipient protuberances makes the young plant look characteristically like a World War 1 German army hat. The surface is usually smooth, and the colour pale greyish-pink to yellow-pink in well-lit situations. The cell surface (SEM) is both of the Phymatolithon- and Leptophytum-types. The surface texture is granular due to the presence of numerous tightly packed, pustulate trichocyte fields that are easily visible with a hand lens.

Thalli are monomerous, and dorsiventrally organised. In crustose areas, the medullary filaments comprise no more than 55% of the thallus thickness and consist of an occasionally coaxial, but predominantly plumose (non-coaxial) core (Pl. 52, Figs 2 & 5). Cells of medullary filaments are square to rectangular and measure 4-31 µm long X 6-20 µm in diameter. Cell fusions are abundant (Pl. 52, Fig. 5). Secondary pit connections have not been seen. Downward curving filaments are present, and are terminated by an epithallial cell (Pl. 52, Fig. 6).

The cortex is relatively thick (up to 75% of thallus) in crustose parts and cortical filaments are composed of cells that are square to elongate, and measure 6-15 µm long X 4-11 µm in diameter (Pl. 52, Fig. 2). Cell fusions are abundant (Pl. 52, Fig. 3). Secondary pit connections have not been seen. Buried trichocyte fields occur frequently in the cortex (Pl. 53, Fig. 7). Subepithallial initials are square to rectangular (Pl. 52, Fig. 3), and measure 5-12 µm long X 5-10 µm in diameter. Epithallial cells (Pl. 52, Fig. 3) are squat to elliptical and measure 3-6 µm long X 5-10 µm in diameter, and occur in 1-3 (mostly 2-3 but up to 4 when shedding) cell layers. Fields of rectangular to elongate trichocytes (Pl. 52, Fig. 4) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes taper slightly at their dorsal ends and measure 15-32 µm long X 9-16 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields.

Protuberances are composed of a thick central core of medullary filaments with vertically oriented cells arranged in a coaxial manner. From this central core arise the cortical filaments composed of cells that are oriented perpendicularly to the long axis of the protuberance. The protuberances branch dichotomously and are predominantly unfused (Pl. 51, Fig. 1).

Reproduction

Gametangial plants are monoecious (Pl. 54, Fig. 13). Spermatangial conceptacles are smaller than sporangial conceptacles, and measure 157-187 µm in external diameter. Spermatangial conceptacles are more-or-less flush with the surrounding thallus surface (Pl. 54, Figs 13 & 14). They have elliptical chambers that measure 67-110 µm in diameter X 22-37 µm high, with the roof 45-56 µm (3-6 cells) thick. Simple spermatangial systems are borne only on the floor of the low-elliptical chamber (Pl. 54, Figs 14 & 15). Spermatangial conceptacles containing apparently viable spermatangia are often seen buried in the thallus.

Carpogonial conceptacles are also small but larger than Spermatangial conceptacles and measure c. 300 µm in external diameter (Pl. 55, Fig. 16). Carpogonial conceptacles are more-or-less flush to only slightly raised above the surrounding thallus surface (Pl. 55, Fig. 16). They have elliptical chambers that measure 87-145 µm in diameter X 35-50 µm high, with the roof 42-62 µm thick. Three-celled carpogonial branches occur across the chamber floor (Pl. 55, Fig. 17). Carpogonial conceptacles containing apparently viable carpogonia are often seen buried in the thallus. Carposporangia, developing in carpogonial conceptacles after presumed karyogamy, develop only from peripheral carpogonial branches.

Carposporangial conceptacles are large, flush to slightly raised above the surrounding thallus surface, and measure 350-550 µm in external diameter (Pl. 54, Fig. 13; Pl. 55, Fig. 18). Carposporangial conceptacles have elliptical to bean-shaped chambers that measure 125-187 µm in diameter X 34-56 µm high, with the roof 31-56 µm thick. The central fusion cell is continuous and more-or-less discoid (Pl. 55, Fig. 19), and the gonimoblast filaments are borne peripherally. Gonimoblast filaments are 8-10 cells long including a terminal carpospore that measures 27-37 µm in length X 21-30 µm in diameter. Mature carpospores enlarge until they almost fill the conceptacle chamber (Pl. 54, Fig. 13).

Tetrasporangial conceptacles are slightly raised above the rest of the thallus surface, measuring 275-600 µm in external diameter (Pl. 53, Fig. 8). Their chambers are elliptical (Pl. 53, Figs 7-10), and measure 160-225 µm in diameter X 65-115 µm high, with the roof 31-45 µm (4-8 [mostly 5-6] cells; incl. epithallial cell) thick. The conceptacle floor is located 9-17 cells below the surrounding thallus surface. The roof is formed from filaments interspersed among the sporangia and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 53, Fig. 12). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. A small central columella is present in young conceptacles (Pl. 53, Figs 10 & 11), but as the sporangia expand they crush the columella (Pl. 53, Fig. 9). Zonately divided tetrasporangia are located peripherally in the tetrasporangial conceptacles. Sporangia measure 40-73 µm long X 17-41 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 53, Figs 7 & 9), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Key features

Hydrolithon gardineri is characterised by the following **combination** of characters: 1) thallus moderately thick, adherent, producing narrow terete, loosely dichotomously branched, predominantly unfused protuberances; 2) thallus monomerous; 3) medullary filaments predominantly plumose in crustose part of thallus and are only occasionally coaxial; 4) tetrasporangial conceptacles that are only slightly raised above the thallus surface; 5) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 6) within fields, trichocytes are not separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 9) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is commonly 5-6 cells thick; 11) the sporangial conceptacle floor is commonly 9-17 cells below the surrounding thallus surface.

Remarks

Hydrolithon gardineri is a fairly well-known species throughout the tropical and sub-tropical Indo-Pacific region (Littler & Littler 2003). Like H. onkodes, its taxonomy has been fairly well documented (Verheij 1993, 1994; Littler & Littler 2003), but unlike H. onkodes, it was not until a year later that Lithophyllum gardineri was formally transferred to the genus Hydrolithon (see Verheij 1993, 1994). Since then, a host of different taxa have been synonymised with Hydrolithon gardineri (see above and Silva et al. 1996) and it appears that within the genus Hydrolithon, the gross morphology of H. gardineri is what characterises this taxon. With this in mind, it seems likely that a greater number of taxa will prove to be synonymous with Hydrolithon gardineri (see latter part of this paper).

Basionym

Lithophyllum oligocarpum Foslie 1906a: 22

Pl. 56-60, Figs 1-22; Pl. 61-63, Figs 1-12.

Current Placement/Name

Hydrolithon onkodes (Heydrich) Penrose & Woelkerling 1992: 83 (determined by Afonso-Carrillo & Sansón 1999: 167).

Pl. 90-95, Figs 1-23.

Holotype

TRH. Puerto Orotava, Tenerife, Canary Islands; unnumbered. Previous references to typification were by Adey & Lebednik 1967: 47 (as Lithophyllum), Adey 1970: 10 (as Porolithon), Woelkerling 1993: 169 and Woelkerling & Lamy 1998: 320. Holotype fragments have been reported for PC but these are apparently missing (Woelkerling and Lamy 1998).

Synonyms

Homotypic synonyms:

Porolithon oligocarpum (Foslie) Foslie 1909: 57 (see also Adey 1970: 10; Afonso-Carrillo 1982: 256; John et al. 1994: 63; Lawson et al. 1995: 112).

Porolithon onkodes (Heydrich) Foslie var. oligocarpa (Foslie) Lemoine 1929.

Etymology

"oligocarpum", oligo = few; carpus = fruit, fruited (Stearn 1973). Foslie (1906a) did not explain the origin of the epithet, but it presumably makes reference to a relative scarcity of reproductive material.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype material housed at TRH (Pl. 56, Fig. 1). The holotype itself is smooth and featureless, lacking any protuberances (Printz 1929: Pl. 67, Fig. 12). Any marked irregularities in surface structures appears to have been formed by the crust conforming to the rocky substratum over which it was growing at the time. A small fragment from the holotype was sent on loan for the purposes of this study. The thallus is adherent, measuring up to 1875 µm thick, with a margin that is free, entire to lobed, but lacking an orbital ridge (Pl. 57, Figs 6 & 8; Pl. 59, Fig. 14). The cell surface (SEM) is of the *Leptophytum*-type (Pl. 57, Fig. 2). The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate trichocyte fields (Pl. 57, Fig. 3).

The thallus is monomerous and dorsiventrally organised (Pl. 57, Figs 4, 6, 8 & 9; Pl. 59, Figs 14 & 16). The medullary filaments comprise 15-24% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 57, Figs 4, 6, 8 & 9; Pl. 59, Figs 14 & 16), with cells that are square to rectangular and measure 5-50 µm long X 4-19 µm in diameter. Cell fusions are abundant. Secondary pit connections have not been seen.

The cortical filaments comprise up to 85% of the thallus thickness (Pl. 57, Figs 4 & 6; Pl. 59, Fig. 14) with cells that are square to rectangular and measure 5-2 µm long X 6-12 µm in diameter. Cell fusions are abundant (Pl. 57, Fig. 7). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 57, Fig. 5). Subepithallial initials are square to rectangular (Pl. 59, Fig. 15), and measure 7-19 µm long X 7-12 µm in diameter. Epithallial cells (Pl. 59, Fig. 15) are squat to elliptical and measure 3-7 µm long X 7-13 µm in diameter, and occur in 1-13 cell layers (mostly 2-3 but up to 4 when shedding). Fields of squarish to elongate trichocytes commonly occur at the thallus surface in tightly packed, pustulate horizontal fields (Pl. 57, Fig. 3). These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are <u>not</u> separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 15-43 µm long X 9-21 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 57, Fig. 5).

Reproduction

Type fragment lacked gametangial material.

Sporangial conceptacles are slightly sunken to flush to only slightly raised above the rest of the thallus and measure 250-450 µm in external diameter (Pl. 58, Figs 10-13; Pl. 60, Fig. 17). Their chambers (Pl. 58, Figs 12 & 13; Pl. 60, Figs 17 & 18) are elliptical to bean-shaped, and measure 200-295 µm in diameter X 60-110 µm high, with the roof 43-62 µm (5-12 [mostly 5-9] cells; incl. epithallial cell) thick. The conceptacle floor is located 4-14 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments peripheral to the conceptacle chamber and not from filaments interspersed among the sporangia (Pl. 60, Figs 21 & 22). These cells protrude into the pore canal as papillae, and are oriented more-or-less parallel to the roof surface (Pl. 60, Figs 20 & 22). The pore-canal is typically funnel-shaped measuring c. 25 µm at its apex to c. 62 µm at its base. There is a central columella present (giving the conceptacle chamber its bean-shape) (Pl. 60, Fig. 17), and the zonately divided tetrasporangia are located peripheral to it. Tetrasporangia measure 37-74 µm long X 12-43 µm in diameter.

Bisporangia were also found (Pl. 60, Fig. 19), measuring 31-62 μm long X 25-29 μm in diameter. Sporangial conceptacles often become buried in the thallus (Pl. 58, Fig. 12; Pl. 60, Fig. 18), and often contain apparently viable sporangia. Both partly infilled and open conceptacles have been observed buried in the thallus (Pl. 58, Fig. 13; Pl. 60, Fig. 18).

Description of representative specimens

Representative specimens examined

Canary Islands: Puerto de la Cruz ("Puerto Orotava"), Tenerife (J Afonso-Carrillo, 12.xi.1999, UWC: 00-CI-01).

Habitat and Phenology

Little is known of the habitat of the type material ascribed to Lithophyllum oligocarpum since this taxon has never been described in a modern context. Earlier reports had not included habitat descriptions for this taxon. In the Canary Islands, however, Lithophyllum oligocarpum is relatively common in tide pools, in the lower eulittoral zone, and the subtidal to depths of up 10 m, mainly on exposed habitats. The formation of sporangial conceptacles and maturation of sporangia have only been recorded during July and August (summer); sexual plants have never been collected (Afonso-Carrillo pers. comm.).

Distribution

Azores (Lemoine 1966; Lawson et al. 1995), Canary Islands (Foslie 1906a; Lemoine 1966; Afonso-Carrillo 1982; Afonso-Carrillo et al. 1984; Afonso-Carrillo & Sansón 1999; This study), Cape Verde Islands (Lemoine 1966; Lawson et al. 1995), Gulf of Guinea (Lemoine 1966; Lawson et al. 1995).

Habit and Vegetative Structure

The following description is based on a representative sample sent from the type locality in the Canary Islands by Julio Afonso-Carrillo (Pls 61-63, Figs 1-12). The specimen is smooth and featureless, lacking any protuberances (Pl. 61, Fig. 1). Any marked irregularities in surface structures appears to have been formed by the crust conforming to the rocky substrate over which it was growing at the time. The thallus is adherent, measuring up to 1400 µm thick, with a margin that is also generally adherent, entire to lobed, but lacking an orbital ridge. The cell surface (SEM) is of the <u>Leptophytum</u>-type. The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate trichocyte fields.

The thallus is monomerous and dorsiventrally organised (Pl. 62, Figs 2 & 7). The medullary filaments comprise 14-39% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 62, Figs 2, 6 & 7), with cells that are square to rectangular and measure 10-33 µm long X 5-20 µm in diameter. Cell fusions are abundant (Pl. 62, Figs 6 & 7). Secondary pit connections have not been seen.

The cortical filaments comprise the bulk of the thallus thickness (up to 86%) with cells that are square to rectangular and measure 5-20 µm long X 5-12 µm in diameter. Cell fusions are abundant (Pl. 62, Fig. 4). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 62, Fig. 5). Subepithallial initials are square to rectangular (Pl. 62, Fig. 4), and measure 5-20 µm long X 6-11 µm in diameter. Epithallial cells (Pl. 62, Fig. 4) are squat to elliptical and measure 4-9 µm long X 6-10 µm in diameter, and occur in 1-2 cell layers (up to 4 when shedding). Fields of squarish to elongate trichocytes (Pl. 62, Fig. 3) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are <u>not</u> separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 16-40 µm long X 9-19 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 62, Fig. 5).

Reproduction

The representative specimen lacked gametangial material.

Tetrasporangial conceptacles are slightly sunken to flush to only slightly raised above the rest of the thallus and measure 225-400 µm in external diameter (Pl. 63, Fig. 8). Their chambers (Pl. 63, Figs 8 & 9) are elliptical to bean-shaped, and measure 200-225 µm in diameter X 70-90 µm high, with the roof 43-68 µm (6-10 cells; incl. epithallial cell) thick (Pl. 63, Fig. 11). The conceptacle floor is located 4-16 cells below the surrounding thallus surface. The roof is formed from filaments peripheral to the conceptacle chamber and not from filaments interspersed among the sporangia (Pl. 63, Figs 10 & 11). These cells protrude into the pore canal as papillae, and are oriented more-or-less parallel to the roof surface (Pl. 63, Figs 11 & 12). The pore-canal is less funnel-shaped than in the type specimen. There is a central columella present (giving the conceptacle chamber its bean-shape) (Pl. 63, Fig. 9) although this is not evident in all conceptacles, as it appears to be lost as the sporangia enlarge. Zonately divided tetrasporangia are located peripherally in the conceptacle chamber, and measure 42-87 µm long X 37-62 µm in diameter. Bisporangia have not been seen. Sporangial conceptacles often become buried in the thallus (Pl. 63, Fig. 9), and often contain apparently viable sporangia. Both partly infilled and open conceptacles have been observed buried in the thallus.

Key features

Lithophyllum oligocarpum is characterised by the following **combination** of characters: 1) thallus thick, adherent, smooth, lacking protuberances; 2) thallus monomerous; 3) medullary filaments plumose; 4) tetrasporangial conceptacles that are slightly sunken to flush to only slightly raised above the rest of the thallus surface; 5) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 6) within fields, trichocytes are <u>not</u> separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals <u>not</u> lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments peripheral to the conceptacle chamber and not from filaments interspersed among the sporangia; 9) the tetrasporangial pore canal is lined by narrow filaments that tilt into the pore canal, are orientated more-or-less parallel to the roof surface, and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is commonly 6-10 cells thick; 11) the sporangial conceptacle floor is commonly 4-16 cells below the surrounding thallus surface.

Remarks

In a study of the calcareous algae of the Canary Islands, Lemoine (1929) treated <u>Porolithon oligocarpum</u> as a variety of <u>Porolithon onkodes</u>. In a reappraisal, Penrose & Woelkerling (1992) considered <u>Hydrolithon</u> and <u>Porolithon</u> to be congeneric and <u>Porolithon</u> was considered to be a heterotypic synonym for <u>Hydrolithon</u>. Still later, Afonso-Carrillo (in Afonso-Carrillo & Sansón 1999: 167) re-examining the type of Lithophyllum oligocarpum and material from the type locality, came to the conclusion, like Lemoine (1929), that <u>Porolithon oligocarpum</u> was indeed a variety of <u>Porolithon onkodes</u> and thus a heterotypic synonym of <u>Hydrolithon onkodes</u> (Heydrich) Penrose & Woelkerling (1992).

In their reappraisal, Penrose & Woelkerling (1992) showed that Hydrolithon is separated from *Spongites* on the basis of the tetrasporangial roof development. In *Hydrolithon*, the pore canals of the tetrasporangial conceptacles are lined by a ring of conspicuous, enlarged cells that arise from filaments interspersed among the sporangial initials. These cells do not protrude into the pore canal and are oriented more-or-less perpendicularly to the roof surface. In *Spongites*, the pore canals of the tetrasporangial conceptacles lack the ring of conspicuous, enlarged cells and the roof is formed from cells that arise from the periphery. These cells protruded into the pore canal and are oriented more-or-less parallel to the roof surface. Based on Penrose & Woelkerling's (1992) findings, this research has shown (characters 7, 8 and 9 above) that *Lithophyllum oligocarpum* conforms to the sporangial conceptacle development characteristic of the genus Spongites and not *Hydrolithon*. *Lithophyllum oligocarpum* should therefore be referred to as *Spongites oligocarpus* (Foslie) Maneveldt & Keats comb. nov.

It should be noted, however, that like *S. africanum*, *L. oligocarpum* is also remarkably similar to *Pneophyllum conicum* Keats, Chamberlain & Baba (1997) (see Table 3). The genera *Spongites* and *Pneophyllum* are distinguished primarily on the development of the sporangial conceptacle roof. In *Spongites*, the sporangial conceptacle roof is formed from peripheral roof filaments only, while in *Pneophyllum*, the conceptacle roof is formed from both peripheral roof filaments as well as filaments interspersed among the sporangia. In *Pneophyllum*, however, the conceptacle roof development is only evident in developing young (immature) sporangial conceptacles; it is seldom evident in the mature conceptacles, and therefore appears like that of *Spongites*. As only mature sporangial conceptacles were seen in *L. oligocarpum* during this study and reported on by Afonso-Carrillo & Sansón (1999), the *Pneophyllum*-type sporangial conceptacle roof development cannot be ruled out as a possibility. While *L. oligocarpum* and *P. conicum* (see Keats et al. 1997) appear superficially similar, they differ with respect to their number of epithallial cell layers, the condition of their medullary filaments (coaxial vs. plumose), and the absence and presence respectively of a single elongated cell in their sporangial conceptacle walls (Table 3). These differences are consistent and until such time as plants bearing young, developing (immature) sporangial conceptacles are examined to fully evaluate the taxonomic placement of L. oligocarpum, this species conforms to the generic description of Spongites.

Like S. africanum, this species also displays a very interesting feature. It was reported that Porolithon (Adey et al. 1982: 6) was characterised by among other features, the existence of horizontal fields of pustulate ("pustulous") trichocytes that are not separated by normal cortical cells. Lithophyllum oligocarpum possess this same trichocyte arrangement. This is not surprising as Penrose & Woelkerling (1988) had reported a number of southern Australian taxa, belonging to the genus Spongites, possessing trichocyte fields in horizontal fields and so too have Keats et al. (1997) shown them to occur in P. conicum. A number of earlier reports (see Lemoine 1917; Cabioch 1972) had already highlighted the variability in trichocyte arrangements in taxa ascribed to the defunct genus Porolithon. These results support the view of Penrose & Woelkerling (1988) that trichocyte arrangement is not a diagnostic character at the level of genus but may still, however, be useful for distinguishing species.

Basionym

Lithophyllum onkodes f. pachydermum Foslie 1904: 5

Pl. 64-68, Figs 1-27; Pl. 69-71, Figs 1-9.

Current Placement/Name

Status and disposition uncertain.

Lectotype

TRH. St. Croix (?), US Virgin Islands (West Indies); Ørsted no 548. Previous references to typification were by Adey & Lebednik 1967: 47 (as Lithophyllum pachydermum) and Adey 1970: 11 (as Porolithon pachydermum). Isolectotype material also exists in BM (as Lithophyllum pachydermum).

Synonyms

Homotypic synonyms:

Lithophyllum pachydermum (Foslie) Adey et Lebednik 1967: 47.

Porolithon pachydermum (Foslie) Foslie 1909: 57 (see also Adey 1970: 11).

Etymology

"pachydermum", pachy = thick, stout + derma = skin (Stearn 1973). Foslie (1904) did not explain the origin of the epithet. It could be making reference to an elephant-skin-like surface (as in pachyderm) or simply just be referring to the multiple layers of epithallial cells.

Description of Type

Habit and Vegetative Structure

The following description is based on the isolectotype material housed at BM (Pl. 64, Fig. 1). The type is adherent, measuring up to at least 3025 µm thick. Thalli are flat and smooth, lacking protuberances (Pl. 64, Fig. 1), and have free to adherent margins that are entire to lobed, but lack orbital ridges (Pl. 65, Fig. 6; Pl 67, Figs 15 & 17). The cell surface (SEM) is both of the Phymatolithon- and Leptophytum-type (Pl. 65, Fig. 2). The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate trichocyte fields (Pl. 65, Fig. 3).

The thallus is monomerous and dorsiventrally organised (Pl. 65, Figs 6, 8 & 9; Pl. 67, Figs 15, 17 & 21). The medullary filaments comprise 9-86% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 65, Figs 6, 8 & 9; Pl. 65, Figs 17 & 21), with cells that are square to rectangular and measure 6.2-31 µm long X 3.7-14.9 µm in diameter. Where the medullary filaments comprise a very small portion of the thallus thickness, it often gives the false impression of being dimerous when sectioned parallel to the growing margin (Pl. 67, Figs 16 & 22). Cell fusions are abundant (Pl. 65, Fig. 9; Pl. 67, Fig. 21). Secondary pit connections have not been seen.

The cortical filaments comprise 14-91% of the thallus thickness (Pl. 65, Figs 6 & 8; Pl. 65, Fig. 15), with cells that are square to rectangular and measure 6-17 µm long X 4-12 µm in diameter. Cell fusions are abundant. Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 65, Figs 4 & 7; Pl. 65, Fig. 20). Subepithallial initials are squarish (Pl. 67, Fig. 19), and measure 5-12 µm long X 5-12 µm in diameter. Epithallial cells (Pl. 67, Fig. 19) are squat to elliptical and measure 3-6 µm long X 5-12 µm in diameter, and occur in 1-3 cell layers (mostly 2-3). Fields of squarish to rectangular trichocytes (Pl. 65, Fig. 5; Pl. 67, Fig. 18) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 15-38 µm long X 7-22 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 65, Figs 4 & 7; Pl. 65, Fig. 20).

Reproduction

The type fragment lacked gametangial material.

Tetrasporangial conceptacles are more-or-less flush to only slightly raised above the rest of the thallus, measuring 450-675 µm in external diameter (Pl. 66, Figs 10-12; Pl. 68, Fig. 23). Their chambers (Pl. 66, Fig. 14; Pl. 68, Figs 23-25) are elliptical to bean-shaped, and measure 145-290 µm in diameter X 50-170 µm high, with the roof 31-51 µm (6-11 cells; incl. epithallial cell) thick. The conceptacle floor is located 13-19 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 68, Fig. 27). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. There is a small central columella present (giving the conceptacle chamber its bean-shape) (Pl. 68, Figs 23, 25 & 26), and the zonately divided tetrasporangia are located peripheral to it. Tetrasporangia measure 31-87 µm long X 9-47 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 66, Figs 13 & 14; Pl 68, Fig. 24), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Description of representative specimens

Representative specimens examined

Bermuda: D Keats, 13.ii.2000, UWC: 2000/106B.

Habitat and Phenology

Porolithon pachydermum is one of the most common corallines in the intertidal and shallower areas (<10m) of coral reefs of the Caribbean West Indian coastline (Adey 1978; Littler & Littler 2000). Here it is often the dominant frame builder on algal ridges experiencing very high wave energy and characteristically occurs on the most exposed platforms (Adey 1978; Keats pers. comm.). This species commonly occurs with a mixture of other species belonging to the genera Hydrolithon, Neogoniolithon, and Lithophyllum with Lithophyllum congestum being another prominent feature of mostly medium energy reefs. Porolithon pachydermum has been widely reported from the US Virgin Islands (e.g. Foslie 1909; Printz 1929; Adey & Lebednik 1967; Adey 1978; Littler & Littler 2000).

Distribution

Antilles (Lemoine 1966; Adey 1978; Littler & Littler 2000), Bahamas (Lemoine 1966; Littler & Littler 2000), Bermuda (This study), Mexico (Pacific? – see remarks) (Mendoza-González & Mateo-Cid 1985), US Virgin Islands (Foslie 1904; Lemoine 1964; Adey 1978), Western Caribbean (Berlize, Honduras, Mexico, Panama, San Andrés Island) (Adey 1978; Littler et al. 1995; Littler & Littler 2000).

Habit and Vegetative Structure

Plants are generally adherent and thick. Thalli surfaces are generally smooth and featureless but tend to become warty to lumpy when conforming to an irregular substratum (Pl. 69, Fig. 1). The alga often forms thick crusts as it frequently overgrows itself. Thalli generally lack protuberances, and have free to mostly adherent margins that are entire to lobed, but lack orbital ridges. The thallus surface appears to be frequently grazed. The cell surface (SEM) is both of the Phymatolithon- and Leptophytum-type. Thalli are pale greyish pink in well-lit situations. The surface texture is matt, and granular due to the presence of numerous tightly packed, pustulate trichocyte fields that are easily visible with a hand lens.

On some Caribbean reefs, P. pachydermum has been reported to have a castle-like, three-dimensional honey-combed structure. At the bases of the coralline are found the tubular burrows of the chiton, Choneplax lata Guilding (Littler et al. 1995; Littler & Littler 2000). This form is evidently caused by growth in response to the grazing activities of this chiton (Littler et al. 1995).

The thallus is monomerous and dorsiventrally organised (Pl. 70, Fig. 5). The medullary filaments comprise 9-86% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 68, Fig. 5), with cells that are square to rectangular and measure 6-31 µm long X 4-25 µm in diameter. Where the medullary filaments comprise a very small portion of the thallus thickness, it often gives the false impression of being dimerous when sectioned parallel to the growing margin (Pl. 70, Figs 2 & 6). The medullary filaments in younger thalli typically comprise a larger percentage of the thallus while this seems to decrease as the thallus thickens. Cell fusions are abundant (Pl. 70, Fig. 5). Secondary pit connections have not been seen.

The cortical filaments comprise 14-91% of the thallus thickness (Pl. 70, Fig. 2), with cells that are square to rectangular and measure 5-17 µm long X 4-12 µm in diameter. Cell fusions are abundant (Pl. 70. Fig. 4). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 70. Fig. 3). Subepithallial initials are square to rectangular (Pl. 70, Fig. 4), and measure 5-19 µm long X 5-12 µm in diameter. Epithallial cells (Pl. 70, Fig. 4) are squat to elliptical and measure 3-7 µm long X 5-12 µm in diameter, and occur in 1-3 cell layers (mostly 2-3). Fields of squarish to elongate trichocytes (Pl. 70, Fig. 2) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 15-46 µm long X 7-27 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 70. Fig. 3).

Reproduction

Gametangial plants have not been seen.

Tetrasporangial conceptacles are more-or-less flush to only slightly raised above the rest of the thallus, measuring 250-675 µm in external diameter (Pl. 71, Figs 7 & 8). Their chambers are predominantly elliptical (but also bean-shaped) (Pl. 71, Figs 7 & 8), and measure 125-290 µm in diameter X 50-170 µm high, with the roof 31-68 µm (6-11 cells; incl. epithallial cell) thick (Pl. 71, Fig. 9). The conceptacle floor is located 9-19 cells below the surrounding thallus surface. The roof is formed from filaments interspersed among the sporangia and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 71, Fig. 9). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. There is a small central columella present (giving the conceptacle chamber its bean-shape) although this is not evident in all conceptacles, as it appears to be lost as the sporangia enlarge (Pl. 71, Fig. 9). Zonately divided tetrasporangia are, however, located mostly peripherally in the conceptacles. Tetrasporangia measure 31-87 µm long X 9-47 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus, and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Key features

Porolithon pachydermum is characterised by the following **combination** of characters: 1) thallus thick, adherent, generally lacking protuberances but may be warty to lumpy; 2) thallus monomerous; 3) medullary filaments plumose, but often gives the false impression of being dimerous; 4) tetrasporangial conceptacles that are slightly sunken to flush to only slightly raised above the thallus surface; 5) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 6) within fields, trichocytes are not separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 9) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is commonly 6-11 cells thick; 11) the sporangial conceptacle floor is commonly 9-19 cells below the surrounding thallus surface.

Remarks

Porolithon pachydermum is a well-known species throughout the Caribbean Sea and the West Indies (e.g. Foslie 1909; Printz 1929; Lemoine 1964, 1966; Adey & Lebednik 1967; Adey 1978; Littler et al. 1995; Littler & Littler 2000). Strange enough, its taxonomy has never been well documented or resolved, and like so many taxa ascribed to the defunct genus Porolithon, P. pachydermum was never formally transferred to the genus Hydrolithon (see Penrose & Woelkerling 1992).

In the proceedings of the fourth International Seaweed Symposium, Lemoine (1964) commented on the species representative of the 8 Melobesioid (as then defined) groups as defined by M.J. Feldmann (1946) in his description of the marine flora of the Atlantic

Islands. Lemoine (1964) named a Pan tropical group of four species comprising: Hydrolithon onkodes (as Porolithon) from the Atlantic and Indo-Pacific regions; Hydrolithon onkodes (as Porolithon) from the Pacific; P.oligocarpum from the East Atlantic; and P. pachydermum from the West Atlantic (see also Lemoine 1966). Lemoine's findings highlighted the close affinity of these four entities and still later, Afonso-Carrillo (in Afonso-Carrillo & Sansón 1999) came to the conclusion (although mistaken – see Porolithon oligocarpum above), like Lemoine (1929), that Porolithon oligocarpum was indeed a variety of Porolithon onkodes and thus a homotypic synonym of Hydrolithon onkodes. There seems to be the suggestion that these four entities are all synonymous and thus all conspecific with Hydrolithon onkodes.

The only record of P. pachydermum outside of Lemoine's (1964, 1966) distribution was by Mendoza-González & Mateo-Cid (1985) who cite this taxon for Pacific Mexico. However, two similar studies (Dreckmann 1991; Fragoso & Rodríguez 2002) of the Pacific Mexican non-geniculate coralline algae found no P. pachydermum, although they did find H. onkodes. In all likelihood, because of the close affinity of these taxa, Mendoza-González & Mateo-Cid (1985) may have confused H. onkodes with P. pachydermum.

Not only does this study show the affinity of Porolithon pachydermum to other Hydrolithon taxa (characters 7,8, and 9), but also this species conforms well to Hydrolithon onkodes. Although Krishnamurthy & Jayagopal (1987) made a similar suggestion, their findings were inconclusive. Adey et al. (1982) on the other hand, considered H. onkodes (as Porolithon) and P. pachydermum to be "pair species". Based on this study, it is concluded that P. pachydermum is indeed a heterotypic synonym for H. onkodes.

Basionym

Lithophyllum praetextatum Foslie 1907a: 31

Pl. 72-74, Figs 1-9.

Current Placement/Name

Status and disposition uncertain.

Holotype

TRH. Easter Island; Farlow no. 16. Previous references to typification were by Adey & Lebednik 1967: 48 (as *Lithophyllum*) and Adey 1970: 11 (as *Porolithon*). The holotype is the only collection of this species identified by Foslie.

Synonyms

Porolithon praetextatum (Foslie) Foslie 1909: 57 (see also Adey 1970: 11)

Etymology

"*praetextatum*", *praetextus* = bordered, fringed + *tum* = then, at that time, and also, but also, if so, furthermore (Stearn 1973). Foslie (1907a) did not explain the origin of the epithet. How this applies to *L. praetextatum* is unclear.

Description of Type

Habit and Vegetative Structure

The following description is based on the type material housed at TRH (Pl. 72, Fig. 1). The type comprises a single specimen measuring roughly 25 mm wide X 40 mm high, whose thallus is dominated by narrow terete, dichotomously branched, generally unfused protuberances. Protuberances taper somewhat toward their distal ends and are bluntly pointed. Individual protuberances measure up to 15 mm in length X 3 mm in diameter.

Since the type comprises only a single fragment, it was decided not to dissect it too much and therefore very little crustose areas were analysed. The thallus is adherent in the crustose areas and is generally flat and smooth. No margins were examined. The cell surface (SEM) is generally of the Leptophytum-type (Pl. 73, Fig. 2). The surface texture is matt and granular due to the presence of tightly packed, pustulate trichocyte fields (Pl. 73, Fig. 3).

The thallus is monomerous, and dorsiventrally organised. In crustose areas, the medullary filaments consist of a central plumose (non-coaxial) core (Pl. 73, Fig. 7) with cells that are square to rectangular and measure 10-25 µm long X 5-11 µm in diameter. Cell fusions are abundant (Pl. 73, Fig. 7). Secondary pit connections have not been seen.

The cortical filaments in crustose parts are composed of cells that are square to rectangular, and measure 4-15 µm long X 4-10 µm in diameter. Cell fusions are abundant (Pl. 73, Fig. 6). Secondary pit connections have not been seen. Buried trichocyte fields occur frequently in the cortex (Pl. 73, Fig. 4). Subepithallial initials are square to rectangular (Pl. 71, Fig. 6), and measure 4-11 µm long X 6-11 µm in diameter. Epithallial cells (Pl. 73, Fig. 6) are squat to elliptical and measure 3-6 µm long X 6-13 µm in diameter, and occur in 1-3 (mostly 2-3 but up to 4 when shedding) cell layers. Fields of rectangular to elongate trichocytes (Pl. 73, Fig. 5) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes taper slightly at their dorsal ends and measure 12-31 µm long X 6-19 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 73, Fig. 4).

Protuberances are composed of a thick central core of medullary filaments with vertically oriented cells arranged in a coaxial manner. From this central core arise the cortical filaments composed of cells that are oriented perpendicularly to the long axis of the protuberance. The protuberances branch dichotomously and are predominantly unfused.

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are rare and subsequently, it was decided not to dissect any of the last remaining conceptacles. Tetrasporangial conceptacles are flush to only slightly raised above the rest of the thallus surface (Pl. 74, Figs 8 & 9), measuring 300-370 µm in external diameter. Sporangia measure 37-43 µm long X 19-28 µm in diameter. No other sporangial features were obtained for this specimen.

Distribution

Chile (Easter Island) (Foslie 1907a).

Key features

Lithophyllum praetextatum is characterised by the following (limited) **combination** of characters: 1) thallus adherent, producing narrow terete, predominantly unfused protuberances; 2) thallus monomerous; 3) medullary filaments predominantly plumose in crustose part of thallus; 4) tetrasporangial conceptacles that are flush to only slightly raised above the thallus surface; 5) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 6) within fields, trichocytes are not separated by the cells of normal cortical filaments.

Remarks

Not only does the type of Lithophyllum praetextatum comprise but a single fragment, it bears very little fertile material with which to perform a critical analysis. It was decided, during the course of this analysis, not to dissect too much material for fear that the type would ultimate be denuded of all fertile material. Therefore there are too few intact features to make an informed decision as to where Lithophyllum praetextatum belongs. If it is assumed that Foslie's (1907a) reasons for placing Lithophyllum praetextatum in Porolithon were justified, we can then go on to make a more informed decision based solely on the characters featured above. It is my opinion, that Lithophyllum praetextatum is synonymous with Hydrolithon gardineri and that the former taxa be subsumed in H. gardineri Verheij & Prud'homme van Reine (1993). Since 1993, a host of taxa have been synonymised with Hydrolithon gardineri (see Lithophyllum gardineri above and Silva et al. 1996) and it appears that within the genus Hydrolithon, the gross morphology of H. gardineri is what characterises this taxon. With this in mind, it seems likely that a greater number of taxa, like Lithophyllum praetextatum, will prove to be synonymous with Hydrolithon gardineri (see previous references to Hydrolithon gardineri). I would also suggest that further study of the type material from Easter Island would still be worthwhile to confirm the above conclusion.

Basionym

Lithophyllum reinboldii Weber van Bosse & Foslie in Foslie 1901b: 5

Pl. 75-79, Figs 1-21.

Current Placement/Name

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie 1909: 55 (see Penrose and Woelkerling (1992: 83).

Pl. 80-84, Figs 1-21.

Lectotype

TRH. Moearas Reef, east coast of Borneo (East Kalimantan), Indonesia; Siboga Expedition collection 38. Type designated by Adey in Adey & Lebednik (1967: 32). Previous references to typification were by Dawson 1960a: 28 (as *Hydrolithon*), Adey & Lebednik 1967: 32 (as *Goniolithon*), Adey 1970: 11 (as *Hydrolithon*), Adey et al. 1982: 26 (as *Hydrolithon*), Penrose & Woelkerling 1988: 161, 1992: 83 (as *Hydrolithon*) and Verheij & Woelkerling 1992: 284 (as *Lithophyllum*). Isolectotype material also exists in TRH (Siboga Expedition collections 57 and 74) and L (see Woelkerling 1993).

Synonyms

Homotypic synonyms:

Goniolithion reinboldii (Weber van Bosse & Foslie in Foslie) Foslie 1905: 7 (see also Weber-van Bosse 1904: 5; De Toni 1905: 1801; Mazza 1917: 194-197; Printz 1929: 31; Hackett 1977: 18).

Porolithon reinboldii (Weber van Bosse & Foslie in Foslie) Lemoine 1911: 166.

Spongites reinboldii (Weber van Bosse & Foslie in Foslie) Penrose & Woelkerling 1988: 173 (see also Kalugina-Gutnik et al. 1992: 17; Titlyanova et al. 1992: 43 [as *Spongines reindoldii*]).

Etymology

'*reinboldii*', named after German phycologist T. Reinbold.

Description of Type

Habit and Vegetative Structure

The isolectotype material from TRH (Siboga Expedition collections 57 and 74) was examined during this study (Pl. 75, Fig. 1). Both specimens are free-living rhodoliths. The fragment marked S.E. 57 is the smaller of the two and measures roughly 50-55 mm in diameter. The larger of the two fragments (marked S.E. 74) measures roughly 70-85 mm in diameter. The specimens are both lumpy with more-or-less rounded, knobbly protuberances that measure up to 7 mm in length X 12 mm in diameter. Protuberances are dense and tightly packed. The thallus is adherent, measuring 1700- 2400 µm thick in crustose areas. No margins have been observed. The cell surface (SEM) is neither of the *Phymatolithon*- nor the *Leptophytum*-type (Pl. 76, Fig. 2), but differs from both in that the outer surface is thick and rounded, possessing a minute central pore does exist (see Chamberlain 1990).

The thallus is dimerous, consisting of a single layer of basal filaments from which arise the erect filaments that make up most of the thallus (Pl. 76, Fig. 5; Pl. 78, Figs 14-17). Cells of the basal filaments are book-shaped (Pl. 78, Figs14-17). In primary-filament view, cells of the basal filaments are more-or-less square, and measure 16-41 µm long X 12-36 µm in diameter. In filament cross sections, basal cells are rectangular to elongate, and measure 16-41 µm long X 6-12 µm in diameter.

Cells of erect filaments are strongly horizontally arranged (Pl. 78, Fig. 13) due to extensive connections by broad cell fusions. This phenomenon appears to increase with depth in the thallus. In their unfused, uninflated state, cells of the erect filaments are square to elongate and measure 7-24 µm long X 5-11 µm in diameter. When the cells of the erect filaments fuse, they are typically spherical to elongate, and measure 16-50 µm long X 12-29 µm in diameter. Secondary pit connections were not seen. Subepithallial initials are square to elongate (Pl. 76, Figs 3 & 4; Pl. 78, Fig. 12), and measure 10-21 µm long X 6-14 µm in diameter. Epithallial cells (Pl. 76, Figs 3 & 4; Pl. 78, Fig. 12) are squat to elliptical, occur singly, and measure 5-7 µm long X 7-14 µm in diameter. Trichocytes are bottle-shaped and common at the thallus surface and occur singly or paired (Pl. 76, Fig. 4; Pl. 78, Fig. 11). Trichocytes (except pairs) are separated from one another by the cells of one or generally more, normal erect filaments and trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes measure 25-50 µm long X 17-26 µm in diameter. They are often overgrown and buried within the thallus.

Reproduction

The type lacks gametangial material.

Sporangial conceptacles are slightly raised above the thallus surface, measuring 270-650 µm in external diameter (Pl. 77, Figs 7-9; Pl. 79, Figs 18 & 19). Their chambers (Pl. 77, Figs 6 & 9; Pl. 79, Figs 18 & 19) are elliptical and measure 200-270 µm in diameter X 125-175 µm high, with the roof 43-68 µm (4-5 cells; incl. epithallial cell) thick (Pl. 77, Fig. 10; Pl. 79, Figs 20 & 21). The conceptacle floor is flush with the surrounding thallus surface to 9 cells below the thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 77, Fig. 10; Pl. 79, Figs 20 & 21). The pore is slightly sunken dorsally (Pl. 77, Fig. 10; Pl. 79, Fig. 21) and the pore canal also narrows dorsally, and is lined by a single elongate cell (oriented more-or-less vertically) plus an epithallial cell that tilts slightly into the pore, giving it its tapered appearance. The pore-canal is typically funnel-shaped measuring c. 18 µm at its apex and c. 31 µm at its base. There were no signs of a central columella. Zonately divided tetrasporangia are plump (Pl. 79, Fig. Insert), and become spherical and almost fill the chamber when mature, measuring 94-140 µm long X 34-94 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 77, Fig. 6; Pl. 79, Fig. 18), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Description of representative specimens

Representative specimens examined

Fiji: Dravuni, Great Astrolabe Reef (D Keats, 2.vi.1994, UWC: 94/1041); Fish Patch, Suva Barrier Reef (D Keats, 5.viii.1994, UWC: 94/1150; 5.x.1994, UWC: 94/1244, 3.xii.1995, UWC: 95/1560); Nukalau Island, Suva Lagoon (D. Keats, 8.xi.1994, UWC: 94/1264; 5.xii.1994, UWC: 94/1382); Suva Lagoon (D Keats, 13.xi.1999, UWC: 99/FJ-01).

Habitat and Phenology

Hydrolithon reinboldii occurs attached to coral reef substrata on the outer side of windward reefs, leeward reefs, and lagoonal patch reefs, but is most abundant encrusting shells, pieces of coral, and forming rhodoliths in the rubble zone of windward reefs at c. 10-15 m depth. It also occurs intertidally on wave-exposed areas of some reefs (Keats pers. comm.).

Distribution

Australia (Penrose & Woelkerling 1992; Verheij 1993, 1994; Ringeltaube & Harvey 2000; Littler & Littler 2003), Borneo (Lemoine 1911; Adey et al. 1982), Caroline Islands (Lemoine 1911), Comores (Segonzac 1984; Silva et al. 1996), China (Zhang & Zhou 1978), Djibouti (Segonzac 1984), El Salvador (Adey et al. 1982), French Polynesia (Payri et al. 2000, Littler & Littler 2003), Fiji (Littler & Littler 2003; This study), Guam (Gordon et al. 1976; Adey et al. 1982), Hawaii (Adey et al. 1982), India (Adey et al. 1982; Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Indonesia (Foslie 1901b, 1909; Penrose & Woelkerling 1992; Verheij 1993, 1994; Silva et al. 1996), Japan (Baba 1987; Iryu & Matsuda 1988; Yoshida 1998), Kenya (Silva et al. 1996), Laccadive Islands (Lemoine 1911; Adey et al. 1982; Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Maldives (Lemoine 1911; Adey et al. 1982; Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Mauritius (Lemoine 1911; Segonzac 1984; Silva et al. 1996), Réunion (Segonzac 1984; Silva et al. 1996), Mexico (Revillagigedo Islands - Pacific) (Dawson 1960a; Adey et al. 1982), Papua New Guinea (Lemoine 1911), Philippines (Adey et al. 1982), Seychelles (Segonzac 1984; Silva et al. 1996; Kalugina-Gutnik et al. 1992; Titlyanova et al. 1992), Samoa (Foslie 1901b; Lemoine 1911), South Sandwich Islands (Lemoine 1911), Sri Lanca (Segonzac 1984; Silva et al. 1996), Tanzania (Zanzibar) (Foslie 1901b; Lemoine 1911; Segonzac 1984; Silva et al. 1996), Timor (Adey et al. 1982), Viet Nam (Adey et al 1982).

Habit and Vegetative Structure

Plants are generally adherent on coral rock, dead coral skeletons, shells, or form free-living rhodoliths (Pl. 80, Fig. 1) (Keats pers. comm.). Thalli measure up to at least 100 mm in diameter and 5 mm thick. Thalli are generally lumpy with more-or-less rounded, knobbly protuberances that measure up to 9 mm in length X 10 mm in diameter. Protuberances are dense and tightly packed. The margin is adherent, entire to lobed, and it lacks orbital ridges.

The surface is irregularly tesselate, and commonly has white scales of sloughing epithallial cells. The cell surface (SEM) is neither of the Phymatolithon- nor the Leptophytum-type (Pl. 81, Figs 2 & 3). It often, however, appears Leptophytum-type after sloughing has occurred (Pl. 81, Fig. 2). Plants are usually deep lavender, with a matt and chalky texture.

The thallus is dimerous, consisting of a single layer of basal filaments from which arise the erect filaments that make up most of the thallus (Pl. 81, Figs 5 & 7; Pl. 83, Figs 12, 16 & 17). Cells of the basal filaments are book-shaped (Pl. 81, Fig. 7; Pl. 83, Figs 12, 16 & 17). In primary-filament view, cells of the basal filaments are more-or-less square, and measure 10-42 µm long X 12-36 µm in diameter. In filament cross sections, basal cells are rectangular to elongate, and measure 10-42 µm long X 6-12 µm in diameter. Cell fusions are common (Pl. 81, Fig. 7; Pl. 83, Fig. 17). Thalli rarely become secondarily monomerous, and when they do it is probably in response to wound healing.

Cells of erect filaments are strongly horizontally arranged (Pl. 81, Fig. 5; Pl. 83, Figs 13 & 15) due to extensive connections by broad cell fusions. This phenomenon appears to increase with depth in the thallus. In their unfused, uninflated state, cells of the erect filaments are square to elongate and measure 7-24 µm long X 5-12 µm in diameter. When the cells of the erect filaments fuse, they are typically spherical to elongate, and measure 16-50 µm long X 12-31 µm in diameter. Secondary pit connections were not seen. Subepithallial initials are square to elongate (Pl. 81, Fig. 6; Pl. 83, Fig. 14), and measure 9-24 µm long X 6-14 µm in diameter. Epithallialcells (Pl. 81, Fig. 6; Pl. 83, Fig. 14) are squat to elliptical, occur singly (sometimes 2 when shedding), and measure 5-8 µm long X 6-14 µm in diameter. Trichocytes are bottle-shaped and common at the thallus surface and occur singly or in pairs (Pl. 81, Figs 4 & 6; Pl. 83, Fig. 14). Trichocytes (except pairs) are separated from one another by the cells of one or generally more, normal erect filaments and trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes measure 25-50 µm long X 15-26 µm in diameter. They are often overgrown and buried within the thallus.

Protuberances are radially organised, with a central core of filaments composed of elongate cells, from which radiate out filaments composed of cells similar to those of the erect filaments of crustose areas. Cells of filaments within protuberances commonly show strong layering.

Reproduction

Gametangial material has not been seen.

Sporangial conceptacles are slightly raised above the thallus surface, measuring 190-900 µm in external diameter (Pl. 82, Figs 8-10; Pl. 84, Figs 18 & 19). Their chambers are elliptical (Pl. 82, Fig. 10; Pl. 84, Figs 18 & 19) and measure 160-500 µm in diameter X 90-175 µm high, with the roof 37-68 µm (4-5 cells; incl. epithallial cell) thick (Pl. 82, Fig. 11; Pl. 84, Fig. 19). The conceptacle floor is flush with the surrounding thallus surface to 9 cells below the thallus surface. The roof is formed from filaments interspersed among the sporangia and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 82, Fig. 11; Pl. 84, Fig. 21). The pore canal narrows dorsally, and is lined by a single elongate cell (oriented more-or-less vertically) plus an epithallial cell that tilts slightly into the pore, giving it its tapered appearance. The pore is sunken and the pore-canal is typically funnel-shaped (Pl. 82, Fig. 11; Pl. 84, Fig. 21) measuring c. 18 µm at its apex and c. 31 µm at its base. There were no signs of a central columella. Zonately divided sporangia develop across the conceptacle floor. Tetrasporangia are plump, and become spherical and almost fill the chamber when mature (Pl. 84, Fig. 20), measuring 68-161 µm long X 27-143 µm in diameter. Bisporangia, measuring 62-124 µm long X 43-105 µm in diameter, were also seen (Pl. 84, Fig. insert). Sporangial conceptacles often become buried in the thallus (Pl. 82, Fig. 10; Pl.

84, Fig. 18), and often contain apparently viable sporangia. Although not common, infilled conceptacles have been observed.

Key features

Hydrolithon reinboldii is characterised by the following **combination** of characters: 1) thallus thick, adherent, often protuberant, also occurring as free-living rhodoliths with an obviously tesselate surface; 2) primary thallus dimerous; 3) has a single basal layer of non palisade cells; 4) cells of erect filaments are strongly horizontally arranged due to extensive connections by broad cell fusions; 5) sporangial conceptacles that are only slightly raised above the thallus surface; 6) trichocytes present, both at the surface and immersed in the thallus, commonly occurring singly and in pairs; 7) trichocytes quite often separated by the cells of normal erect filaments; 8) the sporangial conceptacle pore is sunken; 9) the base of sporangial conceptacle pore canals consistently lined by a ring of conspicuous, enlarged, domed cells; 10) the enlarged cell in the sporangial pore canal subtends a single epithallial cell that tilts slightly into the pore and gives it a tapered appearance in vertical section i.e. the sporangial conceptacle pore canal is more-or-less funnel shaped; 11) the sporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 12) the sporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 13) the tetrasporangial conceptacle roof is commonly 4-5 cells thick; 14) the sporangial conceptacle floor is commonly 0-9 cells below the surrounding thallus surface.

Remarks

Hydrolithon reinboldii, the type of the genus Hydrolithon, has been the subject of a number of studies (e.g. Dawson 1960a; Gordon et al. 1976; Adey et al. 1982; Krishnamurthy

& Jayagopal 1987; Penrose & Woelkerling 1988). All earlier reports of this species, however, generally dealt only with vegetative characters. It was not until Penrose & Woelkerling's (1992) reappraisal, that the sporangial conceptacle anatomy and roof development in *Hydrolithon reinboldii* was seen as an important character separating *Hydrolithon* (sensu stricto) from *Spongites* (sensu stricto). Similarly, this study has opted to describing all features possible in case they too would be useful as diagnostic features.

Basionym

Porolithon castellum Dawson 1960b: 41

Pl. 96-100, Figs 1-27.

Current Placement/Name

Status and disposition uncertain.

Holotype

USNC. North side of Isla del Caño, Costa Rica; E.Y. Dawson, no 21094.

Isotype material exists at UC and USNC. The isotype material from UC was examined during this study.

Synonyms

None

Etymology

'castellum', Dawson (1960b) did not explain the origin of the epithet, but it presumably makes reference to the pinnacled 'fairy castle'-like form of slender, laterally fused columns.

Description of Type

Habit and Vegetative Structure

The following description is based on the isotype material housed at UC (Pl. 96, Fig. 1). The isotype fragments from UC comprises 2 fragments: the larger of the two is roughly 60 mm high by 20 mm (at base) in diameter; the smaller of the two fragments is roughly 40 mm high by 23 mm (at base) in diameter. The thallus is castle-like, resembling a miniature mountain, bearing individual to fused vertical columns. Dawson (1960b) did, however, make reference to well developed much larger, subtidal “pinnacled, ‘fairy castle’ form of slender, laterally fused columns”. The type fragments are adherent, measuring up to 600 µm in crustose areas. The crustose parts of the thalli are generally smooth and have free margins that are entire to lobed, but lack orbital ridges (Pl. 97, Fig. 7). The cell surface (SEM) is somewhat between the Leptophytum- and Phymatolithon-type (Pl. 97, Fig. 2). The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate trichocyte fields (Pl. 97, Figs 3 & 5).

The thallus is monomerous, and dorsiventrally organised in crustose areas (Pl. 97, Figs 7-9; Pl. 99, Figs 16 & 20). The medullary filaments comprise 37-50% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 97, Fig. 8; Pl. 99, Fig. 20), with cells that are square to rectangular and measure 5-30 µm long X 5-19 µm in diameter. Cell fusions are abundant (Pl. 97, Fig. 8; Pl. 99, Fig. 20). Secondary pit connections have not been seen.

The cortical filaments comprise up to 63% of the thallus thickness (Pl. 97, Fig. 7), with cells that are square to rectangular and measure 5-17 µm long X 5-16 µm in diameter. Cell fusions are abundant (Pl. 97, Fig. 6; Pl. 99, Fig. 18). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 97, Fig. 4; Pl. 99, Fig. 21). Subepithallial initials are square (Pl. 97, Fig. 6; Pl 99, Fig. 18), and measure 6-12 µm long X 6-12 µm in diameter. Epithallial cells (Pl. 97, Fig. 6; Pl 99, Fig. 18) are squat to elliptical and measure 3-6 µm long X 6-12 µm in diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 4 when shedding). Fields of squarish to elongate trichocytes (Pl. 97, Fig. 4; Pl. 99, Fig. 17) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 16-37 µm long X 9-29 µm in diameter. Trichocytes end abruptly at their dorsal ends and the remains of the hairs that stain darkly are still visible (Pl. 99, Fig. 19). They are often overgrown and buried within the thallus in horizontal fields (Pl. 97, Fig. 4; Pl. 99, Fig. 21).

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are flush to slight sunken below the thallus surface, measuring 265-455 µm in external diameter (Pl. 98, Figs 10-12; Pl. 100, Fig. 22). Their chambers (Pl. 98, Figs 12 & 13; Pl. 100, Figs 22, 23 & 25) are elliptical to bean-shaped, and measure 225-285 µm in diameter X 50-100 µm high, with the roof 31-62 µm (6-10 cells; incl. epithallial cell) thick. The conceptacle floor is 12-17 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 98, Fig. 15; Pl. 100, Fig. 26). This ring of enlarged cells is substantially smaller than those commonly found in other species of Hydrolithon. While the ring of enlarged cells is typically 2/3 the length of the conceptacle pore in most species of Hydrolithon, it is generally only 1/4 to 1/3 the length of the conceptacle pore in Porolithon castellum. Above the enlarged cells, the tetrasporangial pore canal is often lined by narrow filaments that may tilt slightly into the pore canal and create the appearance of papillae (Pl. 100, Figs 26 & 27). There is a small central columella present (giving the conceptacle chamber its bean-shape) (Pl. 98, Fig. 12; Pl. 100, Fig. 25), and the zonately divided tetrasporangia are located peripheral to it. Tetrasporangia measure 37-74 µm long X 25-56 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 98, Fig. 14; Pl. 100, Fig. 23), and often contain apparently viable sporangia (Pl. 100, Fig. 24); infilled conceptacles have not been observed.

Distribution

Costa Rica (Pacific) Dawson 1960b.

Key features

Porolithon castellum is characterised by the following **combination** of characters: 1) thallus "castle-" or mountain-like, with vertical columns; 2) thallus monomerous; 3) medullary filaments plumose in crustose part of thallus; 4) tetrasporangial conceptacles that are flush to only slightly below the thallus surface; 5) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 6) within fields, trichocytes are not separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of enlarged, domed cells; 8) these enlarged cells are smaller than in other Hydrolithon taxa and typically only 1/4 to 1/3 the length of the conceptacle pore; 9) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 10) above the enlarged cells, the tetrasporangial pore canal is lined by narrow filaments that may tilt slightly into the pore canal and create the appearance of papillae; 11) the tetrasporangial conceptacle roof is commonly 6-10 cells thick; 12) the sporangial conceptacle floor is commonly 12-17 cells below the surrounding thallus surface.

Remarks

According to Dawson (1960b) Porolithon castellum is a very visible feature in shallow intertidal areas and the subtidal of Isla del Caño, Costa Rica. Dawson refers to well developed subtidal specimens that “represent this species as one of the most distinctive of the genus”. Dawson makes a special reference to the “pinnacled, ‘fairy castle’ form of slender, laterally fused columns … all arising from a thin basal crust” and notes that this species is “unlike anything heretofore described”. Foslie (1900a) had already described just such a species from the Gilbert Islands, Kiribati, in the western Pacific, a species he named Lithophyllum craspedium. The plants identified by Dawson (1960b) as Porolithon castellum are, in all probability, very young specimens of Hydrolithon craspedium (see Pl. 37). Its characteristic castle-like, massive, mountain-like structure with broad, thick vertical columns would make this specimen stand out against the rest of the reef.

Besides it gross morphology, Porolithon castellum is also quite unique in its tetrasporangial roof anatomy. Unlike most Hydrolithon, the ring of enlarged cells that typically lines the pore canal in tetrasporangial conceptacles is rarely visible. This is so because these cells are substantially smaller than in most Hydrolithon and when visible, are quite often 1/4 to 1/3 the length of the conceptacle pore canal. In most Hydrolithon taxa, these enlarged pore canal cells are roughly 2/3 to 3/4 the length of the conceptacle pore canal. In H. craspedium, however, the enlarged cells lining the tetrasporangial pore canal are also typically 1/3 the length of the pore canal. Porolithon castellum, therefore, conforms well to the description of H. craspedium and is therefore a heterotypic synonym for Hydrolithon craspedium. Dawson’s (1960b) account is therefore the first recorded collection of H. craspedium for the Eastern Pacific.

Basionym

Porolithon cocosicum Lemoine 1930: 49 (see also Chapman 1971: 169)

Pl. 101-102, Figs 1-8; Pl. 103-106, Figs 1-17.

Current Placement/Name

Status and disposition uncertain.

Holotype

BM. Cocos Island, Pacific Ocean (St. George Expedition of 1923-1924); algal box collection no. 316. Previous references to typification were by Tittley et al. 1984: 13. Holotype fragments exist in PC

Synonyms

None

Etymology

'cocosicum' after the Cocos Island from where collected.

Description of Type

Habit and Vegetative Structure

The following description is based on the BM slide no. 5369 (gametangial material) (Pl. 101 & 102) and the holotype fragment sent on loan from PC (sporangial fragments) (Pl. 103-106). Fragments are adherent, measuring up to 330 µm thick. Thalli are smooth and featureless, lacking protuberances but may also be slightly warty to low lumpy (Lemoine 1930: Pl. 4, Fig 4). Margins have not been observed. The cell surface (SEM) is of the

Phymatolithon-type (Pl. 103, Fig. 1). The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate trichocyte fields (Pl. 103, Fig. 2).

The thallus is monomerous and dorsiventrally organised. The medullary filaments comprise 8-52% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 101, Fig. 4; Pl. 105, Fig. 13), with cells that are square to rectangular and measure 6-25 μm long X 6-15 μm in diameter. Cell fusions are abundant (Pl. 101, Fig. 4; Pl. 105, Fig. 13). Secondary pit connections have not been seen.

The cortical filaments comprise up to 92% of the thallus thickness with cells that are square to rectangular and measure 5-21 μm long X 5-12 μm in diameter. Cell fusions are abundant (Pl. 101, Fig. 3; Pl. 103, Fig. 3; Pl. 105, Fig. 12). Secondary pit connections were not seen. Buried trichocyte fields frequently occur in the cortex (Pl. 101, Fig. 2; Pl. 105, Fig. 11). Subepithallial initials are square to rectangular (Pl. 101, Fig. 3; Pl. 103, Fig. 3; Pl. 105, Fig. 12), and measure 6-19 μm long X 5-12 μm in diameter. Epithallialcells (Pl. 101, Fig. 3; Pl. 103, Fig. 3; Pl. 105, Fig. 12) are squat to elliptical and measure 4-7 μm long X 5-12 μm in diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 5 when shedding). Fields of squarish to rectangular trichocytes (Pl. 101, Fig. 1; Pl. 105, Fig. 10) commonly occur at the thallus surface in tightly packed, pustulate horizontal fields. These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are not separated by the cells of normal cortical filaments. Individual trichocyte chains typically comprise 2 cells; a megacell and a support cell. Individual trichocytes measure 15-37 μm long X 9-20 μm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 101, Fig. 2; Pl. 105, Fig. 11).

Reproduction

Gametangial plants are monoecious (Pl. 102, Fig. 5). Spermatangial conceptacles are small, measuring about 125-200 µm in external diameter. Spermatangial conceptacle roofs are usually more-or-less flush with the surrounding thallus surface, but are sometimes slightly raised. The conceptacle chamber is wide and shallow to elliptical, measuring 93-155 µm in diameter X 22-37 µm high, with the roof 19-37 µm thick (Pl. 102, Figs 5 & 6). Spermatangial conceptacles are often seen buried in the thallus; infilling has not been observed (Pl. 102, Fig. 5). Simple spermatangial systems are borne only on the floor of the conceptacle chamber (Pl. 102, Fig. 6).

Carpogonial conceptacles have not been observed.

Carposporangial conceptacles are relatively large, measuring 300-450 µm in external diameter. Chambers of carposporangial conceptacles are elliptical to bean-shaped, and measure 175-374 µm in diameter X 56-109 µm high with the roof 56-62 µm thick (Pl. 102, Figs 5 & 8). The pore canal is lined with small filaments. The continuous central fusion cell is narrow and thick, with gonimoblast filaments borne peripherally (Pl. 102, Figs 7 & 8). Gonimoblast filaments are 9-11 cells long including a terminal carpospore that measures 31-62 µm long X 31-43 µm in diameter. Mature carpospores almost fill the conceptacle chamber.

Tetrasporangial conceptacles are slightly sunken to flush to slightly raised above the rest of the thallus surface and measure 275-450 µm in external diameter (Pl. 104, Figs 4-7; Pl. 106, Figs 14 & 15). Their chambers (Pl. 104, Figs 6 & 7; Pl. 106, Figs 14 & 15) are elliptical to spherical, and measure 175-300 µm in diameter X 60-150 µm high, with the roof 43-56 µm (7-11 cells) thick (Pl. 104, Fig. 9; Pl. 106, Fig. 17). The conceptacle floor is located 12-20 cells below the thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 104, Fig. 9; Pl. 106, Fig.

17). The pore-canal filaments are usually oriented more-or-less vertically, and do not tilt markedly into the pore. A central columella has not been seen. Zonately divided tetrasporangia are, however, located peripherally in the conceptacle chamber (Pl. 104, Fig. 8; Pl. 106, Fig. 16). Sporangia measure 35-99 µm long X 15-53 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 104, Fig. 6; Pl. 106, Figs 14 & 15), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Distribution

Cocos Island (Costa Rica, Pacific Ocean) (Lemoine 1930), Fiji (Chapman 1971).

Key features

Porolithon cocosicum is characterised by the following **combination** of characters: 1) thallus thin, adherent, generally lacking protuberances but may be slightly warty to low lumpy; 2) thallus monomerous; 3) medullary filaments plumose; 4) tetrasporangial conceptacles that are slightly sunken to flush to only slightly raised above the thallus surface; 5) Plants commonly with up to 5 layers of epithallial cells; 6) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 7) within fields, trichocytes are not separated by the cells of normal cortical filaments; 8) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 9) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 10) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 11) the tetrasporangial conceptacle roof is commonly 7-11 cells thick; 12) the sporangial conceptacle floor is commonly 12-20 cells below the surrounding thallus surface.

Remarks

In her description of this taxon, Lemoine (1930: 49) distinguished Porolithon cocosicum from P. onkodes Heydrich (from the Pacific) (see also Lemoine 1911) and P. onkodes f. pachyderma Foslie (from the western Atlantic) by having a monomerous thallus (with a thick medullary region) as apposed to having both a monomerous (with a thin medullary region) and a dimerous thallus she considered diagnostic of the latter two taxa. What this study has shown (e.g. Pl. 26, Figs 3 & 18; Pl. 67, Figs 16 & 22; Pl. 70, Figs 2 & 6) is that when extremely thin monomerous thalli are sectioned parallel to the growing margin or at right angles to the growing thallus, it gives the false impression of a dimerous thallus. This may be what led Lemoine (1911, 1930) to conclude that P. onkodes and P. onkodes f. pachyderma bore both monomerous and dimerous thalli. Like earlier researchers (e.g. Penrose & Woelkerling 1988; Keats & Chamberlain 1994) this study has not recorded any dimerous thalli in H. onkodes. Based on the key characters listed above, the description of Porolithon cocosicum matches perfectly that of H. onkodes. Porolithon cocosicum is, therefore, conspecific with H. onkodes and should therefore be regarded as a heterotypic synonym of Hydrolithon onkodes.

Basionym

Porolithon marshallense W.R. Taylor ("marshallensis") 1950: 128-129

Pl. 107-111, Figs 1-18; Pl. 112-114, Figs 1-15.

Current Placement/Name

Status and disposition uncertain.

Holotype

MICH. Kabelle Island, Rongelap Atoll, Marshall Islands; Taylor no. 46-627. Previous references to typification were by Woelkerling & Lamy 1998: 389 (as Porolithon).

Isotype

Isotype material also exists in BM (algal collection box 1015) and PC (Taylor no. 46-627). Isotype material from both BM and PC were analysed during this study.

Synonyms

Homotypic synonyms:

Spongites marshallensis (Taylor) Dreckmann ("marshallense") 1991: 35.

Heterotypic synonyms:

Lithophyllum gardineri Foslie forma obpyramidatum Foslie 1907a: 30 ("obpyramidata") (Taylor 1950: 128).

Porolithon gardineri (Foslie) Foslie forma abbreviatum (Foslie) R.K.S. Lee 1967: 991 ("abbreviata").

Etymology

'marshallensis' after the Marshall Islands from where collected.

Description of Type

Habit and Vegetative Structure

The following description is based on the type material housed at BM (Pl. 107-111) and PC (Pl. 112-114). The BM type consists of a single specimen roughly 35 mm high X 25 - 50 mm in diameter (Pl. 105, Fig. 1). The PC material sent on loan comprised a few unfused terete protuberances. The type material bears numerous terete, dichotomously branched, generally unfused protuberances measuring up to 6 mm in diameter X up to 30 mm in length. Protuberances are blunt ending. The thallus in the crustose areas is adherent, measuring up to 550 µm thick, and is generally flat and smooth. The margins are free to adherent, and entire to lobed, but lack orbital ridges (Pl. 108, Fig. 6). The cell surface (SEM) is both of the Phymatolithon- and Leptophytum-types (Pl. 108, Figs 2 & 4; Pl. 112, Fig. 1). The surface texture is matt and granular due to the presence of numerous tightly packed, pustulate trichocyte fields (Pl. 108, Fig. 3; Pl. 112, Figs 2 & 3).

The thallus is monomerous, and dorsiventrally organised (Pl. 108, Figs 6 & 9). In crustose areas, the medullary filaments comprise up to 45% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 108, Figs 8 & 9), with cells that are square to rectangular and measure 9-25 µm long X 6-15 µm in diameter. Cell fusions are abundant (Pl. 108, Fig. 8). Secondary pit connections have not been seen.

The cortical filaments comprise up to 60% of the thallus thickness in crustose parts and are composed of cells that are square to elongate, and measure 4-21 µm long X 4-19 µm in diameter (Pl. 108, Fig. 6). Cell fusions are abundant (Pl. 108, Fig. 7; Pl. 112, Fig. 5; Pl. 114, Fig. 11). Secondary pit connections have not been seen. Buried trichocyte fields occur frequently in the cortex (Pl. 108, Fig. 5; Pl. 110, Fig. 13; Pl. 111, Fig. 17; Pl. 112, Fig. 4; Pl. 113, Figs 8 & 9; Pl. 114, Fig. 13). Subepithallial initials are square to rectangular (Pl. 108,

Fig. 7; Pl. 110, Fig. 14; Pl. 112, Fig. 5; Pl. 114, Fig. 11), and measure 5-19 µm long X 6-13 µm in diameter. Epithallial cells (Pl. 108, Fig. 7; Pl. 110, Fig. 14; Pl. 112, Fig. 5; Pl. 114, Fig. 11) are squat to elliptical and measure 3-7 µm long X 6-12 µm in diameter, and occur in 1-3 (mostly 2-3 but up to 4 when shedding) cell layers. Fields of rectangular to elongate trichocytes commonly occur at the thallus surface in horizontal pustulate fields (Pl. 108, Fig. 3; Pl. 110, Fig. 12; Pl. 112, Fig. 3; Pl. 114, Fig. 12). These trichocytes give the thallus a distinctive granular appearance when they occur at the surface. Within fields, individual trichocytes are <u>not</u> separated by the cells of normal cortical filaments. Individual trichocyte chains comprise only 2 cells; a megacell, and a support cell. Individual trichocytes measure 19-43 µm long X 7-22 µm in diameter. They are often overgrown and buried within the thallus in horizontal fields (Pl. 108, Fig. 5; Pl. 110, Fig. 13; Pl. 111, Fig. 17; Pl. 112, Fig. 4; Pl. 113, Figs 8 & 9; Pl. 114, Fig. 13).

Protuberances are composed of a thick central core of medullary filaments with vertically oriented cells arranged in a coaxial manner. From this central core arise the cortical filaments composed of cells that are oriented perpendicularly to the long axis of the protuberance. The protuberances branch dichotomously and are predominantly unfused.

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are slightly sunken to flush to only slightly raised above the rest of the thallus surface (Pl. 109, Figs 10 & 11; Pl 111, Figs 15 & 17; Pl. 113, Figs 6-9; Pl. 1142, Fig. 14), measuring 195-425 µm in external diameter. Their chambers (Pl. 111, Figs 15-17; Pl. 113, Figs 8 & 9; Pl. 114, Fig. 14) are elliptical to bean-shaped, and measure 165-200 µm in diameter X 78-150 µm high, with the roof 25-41 µm (4-6 [mostly 5-6] cells; incl. epithallial cell) thick (Pl. 113, Fig. 10). The conceptacle floor is located 8-17 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 111, Fig. 18; Pl. 113, Fig. 10; Pl. 114, Fig. 15). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. A small central columella is present and zonately divided tetrasporangia are located peripherally to it (Pl. 111, Fig. 16; Pl. 113, Fig. 8). Tetrasporangia measure 43-87 μm long X 19-43 μm in diameter. Bisporangial Plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 111, Fig. 16; Pl. 113, Fig. 9), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Distribution

Marshall Islands (Taylor 1950; Lee 1967), Mexico (Pacific) (Dreckmann 1991).

Key Features

Porolithon marshallense is characterised by the following **combination** of characters: 1) thallus moderately thick, adherent, producing narrow terete, dichotomously branched, predominantly unfused protuberances; 2) thallus monomerous; 3) medullary filaments plumose in crustose part of thallus; 4) tetrasporangial conceptacles that are slightly sunken to flush to only slightly raised above the thallus surface; 5) trichocytes present, both at the surface and immersed in the thallus, consisting of numerous horizontally oriented, pustulate fields which give the thallus a distinctive granular appearance when they occur at the surface; 6) within fields, trichocytes are not separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 9) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is commonly 5-6 cells thick; 11) the sporangial conceptacle floor is commonly 8-17 cells below the surrounding thallus surface.

Remarks

In his review of the marine plants of Bikini Island and other Marshall Islands, W.R. Taylor (1950) had considered Porolithon marshallense conspecific with Lithophyllum gardineri Foslie forma obpyramidatum Foslie 1907a: 30 ("obpyramidata"). Later, R.K.S. Lee (1967) reduced Porolithon marshallense to synonymy under the combination P. gardineri forma abbreviatum (as “abbreviata”). Still later Verheij (1993) considered Lithophyllum gardineri forma obpyramidata and Lithophyllum coarctatum to be heterotypic synonyms for Lithophyllum gardineri and thus conspecific with Hydrolithon gardineri. Porolithon marshallense conforms well to the characters that I have considered diagnostic of Hydrolithon gardineri so it is concluded that Porolithon marshallense is conspecific with Hydrolithon gardineri.

TYPE MATERIAL NOT OBTAINED

1. Basionym (& Herbarium)

Porolithon colliculosum Masaki 1968: 43-44 (HAK) (see also Yoshida 1998: 564)

Current Placement/Name

Status and disposition uncertain.

Synonyms

None, although *Neogoniolithon colliculosum* (Masaki) Baba 1987: 196 (never published).

From Masaki's description and diagrams, *Porolithon colliculosum* appears more closely related to Spongites (sensu strictu) than either Porolithon (as Hydrolithon) or *Neogoniolithon*. In *Porolithon colliculosum* (Masaki 1968: Pl. 71-72; Baba 1987: Fig. 114) the sporangial conceptacle roof is formed from filaments peripheral to the chamber and the sporangial initials. This type of conceptacle roof development is not found in species now ascribed to *Hydrolithon*. There is also no mention of a ring of enlarged cells at the base of the sporangial conceptacle pore that are also very characteristic of *Porolithon*. Baba (1987: 199) cites the development of the conceptacle roof as the reason for his placement of this taxon in *Neogoniolithon* not realising that *Spongites* also has this type of sporangial conceptacle roof development. The spermatangia within the spermatangial conceptacles (Masaki 1968, Pl. 72, Fig. 3; Baba 1987: 199, Fig. 115) are restricted to the conceptacle floor, one of the diagnostic characters of Spongites; in Neogoniolithon, spermatangia are located on the floor, walls and roof of the conceptacle chamber. Furthermore, gonimoblast filaments are characteristically across the conceptacle floor in *Neogonioithon*, while they are peripheral in *Spongites* as is clearly evident in *Porolithon colliculosum* (Masaki 1968: Pl. 72, Fig. 4).

2. Basionym (& Herbarium)

Porolithon orbiculatum Masaki 1968: 44-46 ("orbicularis") (HAK) (see also Baba 1987: 321; Yoshida 1998: 564)

Presently valid name

Status and disposition uncertain.

Synonyms

None.

From Masaki's description and diagrams, Porolithon orbiculatum appears to be a Spongites. In Porolithon orbiculatum (Masaki 1968: Pls 69 & 70, Fig. 1-3) the sporangial conceptacle roof lacks the enlarged cells typical of the base of the conceptacle pore and also appears to be formed from filaments peripheral to the conceptacle chamber and the sporangial initials. Both Porolithon colliculosum and Porolithon orbiculatum bear numerous trichocytes in horizontal fields. This may have been the reason for Masaki's designation of these taxa as Porolithon. We now know that trichocyte arrangements and grouping are not reliable characters for separating taxa at the generic level (see Lemoine 1917; Cabioch 1972; Mendoza & Cabioch 1986; Penrose & Woelkerling 1988; Keats et al. 1997).

In Baba's (1987) description of Porolithon orbiculatum, however, the sporangial conceptacle was shown to possess the enlarged cells at the base of the conceptacle pore canal, a character diagnostic of Hydrolithon. Although Baba's (1987: 365, Fig. 157) diagram shows development of the sporangial conceptacle roof from both filaments interspersed among and peripheral to the sporangial initials (a character diagnostic of Pneophyllum), he does make mention of the fact that the peripheral derivatives of the roof are still from sterile initials located at the periphery of the conceptacle chamber (Baba 1987: 322). This is unlike the development of the roof from peripheral roof filaments that characterize Spongites and partly Pneophyllum. This taxon requires a modern examination in light of these observations.

3. Basionym (& Herbarium)

Porolithon somaliae Raineri 1929: 412-416 (TO)

Presently valid name

Hydrolithon somaliae (Raineri) P. Silva in Silva et al. 1996: 240

Synonyms

None.

I was unable to trace the whereabouts of this specimen despite suggestions by Paul Silva (pers. comm.) that the Rainer types resided at TO.

4. Basionym (& Herbarium)

Porolithon sonorense Dawson ("sonorensis") 1944: 273 (see also Dawson 1960a: 25-26) (AHFH – transferred to LAM, see Anderson 1991: 35)

Presently valid name

Status and disposition uncertain.

Synonyms

Spongites sonorensis (Dawson) Dreckmann 1991: 35.

Herbarium policy prevented the loan and examination of this specimen.

Dawson's description of Porolithon sonorense (1944, 1960a) is simply not enough to go by. The only real reference to any 'Porolithon' character is the trichocytes that appear in horizontal fields. The gross morphology of Porolithon sonorense is, however, quite distinct from any other described Porolithon. This is not saying much though as the trichocyte arrangements and grouping are not reliable characters for separating taxa at the generic level (see Lemoine 1917; Cabioch 1972; Mendoza & Cabioch 1986; Penrose & Woelkerling 1988; Keats et al. 1997). Also, Dreckmann (1991: 35) provided no description of this taxon; a mere mention of the taxon was provided in a species list of calcareous algae from Pacific Mexico. This taxon requires a modern examination in light of these observations.

DISCUSSION

From the descriptions above it is evident that a number of taxa are conspecific (Tables 4 & 5). It appears that within the group, the gross morphology is quite often a useful character in delineating those taxa ascribed to Porolithon. We should, however, bear in mind that this very character (gross morphology) has most likely been the reason for much of the varied names by which these taxa had been referred to. It has only been through more recent ecological studies (e.g. Littler et al. 1995; see also Littler & Littler 2000, 2003) that morphology in response to environmental factors has shown the variable nature of the morphology of many coralline algae. None-the-less, these ecological studies have shown that we can use the gross morphology (once we have identified the response) to delineate taxa at least to a degree of accuracy.

Based on the collective analyses of the taxa described above, the characteristics of the taxa ascribed to the now defunct genus Porolithon are:

1. thallus non-geniculate;
2. cells of contiguous vegetative filaments normally joined by cell fusions;
3. secondary pit connections absent or rare;
4. sporangia lacking apical plugs and borne within uniporate conceptacles.

The above four characters group this taxon into the subfamily Mastophoroideae (Setchell 1943: 134 - as 'Mastophoreae')

5. thallus monomerous or dimerous and lacking a basal layer of palisade cells throughout;
6. in monomerous thalli, medullary filaments predominantly plumose (non-coaxial);
7. trichocytes present, occurring singly, in small horizontal groups separated by vegetative filaments, or in large tightly packed, pustulate horizontal fields lacking vegetative filaments interspersed among the trichocytes;

8. the base of sporangial conceptacle pore canals are lined by a ring of conspicuous, enlarged, domed cells;
9. these enlarged cells do not protrude into the pore canal, and are oriented more-or-less perpendicularly to the roof surface;
10. the sporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them;
11. the sporangial pore canal is not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae,
12. Spermatangial conceptacles containing simple spermatangial systems that are restricted to the conceptacle floor;
13. gonimoblast filaments borne from the margin of the fusion cell.

These latter nine characters are collectively diagnostic of the genus *Hydrolithon* (*sensu strictu*) as proposed by Penrose & Wolkerling (1988, 1992). Based on the above analyses, however, there appears to be two groups of taxa within the confines of the genus *Hydrolithon* (*sensu strictu*). These two groups separate out from one another based collectively on: 1) the number of epithallial layers; 2) the trichocyte arrangement and 3) the thallus construction (Table 5).

Group 1 is characterised by:

1. a single layer of epithallial cells (up to 2 or 3 cells only when shedding);
2. trichocytes occurring singly, in pairs and/or in small horizontal groups, quite often separated from one another by normal vegetative filaments; and
3. thallus construction always/primarily dimerous.

Group 2 is characterised by:

1. 2-3 layers of epithallial cells (and up to 5 cells when shedding);
2. trichocytes occurring in large tightly packed, pustulate horizontal fields without any vegetative filaments between the individual trichocytes; and
3. thallus construction always/primarily monomerous.

It seems logical to suggest, therefore, that within the genus Hydrolithon, there are at least two subgenera. I suggest that Group 1 comprise the subgenus Hydrolithon with H. reinboldii representative of the subgenus. Group 2 should comprise the subgenus Porolithon with H. onkodes representative of this subgenus.

Key to the taxa ascribed to the defunct genus Porolithon (excluding species of which material has not been obtained)

1. Thallus dimerous; commonly comprised of only 1 layer of epithalial cells; trichocytes most often occurring singly, occasionally in pairs and/or small horizontal rows …... **2**

Thallus monomerous; commonly comprised of 2-3 layers of epithalial cells; trichocytes occurring in large horizontal pustulate fields without any vegetative filaments between the individual trichocytes ….……………………………….………. **4**

2. Plants commonly composed of applanate branches that overgrow one another; sporangial conceptacle pores not sunken ………..…………………... **H. improcerum**

Plants rarely with applanate branches that overgrow one another; sporangial conceptacle pores sunken ……………………………………..…………...……... **3**

3. Cells of erect filaments strongly horizontally arranged ………………..... **H. reinboldii**

Cells of erect filaments not strongly horizontally arranged ..……....… **H. boergesenii**

4. Plants forming massive mountain-like upgrowths when mature or are fruticose …... **5**

Plants smooth, warty, lumpy or occasionally lobed …......………..…..…. **H. onkodes**

………...…... (incl. **P. antillarum**, **P. pachydermum**, **P. sandvicense**, **P. cocosicum**)

5. Plants forming massive mountain-like upgrowths when mature …….. **H. craspedium**

……………………………………………………………….. (incl. **P. castellum**)

Plants fruticose, producing narrow, terete, somewhat dichotomously branched and generally unfused protuberances ……………………………….…...…… **H. gardineri**

…..…..... (incl. **P. aequinoctiale**, **P. coarctatum**, **P. praetextatum**, **P. marshallense**)

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Table 1. Taxa that have been ascribed to the now defunct genus *Porolithon* Foslie 1909.

Original Foslie species (Type species in bold)

1. *Porolithon aequinoctiale* (Foslie) Foslie 1909: 57.
   Lithophyllum aequinoctiale Foslie 1909: 46.
2. *Porolithon africanum* (Foslie) Foslie 1909: 57.
   Lithophyllum africanum Foslie 1900c: 3
3. *Porolithon antillarum* (Foslie et Howe) Foslie 1909: 57.
   Lithophyllum antillarum Foslie et Howe 1906: 579.
4. *Porolithon coarctatum* (Foslie) Foslie 1909: 57.
   Lithophyllum coarctatum Foslie 1907a: 31.
5. *Porolithon craspedium* (Foslie) Foslie 1909: 57.
   Lithophyllum craspedium Foslie 1900a: 26.
6. *Porolithon gardineri* (Foslie) Foslie 1909: 57.
   Lithophyllum gardineri Foslie 1907a: 30.
7. *Porolithon oligocarpum* (Foslie) Foslie 1909: 57.
   Lithophyllum oligocarpum Foslie 1906a: 22.
8. ***Porolithon onkodes*** **(Heydrich) Foslie 1909: 57.**
   Lithothamnion onkodes **Heydrich 1897: 6.**
9. *Porolithon pachydermum* (Weber v. Bosse et Foslie) Foslie 1909: 57.
   Lithophyllum onkodes f. *pachydermum* Foslie 1904: 5.
10. *Porolithon praetextatum* (Foslie) Foslie 1909: 57.
    Lithophyllum praetextatum Foslie 1907a: 31.
11. *Porolithon sandvicense* (Foslie) Foslie 1909: 57.
    Lithophyllum dentatum f. *sandvicensis* Foslie 1901a: 11.

Additional taxa

12. *Porolithon boergesenii* (Foslie) Lemoine in Børgesen 1917: 178.
    Goniolithon boergesenii Foslie 1901a: 19.
13. *Porolithon castellum* Dawson 1960b: 41.
14. Porolithon cocosicum Lemoine 1930: 49.
15. *Porolithon colliculosum* Masaki 1968: 43.

16 *Porolithon improcerum* (Foslie & Howe) Howe 1920: 587
Goniolithon improcerum Foslie & Howe in Foslie 1907b: 24

17. *Porolithon marshallense* W.R. Taylor ("*marshallensis*") 1950: 128.
18. *Porolithon orbiculatum* Masaki 1968: 44.
19. *Porolithon reinboldii* (Weber-van Bosse & Foslie) Lemoine 1911: 166.
    Lithophyllum reinboldii Weber-van Bosse & Foslie in Foslie 1901b: 5
20. *Porolithon somaliae* Raineri 1929: 412.
21. *Porolithon sonorense* Dawson ("*sonorensis*") 1944: 273.

Table 2. The list of Herbaria cited in Paper 1: Porolithon (Acronyms follow Holmgren et al. 1990).

AHFH	LOS ANGELES: Herbarium, Allan Hancock Foundation, University of Southern California, Los Angeles, California 90089-0371, U.S.A. – transferred to LAM and RSA
BM	LONDON: Herbarium, Botany Department, The Natural History Museum, Cromwell Road, London SW7 5BD, England, U.K.
C	COPENHAGEN: Herbarium, Botanical Museum, University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen K, Denmark
HAK	HAKODATE: Herbarium, Laboratory of Marine Botany, Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido 041, Japan
LAM	LOS ANGELES: Herbarium, Botany Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A.
NY	NEW YORK: Herbarium, New York Botanical Garden, Bronx, New York 10458-5126, U.S.A.
PC	PARIS: Herbier, Laboratoire de Cryptogamie, Muséum National d'Histoire Naturelle, 12 rue Buffon, F-75005 Paris, France
RSA	CLAREMONT: Herbarium, Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711-3157, U.S.A.
TO	TORINO: Erbario, Dipartimento di Biologia Vegetale, Università degli Studi di Torino, Viale Pier Andrea Mattioli 25, I-10125 Torino, Italy
TRH	TRONDHEIM: Herbarium, Museum of Natural History and Archaeology, Department of Botany, University of Trondheim, N-7004 Trondheim, Norway
UC	BERKELEY: University Herbarium, University of California, Berkeley, California 94720, U.S.A.

Table 3. A comparative analysis of the vegetative and reproductive anatomy of Spongites africanum (Foslie) Afonso-Carrillo, Chacana & Sansón (1993), Porolithon oligocarpum (Foslie) Foslie 1909 and Pneophyllum conicum (Dawson) Keats, Chamberlain & Baba (1997) (all measurements are in µm). Cell contents in bold represent unique characters.

Feature:	**S. africanum**	**P. oligocarpum**	**P. conicum**
General thallus form	**fruticose, bearing terete protuberances**	**smooth, lacking protuberances**	**smooth, lacking protuberances**
Thallus construction	monomerous	monomerous	monomerous
No. of epithallial cells	1-3	1-3	**1**
	(mostly 2-3; up to 4 when shedding)	(mostly 2-3; up to 4 when shedding)	**(up to 2 when shedding)**
Epithallial cell: shape	squat to elliptical	squat to elliptical	elliptical to rounded
length	3-10	3-9	3-8
diameter	5-12	6-13	3-10
Subepithallial cell: shape	square to rectangular	square to rectangular	square to rectangular
length	4-19	5-20	6-20
diameter	4-10	6-12	4-13
Trichocyte: arrangement	pustulate horizontal fields	pustulate horizontal fields	pustulate horizontal fields
buried in thallus	yes	yes	yes
Condition of medullary filaments	coaxial	coaxial	coaxial
Thickness (%) of thallus comprising cortical filaments	**33-48**	61-86	50-90

Sporangial conceptacle	flush to only slightly raised	slightly sunken to flush to only slightly raised	**raised**
external diameter	300-650	225-450	270-675
no. of roof cells	7-11	6-10	5-13
chamber diameter	175-315	200-295	220-250
chamber height	65-125	60-110	42-105
depth of floor (cells)	≤ 21	≤ 14	≤ 11
Sporangial distribution	peripheral	peripheral	peripheral
Columella	present	present	present
Single elongate cell in conceptacle wall	no	no	**yes**

Material from types and representative specimens are combined. Additional information from Keats et al. (1997).

Table 4. The present status and conspecificity of the taxa ascribed to the defunct genus *Porolithon*.

Taxon	**Present Status**	**Conspecificty**
Hydrolithon boergensenii	unchanged	
Hydrolithon craspedium	unchanged	
Hydrolithon improcerum	unchanged	
Hydrolithon gardineri	unchanged	
Hydrolithon onkodes	unchanged	
Hydrolithon reinboldii	unchanged	
Lithophyllum aequinoctiale?		*Hydrolithon gardineri*
Lithophyllum antillarum		*Hydrolithon onkodes*
Lithophyllum coarctatum		*Hydrolithon gardineri*
Lithophyllum oligocarpum	*Spongites oligocarpum*	
Lithophyllum pachydermum		*Hydrolithon onkodes*
Lithophyllum praetextatum?		*Hydrolithon gardineri*
Lithophyllum sandvicense		Hydrolithon onkodes
Porolithon castellum		*Hydrolithon craspedium*
Porolithon cocosicum		*Hydrolithon onkodes*
Porolithon marshallensis		*Hydrolithon gardineri*
Spongites africanum	unchanged	

? – these taxa require greater investigation with analysis of additional material from the type localities.

Table 5. A comparative summary of the diagnostic characters in those taxa studied that have been ascribed to the defunct genus Porolithon.

Species	Thallus construction	No. of epithallial cells layers[1]	Trichocyte arrangement	Trichocyte fields pustulate (Yes/No)	No. of cells in sporangial concept. roof	Other
Porolithon aequinoctiale	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	-	Plants fruticose, producing narrow, terete, somewhat dichotomously branched and generally unfused protuberances.
Porolithon africanum	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	7-11	Conforms to generic delimitation of Spongites based on sporangial conceptacle development.
Porolithon antillarum	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	5-11	Upright, lobed, honey-combed in form.
Porolithon boergesenii	dimerous	1	Singly, but also in small groups of 2-3; at surface and buried.	No	4-5	Plants knobby, lumpy to smooth
Porolithon castellum	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	6-10	The thallus is mountain-like, bearing individual to fused, narrow vertical columns.
Porolithon cocosicum	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	7-11	Plants generally smooth and featureless.

Porolithon coarctatum	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	5-6	Plants fruticose, producing narrow, terete, somewhat dichotomously branched and generally unfused protuberances.
Porolithon craspedium	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	5-9	The thallus is massive and mountain-like, bearing broad individual to fused vertical columns.
Porolithon gardineri	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	5-6	Plants fruticose, producing narrow, terete, somewhat dichotomously branched and generally unfused protuberances.
Porolithon improcerum	dimerous	1	Singly, but also in small horizontal fields; at surface and buried.	No	2-3	Plants commonly composed of applanate branches that overgrow another
Porolithon marshallense	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	5-6	Plants fruticose, producing narrow, terete, somewhat dichotomously branched and generally unfused protuberances.
Porolithon oligocarpum	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	6-10	Conforms to generic delimitation of Spongites based on sporangial conceptacle development.

Porolithon onkodes	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	7-11	Plants generally smooth and featureless but may also be upright, lobed and honey-combed in form.
Porolithon pachydermum	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	6-11	Plants generally smooth and featureless but may also be upright, lobed and honey-combed in form.
Porolithon praetextatum	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	-	Plants fruticose, producing narrow, terete, somewhat dichotomously branched and generally unfused protuberances.
Porolithon reinboldii	dimerous	1	Singly, but also in pairs; at surface and buried.	No	4-5	Plants commonly occur as rhodoliths; cells of erect filaments strongly horizontally arranged
Porolithon sandvicense	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	4-12	Upright, lobed, honey-combed in form.

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[1] This excludes cell layers that are in the process of being shed.

FIGURE CAPTIONS

Pl. 1

Goniolithon boergesenii Foslie

Fig. 1. The habit of the type of Goniolithon boergesenii Foslie.

Pl. 2

Goniolithon boergesenii Foslie

Figs 2-6. Vegetative anatomy of the type of Goniolithon boergesenii Foslie.

Fig. 2. The thallus surface showing convex epithallial cells with primary pit connections still visible (arrow) and a solitary trichocyte (T) (scale bar = 15 µm).

Fig. 3. The thallus surface showing relatively thin walled epithallial cells and broad centrally located depressions (scale bar = 15 µm).

Fig. 4. The thallus surface showing variable types of epithallial cells and solitary trichocytes (T) (scale bar = 30 µm).

Fig. 5. A vertical fracture of the outer thallus showing a single epithallial cell (arrow), subepithallial initial (i) and cell fusions (f) (scale bar = 30 µm).

Fig. 6. A vertical fracture of the inner dimerous thallus showing the single basal layer (B) of non-palisade cells and cell fusions (f) (scale bar = 30 µm).

Pl. 3

Goniolithon boergesenii Foslie

Figs 7-10. Sporangial anatomy of the type of Goniolithon boergesenii Foslie.

Fig. 7. Surface view showing numerous sporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 8. A close-up of two sporangial conceptacles (arrows) showing their variable sizes (scale bar = 150 µm).

Fig. 9. A vertical fracture through a sporangial conceptacle showing the open un-infilled chamber (K) (scale bar = 100 µm).

Fig. 10. A vertical fracture through the pore canal (Pc) of a sporangial conceptacle showing the remnants of a ring of enlarged cells (arrow) at the base of the pore canal (scale bar = 30 µm).

Pl. 4

<u>Goniolithon boergesenii</u> Foslie

Figs 11-16. Vegetative anatomy of the type of <u>Goniolithon boergesenii</u> Foslie.

Fig. 11. A vertical section of the dimerous thallus showing a single epithallial cell layer (arrow), subepithallial initial (i), erect filament cell fusions (cf) and fusions between adjacent basal cells (bf) (scale bar = 30 µm).

Fig. 12. A vertical section of the outer thallus showing a single epithallial cell layer (e), subepithallial initial (i) and the first erect filament cell (c) (scale bar = 15 µm).

Fig. 13. A vertical section along the filaments of the basal layer showing the book-shaped basal cells (B) and the primary pit connections (arrows) (scale bar = 15 µm).

Fig. 14. A vertical section across the filaments of the basal layer showing the book-shaped basal cells, their primary pit connections (arrow) and the cell fusions between adjacent basal cells (bf) (scale bar = 15 µm).

Fig. 15. A vertical section of the outer thallus showing a single epithallial cell layer (arrow) and a pair of trichocytes (T) at the surface (scale bar = 30 µm).

Fig. 16. A section through the thallus showing solitary (lower two) and paired (upper two) trichocytes buried in the thallus (scale bar = 30 µm).

Pl. 5

Goniolithon boergesenii Foslie

Figs 17-18. Sporangial anatomy of the type of Goniolithon boergesenii Foslie.

Fig. 17. A vertical section of a slightly raised sporangial conceptacle showing the open conceptacle chamber (K) (scale bar = 60 µm).

Fig. 18. A vertical section through the pore canal (Pc) of the sporangial conceptacle showing the ring of enlarged cells (arrow) at the base of the pore canal (scale bar = 15 µm).

Pl. 6

Goniolithon improcerum Foslie & Howe

Fig. 1. Habit of the type of Goniolithon improcerum Foslie & Howe.

Pl. 7

Goniolithon improcerum Foslie & Howe

Figs 2-7. Vegetative anatomy of the type of Goniolithon boergesenii Foslie.

Fig. 2. The thallus surface showing the applanate branches (D) in dorsal view (scale bar = 120 µm).

Fig. 3. The thallus surface showing a close-up of the applanate branches (scale bar = 60 µm).

Fig. 4. A dorsal view of a damaged surface viewed below the epithallial cells showing the relatively thin cell walls (arrowheads) and the primary pit connections (arrows) (scale bar = 15 µm).

Fig. 5. The surface view showing striated epithallial cells (scale bar = 15 µm).

Fig. 6. The thallus surface showing numerous small groups of trichocytes (arrows) (scale bar = 300 µm).

Fig. 7. A close-up of a group of trichocytes (scale bar = 60 µm).

Pl. 8

Goniolithon improcerum Foslie & Howe

Figs 8-11. Tetrasporangial anatomy of the type of *Goniolithon improcerum* Foslie & Howe.

Fig. 8. Surface view of the thallus showing numerous tetrasporangial conceptacles (arrowheads) (scale bar = 860 µm).

Fig. 9. A close-up of the surface view of the thallus showing tetrasporangial conceptacle pores (arrows) in greater detail. Note the numerous grazing scars on the surface (scale bar = 200 µm).

Fig. 10. A close-up of an individual tetrasporangial conceptacle (arrow) (scale bar = 120 µm).

Fig. 11. A vertical fracture through a tetrasporangial conceptacle showing the open, un-infilled chamber (K) and the pore canal (p) (scale bar = 60 µm).

Pl. 9

Goniolithon improcerum Foslie & Howe

Figs 12-17. Vegetative and reproductive anatomy of the type of *Goniolithon improcerum* Foslie & Howe.

Fig. 12. The system of applanate branching showing solitary and small groups of trichocytes (T). Note how the trichocytes end abruptly at their dorsal ends and the remains of the hairs that stain darkly still visible (arrowheads) (scale bar = 60 µm).

Fig. 13. A vertical section through a single applanate branch showing the single epithallial layer (arrows), subepithallial initial (i), non-palisade basal cell (b) and a solitary buried trichocyte (T) (scale bar = 30 µm).

Fig. 14. A close-up of a series of successive filaments showing the single epithallial layer (e), subepithallial initials (i), non-palisade basal cell (b), and cell fusion between adjacent filaments (f) (scale bar = 15 µm).

Fig. 15. A vertical section showing the bistratose margin with terminating marginal initial (arrowhead), single epithallial layer (e) and single basal layer (b) (scale bar = 15 µm).

Fig. 16. A single raised tetrasporangial conceptacle showing and open un-infilled chamber (K) and peripherally located tetrasporangia (arrows) (scale bar = 60 µm).

Fig. 17. A vertical section through the pore (P) of the tetrasporangial conceptacle showing the enlarged cell (E) that lines the pore canal (scale bar = 15 µm).

Pl. 10

Lithophyllum aequinoctiale Foslie

Fig. 1. Habit of the type of Lithophyllum aequinoctiale Foslie (scale bar = 20 mm).

Pl. 11

Lithophyllum aequinoctiale Foslie

Fig. 2-8. Vegetative anatomy of the type of Lithophyllum aequinoctiale Foslie.

Fig. 2. The thallus surface showing thick epithallial cell walls (arrowheads) surrounding relatively narrow epithallial concavities bearing visible primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. Vertical fracture of the margin (arrow) showing epithallial cells (arrowhead), cortical (C) and medullary filaments (M) (scale bar = 120 µm).

Fig. 4. Vertical fracture of the thallus showing epithallial cells (arrowhead), cortical (C) and medullary filaments (M) (scale bar = 120 µm).

Fig. 5. Thallus surface showing a pustulate trichocyte field (T) (scale bar = 60 µm).

Fig. 6. Vertical fracture of the outer thallus showing multiple epithallial cell layers (arrowheads), a somewhat squat subepithallial initial (arrow) and cell fusions (f) (scale bar = 30 µm).

Fig. 7. Vertical fracture of the thallus surface through a pustulate trichocyte field (scale bar = 60 µm).

Fig. 8. Vertical fracture of the inner thallus showing cortical filaments (C) and plumose medullary filaments (M) (scale bar = 30 µm).

Pl. 12

Lithophyllum aequinoctiale Foslie

Figs 9-10. Spermatangial conceptacle anatomy of the type of Lithophyllum aequinoctiale Foslie.

Fig. 9. Surface view showing numerous flush to only slightly raised spermatangial conceptacles (arrows) (scale bar = 860 µm).

Fig 10. An individual slightly raised spermatangial conceptacle (arrow) (scale bar = 150 µm).

Pl. 13

Lithophyllum aequinoctiale Foslie

Figs 11-15. Vegetative and spermatangial anatomy of the type of Lithophyllum aequinoctiale Foslie.

Fig. 11. Vertical section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and cell fusion (f) (scale bar = 15 µm).

Fig. 12. A vertical section through a trichocyte field (T) at the thallus surface showing a solitary intact hair (arrow) (scale bar = 30 µm).

Fig. 13. Vertical section of the cortical filaments showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 14. A vertical fracture of a spermatangial conceptacle (K) showing simple spermatangia restricted to the conceptacle floor (arrowheads) (scale bar = 30 µm).

Fig. 15. A close-up of the spermatangial conceptacle showing the simple spermatangia located on the conceptacle floor (arrowheads) (scale bar = 15 µm).

Pl. 14

Lithophyllum africanum Foslie

Figs 1-8. Vegetative anatomy of type of the type of Lithophyllum africanum Foslie.

Fig. 1. The thallus surface showing thin epithallial cell walls (arrowheads) surrounding broad epithallial concavities bearing visible primary pit connections (arrows) (scale bar = 15 µm).

Fig. 2. A close-up of the thallus surface showing the thin epithallial cell walls (arrowheads) surrounding broad epithallial concavities bearing visible primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing a large pustulate trichocyte field (scale bar = 60 µm).

Fig. 4. A vertical fracture through a large pustulate trichocyte field at the thallus surface (scale bar = 60 µm).

Fig. 5. A vertical fracture through a relatively thick margin (arrows) showing cortical filaments (C) and plumose medullary filaments (M) (scale bar = 500 µm).

Fig. 6. A vertical fracture through the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initials (i), first cortical cell (c) and cell fusions between adjacent cortical filaments (f) (scale bar = 30 µm).

Fig. 7. A vertical fracture through plumose medullary filaments showing extensive cell fusions between adjacent filaments (f) (scale bar = 30 µm).

Fig. 8. A vertical fracture through the inner thallus showing terminating epithallial cells (arrowheads) (scale bar = 30 µm).

Pl. 15

Lithophyllum africanum Foslie

Figs 9-14. Tetrasporangial anatomy of the type of Lithophyllum africanum Foslie.

Fig. 9. The thallus surface showing numerous tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 10. A close-up of the thallus surface showing flush to only slightly raised tetrasporangial conceptacles (arrows) (scale bar = 300 µm).

Fig. 11. A vertical fracture through a protuberance showing tetrasporangial conceptacles buried just below the thallus surface (scale bar = 1200 µm).

Fig. 12. A vertical fracture of the outer thallus showing a buried tetrasporangial conceptacle (k) and buried trichocyte fields (arrows) (scale bar = 200 µm).

Fig. 13. A vertical fracture of the outer thallus showing a buried tetrasporangial conceptacle bearing remnants of a central columella (c) (scale bar = 120 µm).

Fig. 14. A vertical fracture of the outer thallus showing a somewhat flush tetrasporangial conceptacle with exposed pore (arrow) and open, un-infilled chamber (K) (scale bar = 120 µm).

Pl. 16

Lithophyllum africanum Foslie

Figs 15-17. Vegetative anatomy of the type of Lithophyllum africanum Foslie.

Fig. 15. A vertical section of the outer thallus showing multiple epithallial cell layers (e), subepithallial initial (i), first cortical cell (c) and cell fusions between adjacent cortical filaments (f) (scale bar = 15 µm).

Fig. 16. A vertical section of the outer thallus showing a large trichocyte field (T) (scale bar = 15 µm).

Fig. 17. A vertical section of the cortical filaments showing buried trichocyte fields (T) (scale bar = 60 µm).

Pl. 17

Lithophyllum africanum Foslie

Figs. 18-22. Tetrasporangial anatomy of the type of Lithophyllum africanum Foslie.

Fig. 18. A vertical section through a slightly raised tetrasporangial conceptacle showing the pore (arrow) and the open, un-infilled chamber (K) (scale bar = 60 µm).

Fig. 19. A vertical section through a sunken tetrasporangial conceptacle showing intact tetrasporangia (arrows) (scale bar = 60 µm).

Fig. 20. A vertical section through the pore canal of a tetrasporangial conceptacle showing papillate cells (arrows) lining, and projecting slightly into the pore canal (scale bar = 15 µm).

Fig. 21. A vertical fracture through a tetrasporangial conceptacle showing the orientation of the conceptacle roof filaments (arrows) and their apparent origination from the periphery (scale bar = 30 µm).

Fig. 22. A close-up of the tetrasporangial conceptacle roof showing the orientation of the conceptacle roof filaments (arrows) and their apparent origination from the periphery (scale bar = 15 µm).

Pl. 18

Lithophyllum antillarum Foslie et Howe (BM isotype)

Fig.1. Habit of the type of Lithophyllum antillarum Foslie et Howe (BM isotype). A. Dorsal view. B. Lateral view.

Pl. 19

Lithophyllum antillarum Foslie et Howe (BM isotype)

Figs 2-8. Vegetative anatomy of the type of Lithophyllum antillarum Foslie et Howe (BM isotype).

Fig. 2. The thallus surface showing thin to thick walled epithallial cells (arrowheads) with shallow concave centers and primary pit connections (arrows) still intact (scale bar = 15 µm).

Fig. 3. The thallus surface showing a large pustulate trichocyte field (scale bar = 60 µm).

Fig. 4. A vertical fracture of the margin (arrow) showing epithallial cells (arrowhead), cortical (C) and medullary filaments (M) (scale bar = 150 µm).

Fig. 5. A vertical fracture of the outer thallus showing a pustulate trichocyte field (T) at the surface and trichocytes buried in the thallus, multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 6. A vertical fracture of the thallus showing cortical filaments (C), medullary filaments (M) and a trichocyte field (T) at the surface (scale bar = 120 µm).

Fig. 7. A vertical fracture of the inner thallus showing extensive cell fusions between (f) adjacent medullary filaments (scale bar = 30 µm).

Fig. 8. A vertical fracture of the medullary filaments showing extensive cell fusions between (f) adjacent filaments (scale bar = 30 µm).

Pl. 20

Lithophyllum antillarum Foslie et Howe (BM isotype)

Figs 9-13. Carposporangial conceptacle anatomy of the type of Lithophyllum antillarum Foslie et Howe (BM isotype).

Fig. 9. The surface view showing numerous carposporangial conceptacles (arrows). Note the large number of grazing scars at the surface (scale bar = 1200 µm).

Fig. 10. A close-up of a single raised carposporangial conceptacle (arrow). Note the large number of grazing scars at the surface (scale bar = 150 µm).

Fig. 11. A close-up of a single flush carposporangial conceptacle (arrow) (scale bar = 150 µm).

Fig. 12. A vertical fracture of the thallus showing sunken carposporangial conceptacles (scale bar = 100 µm).

Fig. 13. A close-up of the pore canal showing the small papillate filaments (arrows) lining the pore canal (scale bar = 30 µm).

Pl. 21

Lithophyllum antillarum Foslie et Howe (BM isotype)

Figs 14-20. The vegetation anatomy of the type of Lithophyllum antillarum Foslie et Howe (BM isotype).

Fig. 14. A vertical section of the margin (arrow) (scale bar = 120 µm).

Fig. 15. A vertical section of the outer thallus showing a trichocyte field (T) (scale bar = 30 µm).

Fig. 16. A vertical section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i) and first cortical cell (C) (scale bar = 15 µm).

Fig. 17. A section of the cortical filaments showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 18. A section of the protuberance showing predominantly coaxial medullary filaments with extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Fig. 19. A close-up of plumose medullary filaments showing cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 20. A vertical section of the inner thallus showing terminal epithallial cells (arrowheads) (scale bar = 15 µm).

Pl. 22

Lithophyllum antillarum Foslie et Howe (BM isotype)

Figs 21-23. The reproductive anatomy of the type of Lithophyllum antillarum Foslie et Howe (BM isotype).

Fig. 21. A vertical section of a raised carposporangial conceptacle (scale bar = 60 µm).

Fig. 22. A vertical section of the thallus showing buried tetrasporangial conceptacles with open, un-infilled chambers (k) (scale bar = 120 µm).

Fig. 23. A section of a tetrasporangial conceptacle pore canal (P) showing an enlarged cell (arrow) located at the base of the pore canal (scale bar = 15 µm).

Fig. Insert. A single tetrasporangium (scale bar = 15 µm).

Pl. 23

Lithophyllum antillarum Foslie et Howe (TRH isotype)

Fig. 1. Habit of the type Lithophyllum antillarum Foslie et Howe (TRH isotype) (scale bar = 20 mm).

Pl. 24

Lithophyllum antillarum Foslie et Howe (TRH isotype)

Figs 2-8. Vegetative anatomy of the type of Lithophyllum antillarum Foslie et Howe (TRH isotype).

Fig. 2. Fragment remains of the surface of Lithophyllum antillarum Foslie et Howe (TRH isotype) showing relatively thin walled epithallial cells (arrowheads) with shallow concave centers and primary pit connections (arrows) still intact (scale bar = 15 µm).

Fig. 3. The thallus surface showing a large pustulate trichocyte field (scale bar = 60 µm).

Fig. 4. A vertical fracture through a pustulate trichocyte field (arrow) (scale bar = 60 µm).

Fig. 5. A vertical fracture of the thallus showing buried trichocyte fields (arrows) (scale bar = 150 µm).

Fig. 6. A vertical fracture of the margin (arrow) showing the epithallial cell layer (arrowhead) (scale bar = 60 µm).

Fig. 7. A vertical fracture of the outer thallus showing multiple epithallial cell layers (arrow) and cell fusions (arrowheads) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 8. A vertical fracture of the inner thallus showing cells of cortical filaments (C) and plumose medullary filaments (M) (scale bar = 30 µm).

Pl. 25

Lithophyllum antillarum Foslie et Howe (TRH isotype)

Figs 9-12. Tetrasporangial anatomy of the type of Lithophyllum antillarum Foslie et Howe (TRH isotype).

Fig. 9. The surface view of Lithophyllum antillarum Foslie et Howe (TRH isotype) showing a single intact tetrasporangial conceptacle (arrow) (scale bar = 860 µm). Note the numerous grazing scars.

Fig. 10. A close-up of a single more-or-less flush tetrasporangial conceptacle (arrow) (scale bar = 300 µm).

Fig. 11. A vertical fracture of a shallow buried tetrasporangial conceptacle (scale bar = 120 μm).

Fig. 12. A close-up of the tetrasporangia (scale bar = 30 μm).

Pl. 26

Lithophyllum antillarum Foslie et Howe (TRH isotype)

Figs 13-18. Vegetative anatomy of the type of Lithophyllum antillarum Foslie et Howe (TRH isotype).

Fig. 13. A vertical section of a thallus sectioned at a right angle to the growing thallus showing the epithallial cell layer (arrowhead) and an extremely thin basal region, giving a false impression of being dimerous (arrow) (scale bar = 30 μm).

Fig. 14. A vertical section through a pustulate trichocyte field (T). Note how the trichocytes end abruptly at their dorsal ends and the remains of the hairs that stain darkly still visible (arrowheads) (scale bar = 30 μm).

Fig. 15. A vertical section of the inner thallus showing buried trichocyte fields (arrows) (scale bar = 60 μm).

Fig. 16. A section of the outer thallus showing multiple epithallial cell layers (arrowheads), an undivided subepithallial initial (i), a recently divided subepithallial initial (arrows) and first cortical cell (c) (scale bar = 15 μm).

Fig. 17. A section of a monomerous thallus showing plumose medullary filaments with cell fusions (f) between adjacent filaments (scale bar = 15 μm).

Fig. 18. A magnified view of the thallus sectioned at a right angle to the growing thallus showing an extremely thin basal region, giving a false impression of being dimerous (arrowheads) (scale bar = 15 μm).

Pl. 27

Lithophyllum antillarum Foslie et Howe (TRH isotype)

Figs 19-22. Tetrasporangial anatomy of the type of Lithophyllum antillarum Foslie et Howe (TRH isotype).

Fig. 19. A vertical section of a slightly raised tetrasporangial conceptacle showing exposed pore canal (P), open, un-infilled chamber (K) and peripherally located tetrasporangia (scale bar = 60 µm).

Fig. Insert. A single tetrasporangium (scale bar = 15 µm).

Fig. 20. A vertical fracture of a buried tetrasporangial conceptacle showing exposed pore canal (arrow), open, un-infilled chamber (K) and small central columella (arrowhead) (scale bar = 60 µm)

Fig. 21. A close-up of the tetrasporangial conceptacle pore canal showing the enlarged cells (arrows) located at the base of the pore canal (scale bar = 15 µm).

Fig. 22. Through secondary overgrowth, buried conceptacles may bear papillate cells (arrows) along their pore canals (scale bar = 15 µm).

Pl. 28

Lithophyllum coarctatum Foslie

Fig. 1. Habit of the type of Lithophyllum coarctatum Foslie (scale bar = 20 mm).

Pl. 29

Lithophyllum coarctatum Foslie

Figs 2-7. Vegetative anatomy of the type of Lithophyllum coarctatum Foslie.

Fig. 2. The thallus surface showing thin walled epithallial cells (arrowheads) with shallow central concavities bearing intact to broadened primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing epithallial cells with intact primary pit plugs (arrows) (scale bar = 15 µm). Note the single epithallial cell with a convex outer surface.

Fig. 4. The thallus surface showing a single large pustulate trichocyte field (scale bar = 60 µm).

Fig. 5. A vertical fracture through a single large pustulate trichocyte field (arrow) (scale bar = 60 µm).

Fig. 6. A vertical fracture of the outer thallus showing epithallial cells (arrowheads) and buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 7. A fracture of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and a buried trichocyte field (T) (scale bar = 30 µm).

Pl. 30

<u>Lithophyllum coarctatum</u> Foslie

Figs 8-12. The tetrasporangial anatomy of the type of Lithophyllum coarctatum Foslie.

Fig. 8. The surface showing numerous slightly raised tetrasporangial conceptacle (arrows) (scale bar = 860 µm).

Fig. 9. A single raised tetrasporangial conceptacle (arrow) (scale bar = 120 µm).

Fig. 10. A vertical fracture through a raised tetrasporangial conceptacle showing exposed pore canal (arrow) and open, un-infilled chamber (K) (scale bar = 120 µm).

Fig. 11. A fracture through a shallow sunken tetrasporangial conceptacle showing a degree on infilling (K) (scale bar = 120 µm).

Fig. 12. A fracture through the pore canal of a tetrasporangial conceptacle showing the remnants of a ring of enlarged cells (arrowheads) at the base of the pore canal (scale bar = 30 µm).

Pl. 31

Lithophyllum coarctatum Foslie

Figs 13-16. Vegetative anatomy of the type of Lithophyllum coarctatum Foslie.

Fig. 13. A vertical section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i) and first cortical cell (c) (scale bar = 15 µm).

Fig. 14. A section through coaxial medullary filament of a protuberance showing extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 15. A vertical section through a crustose portion of the thallus showing the monomerous construction comprising plumose medullary filaments with cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 16. A vertical section of the outer thallus through a pustulate trichocyte field (T) (scale bar = 30 µm).

Pl. 32

Lithophyllum coarctatum Foslie

Figs 17-19. The tetrasporangial anatomy of the type of Lithophyllum coarctatum Foslie.

Fig. 17. A vertical section through a raised tetrasporangial conceptacle showing an exposed pore canal (P) and an open, un-infilled chamber (K) (scale bar = 60 µm).

Fig. 18. A vertical section through a buried tetrasporangial conceptacle showing an exposed pore canal (P) and an open, un-infilled chamber (K) (scale bar = 60 µm).

Fig. Insert. A single tetrasporangium (scale bar = 15 µm).

Fig. 19. A vertical section through the pore canal of a tetrasporangial conceptacle showing a ring of enlarged cells (arrows) at the base of the pore canal (scale bar = 15 µm).

Pl. 33

Lithophyllum craspedium Foslie

Figs 1-7. Vegetative anatomy of the type of Lithophyllum craspedium Foslie.

Fig. 1. The thallus surface showing variably thin to thick walled epithallial cells (arrowheads) with deeply concave centres (arrows) (scale bar = 15 µm).

Fig. 2. The thallus surface showing numerous scattered pustulate trichocyte fields (arrows) (scale bar = 300 µm).

Fig. 3. The thallus surface showing a single large pustulate trichocyte field (T) (scale bar = 60 µm).

Fig. 4. A vertical fracture of the thallus showing buried trichocyte fields (arrows) (scale bar = 150 µm).

Fig. 5. A vertical fracture of the thallus showing epithallial cells (arrows), cortical (C) and medullary filaments (M) (scale bar = 60 µm).

Fig. 6. A vertical fracture of the outer thallus showing epithallial cells (arrow), subepithallial initial (i), first cortical cell (c) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 7. A vertical fracture of plumose medullary filaments with extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Pl. 34

Lithophyllum craspedium Foslie

Figs 8-12. Tetrasporangial anatomy of the type of Lithophyllum craspedium Foslie.

Fig. 8. The thallus surface showing numerous flush to slightly raised tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 9. A view of a single raised tetrasporangial (arrow) conceptacle (scale bar = 120 µm).

Fig. 10. A vertical fracture of a raised tetrasporangial conceptacle showing an exposed pore canal (arrow) and open, un-infilled chamber (K) (scale bar = 120 µm).

Fig. 11. A close-up of the tetrasporangia (arrows) (scale bar = 30 µm).

Fig. 12. A vertical fracture of the pore canal (P) of a typical tetrasporangial conceptacle showing the remnants of large cells (arrows) lining the base of the pore canal (scale bar = 30 µm).

Pl. 35

Lithophyllum craspedium Foslie

Figs 13-16. The vegetative anatomy of the type of Lithophyllum craspedium Foslie.

Fig. 13. A vertical section of the thallus showing epithallial cells (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 60 µm).

Fig. 14. A vertical section of the outer thallus showing multiple epithallial cell layers being shed (arrow), a single intact epithallial layer (e), the subepithallial initial (i), the first cortical cell (c), a trichocyte (T) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 15 µm).

Fig. 15. A vertical section of the cortical filaments showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 16. A vertical section of the plumose medullary filaments showing a cell fusion (f) between two adjacent filaments (scale bar = 15 µm).

Pl. 36

Lithophyllum craspedium Foslie

Figs 17-21. The tetrasporangial anatomy of the type of Lithophyllum craspedium Foslie.

Fig. 17. A vertical section of the thallus showing a slightly raised tetrasporangial conceptacles with its exposed pore canal (arrow) at the surface, and another tetrasporangial conceptacle buried within the thallus; both conceptacles have open, un-infilled chambers (K) (scale bar = 150 µm).

Fig. 18. A vertical section of a raised tetrasporangial conceptacle showing its exposed pore canal (arrow), open, un-infilled chamber (K) and more-or-less peripherally arranged tetrasporangia (arrowheads) (scale bar = 30 µm).

Fig. 19. A vertical fracture of the tetrasporangial conceptacle roof showing the more-or-less vertical arrangement of the roof filaments (scale bar = 30 µm).

Fig. 20. A vertical section of a tetrasporangial conceptacle pore canal (P) showing the large cell (arrowhead) at the base of the pore canal subtending narrow pore filaments that may or may not tilt slightly into the pore canal and create the appearance of papillae (scale bar = 15 µm).

Fig. 21. A vertical section of a tetrasporangial conceptacle pore canal (P) showing an intact pore canal filament with a large cell (E) at its base (scale bar = 15 µm).

Pl. 37

Hydrolithon craspedium (Foslie) P. Silva

Fig. 1. The general habit of Hydrolithon craspedium (Foslie) P. Silva (UWC: 94/1112).

Fig. 1A. The habit of a representative specimen of Hydrolithon craspedium (Foslie) P. Silva.

Fig. 1B. Stages in the development (left to right, top to bottom) of Hydrolithon craspedium (Foslie) P. Silva (scales = 50 mm). Thalli thicken up early in development and become distinct forming massive, mountain-like upgrowths bearing broad solitary to fused vertical columns.

Pl. 38

Hydrolithon craspedium (Foslie) P. Silva

Figs 2-7. The vegetative anatomy of Hydrolithon craspedium (Foslie) P. Silva (UWC: 94/1280).

Fig. 2. The thallus surface showing a range of cell types bearing thin (arrowheads) to thick cell walls with broad to relatively narrow concavities respectively, to cells that are completely convex (arrows) with distinct primary pit connections still intact. Some cells still bear intact primary pit plugs (scale bar = 15 µm).

Fig. 3. The thallus surface showing a single large pustulate trichocyte field (scale bar = 60 µm).

Fig. 4. A vertical fracture of the outer thallus showing trichocyte fields (T) both at the surface and buried in the thallus (scale bar = 60 µm).

Fig. 5. A vertical fracture of a free, scrolled margin (scale bar = 300 µm).

Fig. 6. A vertical fracture of the outer thallus showing multiple epithallial cell layers (arrowheads), the subepithallial initial (i), the first cortical cell (c) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 7. A vertical fracture of the lower portion of the thallus showing plumose medullary filaments (scale bar = 30 µm).

Pl. 39

Hydrolithon craspedium (Foslie) P. Silva

Figs 8-12. The tetrasporangial anatomy of Hydrolithon craspedium (Foslie) P. Silva (UWC: 94/1280).

Fig. 8. The thallus surface showing numerous flush to only slightly raised tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 9. A close-up of a single, slightly raised, tetrasporangial conceptacle (arrow) (scale bar = 150 µm).

Fig. 10. A vertical fracture of the thallus showing a slightly raised tetrasporangial conceptacle with an open, un-infilled chamber (K) (scale bar = 120 µm).

Fig. 11. A vertical fracture of the thallus showing buried tetrasporangial conceptacles (k) and trichocyte fields (arrows) (scale bar = 200 µm).

Fig. Insert. A single tetrasporangium (arrow) (scale bar = 15 µm).

Fig. 12. A vertical fracture through the pore (P) of a buried tetrasporangial conceptacle showing the remnants of the enlarged cells (arrowheads) that typically line the pore canal (scale bar = 30 µm).

Pl. 40

Hydrolithon craspedium (Foslie) P. Silva

Figs. 13-14. The vegetative anatomy of Hydrolithon craspedium (Foslie) P. Silva (UWC: 94/1176).

Fig. 13. A vertical section of the outer thallus showing a single large pustulate trichocyte field (arrowheads) (scale bar = 30 µm).

Fig. 14. A vertical section of the outer thallus showing multiple epithallial cell layers (arrowheads), the subepithallial initial (i), the first cortical cell (c) and a cell fusion between three adjacent cortical filaments (scale bar = 15 µm).

Pl. 41

Hydrolithon craspedium (Foslie) P. Silva

Figs 15-19. The tetrasporangial anatomy of Hydrolithon craspedium (Foslie) P. Silva (UWC: 94/1176).

Fig. 15. A vertical section showing a flush tetrasporangial conceptacle with slightly occluded pore (P), open, un-infilled chamber (K), peripherally located tetrasporangia (arrowheads), and small central columella (arrow) (scale bar = 60 µm).

Fig. 16. A section of the thallus showing a buried tetrasporangial conceptacle with peripherally located tetrasporangia and central columella (arrow) (scale bar = 60 µm).

Fig. 17. A vertical fracture of a tetrasporangial conceptacle showing peripherally located tetrasporangia (arrows) (scale bar = 30 µm).

Fig. 18. A vertical fracture of a tetrasporangial pore canal (P) and roof showing the absence of the large cell (arrow) lining the base of the pore canal (scale bar = 15 µm).

Fig. 19. A vertical fracture of a tetrasporangial pore canal (P) and roof showing the presence of a large cell (arrowhead) lining the base of the pore canal (scale bar = 15 µm).

Pl. 42

Lithophyllum dentatum f. sandvicensis Foslie

Figs 1-6. Vegetative anatomy of the type of Lithophyllum dentatum f. sandvicensis Foslie.

Fig. 1. The thallus surface showing relatively thin walled epithallial cells (arrowheads) with broad shallow concave centres (arrows) (scale bar = 15 µm).

Fig. 2. The thallus surface showing a single large pustulate trichocyte field (scale bar = 60 µm).

Fig. 3. A vertical fracture of the thallus showing a single large pustulate trichocyte field at the surface (T) and a trichocyte field buried in the thallus (arrow) (scale bar = 60 µm).

Fig. 4. A vertical fracture of a single thallus lobe showing inner and outer cortical (C) and medullary filaments (M) (scale bar = 500 µm).

Fig. 5. A vertical fracture of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initials (i), first cortical cell (c) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 6. A vertical fracture through the plumose medullary filaments showing extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Pl. 43

Lithophyllum dentatum f. sandvicensis Foslie

Figs 7-11. The tetrasporangial anatomy of the type of Lithophyllum dentatum f. sandvicensis Foslie.

Fig. 7. The thallus surface showing numerous flush to only slightly raised tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 8. A close-up of a single raised tetrasporangial conceptacle (arrow). (scale bar = 120 µm)

Fig. 9. A vertical fracture through the chamber (K) of a tetrasporangial conceptacle (scale bar = 90 µm).

Fig. 10. A close-up of the tetrasporangia (arrows) (scale bar = 30 µm).

Fig. 11. A vertical fracture of the tetrasporangial conceptacle roof showing remnants of large cells (arrowheads) lining the base of the pore canal (scale bar = 30 µm).

Pl. 44

Lithophyllum dentatum f. sandvicensis Foslie

Figs 12-17. The vegetative anatomy of the type of Lithophyllum dentatum f. sandvicensis Foslie.

Fig. 12. A vertical section of the margin (arrowhead) showing epithallial cells (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 30 µm).

Fig. 13. A vertical section of the thallus showing a single large trichocyte field (T) (scale bar = 30 µm).

Fig. 14. A vertical section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and cell fusions (f) between adjacent cortical filaments (scale bar = 15 µm).

Fig. 15. A vertical section of the thallus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 16. A vertical section of a multi-layered, plumose medullary region showing extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 17. A vertical section of the inner thallus showing a 1-3 layered, plumose medullary region (M) showing extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Pl. 45

Lithophyllum dentatum f. *sandvicensis* Foslie

Figs 18-23. The tetrasporangial anatomy of the type of *Lithophyllum dentatum* f. sandvicensis Foslie.

Fig. 18. A vertical section of the thallus showing a wedge-shaped species of coralline (arrows) embedded in the thallus of *Lithophyllum dentatum* f. *sandvicensis* Foslie (scale bar = 30 µm).

Fig. 19. A vertical section of a raised tetrasporangial conceptacle showing an exposed pore canal (arrow) and an open, un-infilled chamber (K) (scale bar = 60 µm).

Fig. 20. A vertical section of a flush tetrasporangial conceptacle showing showing an exposed pore canal (P), an open, un-infilled chamber (K) and a small central columella (arrow) (scale bar = 30 µm).

Fig. 21. A vertical section of the outer thallus showing a raised tetrasporangial conceptacle at the surface with its exposed pore canal (arrow) and open, un-infilled chamber (K), and a sunken conceptacle with peripheral tetrasporangia (arrowheads) and open, un-infilled chamber (K) (scale bar = 60 µm).

Fig. Insert. A single tetrasporangium (scale bar = 15 µm).

Fig. 22. A vertical section of the pore canal (P) showing enlarged cells (E) lining the base of the pore canal (scale bar = 15 µm).

Fig. 23. A vertical section of the outer thallus showing a partly infilled (arrows) tetrasporangial conceptacle (scale bar = 60 µm).

Pl. 46

Lithophyllum gardineri Foslie

Fig. 1. The habit of the type of Lithophyllum gardineri Foslie.

Pl. 47

Lithophyllum gardineri Foslie

Figs 2-8. The vegetative anatomy of the type of Lithophyllum gardineri Foslie.

Fig. 2. The surface of the thallus showing relatively thick walled epithallial cells (arrowheads) with broad to narrow shallow concave centres (arrows) (scale bar = 15 µm).

Fig. 3. The surface of the thallus showing a single large pustulate trichocyte field (T) (scale bar = 60 µm).

Fig. 4. A vertical fracture of the thallus showing epithallial cells (arrow), cortical (C) and medullary filaments (M) (scale bar = 300 µm).

Fig. 5. A vertical fracture through a single large pustulate trichocyte field (arrow) (scale bar = 60 µm).

Fig. 6. A vertical fracture of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 7. A vertical fracture of the inner portion of the thallus showing the plumose medullary filaments terminating in inner epithallial cells (arrowheads) and showing extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Fig. 8.A vertical fracture of the plumose medullary filaments showing extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Pl. 48

Lithophyllum gardineri Foslie

Figs 9-14. Vegetative and tetrasporangial anatomy of the type of Lithophyllum gardineri Foslie.

Fig. 9. A vertical fracture of the margin (arrowhead) showing cortical (C) and medullary filaments (M) (scale bar = 200 µm).

Fig. 10. A vertical fracture of a regenerated margin (arrowhead) showing epithallial cells (arrowhead), cortical (C) and medullary filaments (M) (scale bar = 60 µm).

Fig. 11. A close-up of a single slightly raised tetrasporangial conceptacle (arrow) (scale bar = 120 µm).

Fig. 12. A vertical fracture of the thallus showing a buried tetrasporangial conceptacle (K) (scale bar = 200 µm).

Fig. 13. A vertical fracture of the outer thallus showing a flush tetrasporangial conceptacle with exposed pore canal (arrow) and open, un-infilled chamber (K) (scale bar = 90 µm).

Fig. 14. A vertical fracture of the tetrasporangial pore canal (Pc) with remnants of the enlarged cells (arrowheads) that typically line the base of the pore canal (scale bar = 30 µm).

Pl. 49

Lithophyllum gardineri Foslie

Figs 15-21. The vegetative anatomy of the type of Lithophyllum gardineri Foslie.

Fig. 15. A vertical section of the thallus showing recently shed epithallial cell layers (arrowhead), intact epithallial cells (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 60 µm).

Fig. 16. A vertical section of the outer thallus showing a single large trichocyte field (scale bar = 30 µm).

Fig. 17. A vertical section of the thallus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 18. A section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and a buried trichocyte field (T) (scale bar = 15 µm).

Fig. 19. A section of coaxial medullary filaments from a protuberance showing extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 20. A section of the inner thallus (scale bar = 15 µm).

Fig. 21. A section of plumose medullary filaments showing extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Pl. 50

Lithophyllum gardineri Foslie

Figs 22-24. The tetrasporangial anatomy of the type of Lithophyllum gardineri Foslie.

Fig. 22. A vertical section of the thallus showing raised and flush tetrasporangial conceptacles at the surface (K) and a single buried conceptacle (k) (scale bar = 300 µm).

Fig. 23. A vertical section of a more-or-less flush tetrasporangial conceptacle showing an exposed pore canal (p) and an open, un-infilled chamber (K) (scale bar = 60 µm).

Fig. 24. A vertical section of the pore canal of a buried tetrasporangial conceptacle showing the presence of a ring of enlarged cells (E) located at the base of the pore canal (scale bar = 15 µm).

Pl. 51

Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine

Fig. 1. The general habit forms of Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine.

Pl. 52

Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine

Figs 2-6. The vegetative anatomy of Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine (UWC: 94/1178).

Fig. 2. A vertical section of the thallus showing epithallial cells (arrow), a pustulate trichocyte field (arrowhead), cortical (C) and medullary filaments (M) (scale bar = 120 µm).

Fig. 3. A vertical section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and cell fusions (f) (scale bar = 15 µm).

Fig. 4. A vertical section through a single large pustulate trichocyte field (scale bar = 30 µm).

Fig. 5. A vertical section of the plumose medullary filaments showing cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 6. A vertical section of the inner thallus showing downward curving filaments terminating in inner epithallial cells (arrowheads) (scale bar = 15 µm).

Pl. 53

Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine

Figs 7-12. The tetrasporangial anatomy of Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine (UWC: 94/1178).

Fig. 7. A vertical section of the thallus showing buried sporangial conceptacles (K) and trichocyte fields (arrows) (scale bar = 120 µm).

Fig. 8. A vertical section of a tetrasporangial conceptacle. Note the orientation of the roof filaments that are perpendicular to the thallus surface alluding to development of the roof from filaments interspersed among the sporangia (scale bar = 60 µm).

Fig. 9. A vertical section through the thallus showing buried tetrasporangia (arrows) (scale bar = 30 µm).

Fig. 10. A vertical section of a partially buried sporangial conceptacle showing an intact columella (arrow) (scale bar = 60 µm).

Fig. 11. A transverse section through a tetrasporangial conceptacle showing the peripheral orientation of tetrasporangia (arrowheads) around a central columella (C) (scale bar = 60 µm).

Fig. 12. A section through the pore canal (P) of a tetrasporangial conceptacle showing enlarged cells (arrows) located at the base of the pore canal (scale bar = 15 µm).

Pl. 54

Plate 1


1
Præp. 1371 af ældste ekspl. m/konc.
1368 og 1432 (skrap) af dette ekspl.
1426 af mindste ekspl.
Honolulu
Eugenia. Exp. (?)
Goniolithon (Hydrolithon)
[redacted]
breviclavium
[redacted]
Lith. Monogr. pl. 52
fig. 14-15
8 7 6 5 4 3 2 1 0 1 2 3 4 5 6 7 8 9 10

Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine

Figs 13-15. The spermatangial anatomy of <u>Hydrolithon gardineri</u> (Foslie) Verheij & Prud'homme van Reine (UWC: 94/1189; except Fig. 13).

Fig. 13. A monoecious thallus bearing both spermatangial (S) and carposporangial (C) conceptacles (scale bar = 150 µm). (UWC: 94/1178)

Fig. 14. A vertical section of a spermatangial conceptacle bearing simple restricted to the conceptacle floor (arrowheads) (scale bar = 30 µm).

Fig. 15. A close-up of the spermatangial conceptacle floor showing simple spermatangial (scale bar = 15 µm).

Pl. 55

<u>Hydrolithon gardineri</u> (Foslie) Verheij & Prud'homme van Reine

Figs 16-19. The female anatomy of <u>Hydrolithon gardineri</u> (Foslie) Verheij & Prud'homme van Reine (UWC: 94/1178).

Fig. 16. A vertical section through a carpogonial conceptacle (scale bar = 30 µm).

Fig. 17. A close-up of a carpogonial conceptacle showing carpognial branches across the conceptacle floor bearing terminal trichogynes (t) subtended by a carpogonial cell (C) (scale bar = 15 µm).

Fig. 18. A vertical section through a carposporangial conceptacle (scale bar = 30 µm).

Fig. 19. A close-up of the carposporangial conceptacle showing a thick and narrow central fusion cell (arrowhead) bearing unfertilized carpogonial branches (arrow) at its centre and gonimoblast filaments at its periphery. Gonimoblast filaments may comprise up to 9 cells excluding a terminal carpospore (C) (scale bar = 15 µm).

Pl. 56

Lithophyllum oligocarpum Foslie

Fig. 1. Microscope slides of the type of Lithophyllum oligocarpum Foslie (scale bar = 20 mm).

Pl. 57

Lithophyllum oligocarpum Foslie

Figs 2-9. The vegetative anatomy of the type of Lithophyllum oligocarpum Foslie.

Fig. 2. The thallus surface showing relatively thin walled epithallial cells (arrowheads) bearing broad, shallow concave centres with old primary pit connection still visible (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing a single large pustulate trichocyte field (scale bar = 60 µm).

Fig. 4. A vertical fracture of the thallus showing epithallial cells (arrowhead), cortical (C) and medullary filaments (M) (scale bar = 300 µm).

Fig. 5. A vertical fracture of the thallus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 6. A vertical fracture of free margin (arrow) showing epithallial (arrowhead), cortical (C) and medullary filaments (M) (scale bar = 300 µm).

Fig. 7. A vertical fracture of the outer thallus showing epithallial cells (arrowhead) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 8. A vertical fracture of the free margin showing the plumose medullary filaments (scale bar = 60 µm).

Fig. 9. A vertical fracture of the inner portion of the thallus showing plumose medullary filaments terminating in elongate inner epithallial cells (arrowheads) and bearing extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Pl. 58

Lithophyllum oligocarpum Foslie

Figs 10-13. The tetrasporangial anatomy of the type of Lithophyllum oligocarpum Foslie.

Fig. 10. The thallus surface showing numerous flush to slightly sunken tetrasporangial conceptacles (arrows) (scale bar = 860 μm).

Fig. 11. A close-up of a single flush tetrasporangial conceptacle (arrow) (scale bar = 150 μm).

Fig. 12. A vertical fracture of the thallus showing tetrasporangial conceptacles at the surface (arrow) and buried in the thallus (scale bar = 600 μm).

Fig. 13. A vertical fracture of the outer thallus showing two flush tetrasporangial conceptacles bearing exposed pore canals (arrows) and open, un-infilled chambers (K). Note the third completely infilled chamber (k) (scale bar = 120 μm).

Fig. Insert. A close-up of two tetrasporangia (scale bar = 30 μm).

Pl. 59

Lithophyllum oligocarpum Foslie

Figs 14-16. The vegetative anatomy of the type of Lithophyllum oligocarpum Foslie.

Fig. 14. A vertical section of the margin (arrow), epithallial layer (arrowhead), cortical (C) and medullary filaments (M) (scale bar = 30 μm).

Fig. 15. A vertical section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i) and first cortical cell (c) (scale bar = 15 μm).

Fig. 16. A vertical section of the plumose medullary filaments showing cell fusions (f) between adjacent filaments (scale bar = 15 μm).

Pl. 60

Lithophyllum oligocarpum Foslie

Figs 17-22. The tetrasporangial anatomy of the type of Lithophyllum oligocarpum Foslie.

Fig. 17. A vertical section of a raised tetrasporangial conceptacle showing an exposed pore canal (P), open, un-infilled chamber (K), and remnants of a central columella (arrow) (scale bar = 60 µm).

Fig. 18. A vertical section of the thallus showing two buried tetrasporangial conceptacles (K) with one of the two partly infilled (arrow) (scale bar = 150 µm).

Fig. 19. A section through a sporangial conceptacle showing both a tetra- (arrow) and bisporangium (arrowhead) (scale bar = 30 µm).

Fig. 20. A section through the pore canal of a buried sporangial conceptacle showing the presence of numerous papillate cells (arrows) lining the pore canal and orientated more-or-less parallel to the conceptacle roof (scale bar = 30 µm).

Fig. 21. A section through the sporangial conceptacle chamber and roof showing the orientation and probable origin of the roof filaments. Note the presence of an extensive central columella (C) (scale bar = 30 µm).

Fig. 22. A close-up section of the pore canal (P) and roof of a sporangial conceptacle showing the presence of numerous papillate cells (arrowheads) lining the pore canal and the orientation and probable origin of the roof filaments (arrows) (scale bar = 15 µm).

Pl. 61

Porolithon oligocarpum (Foslie) Foslie (UWC: 00-CI-01)

Fig. 1. The typical habit of Porolithon oligocarpum (Foslie) Foslie from the type locality in the Canary Islands (UWC: 00-CI-01) (scale bar = 20 mm).

Pl. 62

Porolithon oligocarpum (Foslie) Foslie (UWC: 00-CI-01)

Figs 2-7. The vegetation anatomy of Porolithon oligocarpum (Foslie) Foslie from the type locality in the Canary Islands (UWC: 00-CI-01).

Fig. 2. A vertical section of the margin (arrow) showing cortical filaments (C) and a thick plumose medullary region (M) (scale bar = 60 µm).

Fig. 3. A vertical section through a single large pustulate trichocyte field (T). Note how the trichocytes end abruptly at their dorsal ends and the remains of the hairs that stain darkly still visible (arrowheads) (scale bar = 30 µm).

Fig. 4. A vertical section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 5. A section of the thallus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 6. A section of the plumose medullary filaments showing extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 7. A section of the inner portion of the thallus showing the medullary filaments terminating in elongate to domed inner epithallial cells (arrowheads). A single cell fusion (f) is also visible (scale bar = 15 µm).

Pl. 63

Porolithon oligocarpum (Foslie) Foslie (UWC: 00-CI-01)

Figs 8-12. The tetrasporangial anatomy of Porolithon oligocarpum (Foslie) Foslie from the type locality in the Canary Islands (UWC: 00-CI-01).

Fig. 8. A section through a slightly raised tetrasporangial conceptacle showing a slightly occluded pore canal (P) and an open, un-infilled chamber (K) (scale bar = 60 µm).

Fig. 9. A section of the thallus showing numerous buried tetrasporangial conceptacles (K) two of which bear small central columellas (arrowheads) (scale bar = 150 µm).

Fig. 10. A section through the periphery of a tetrasporangial conceptacle showing the orientation and probable origination of the roof filaments (arrows) as well as a single peripheral tetrasporangium (t) (scale bar = 15 µm).

Fig. 11. A section of the tetrasporangial conceptacle roof showing papillate cells (arrowheads) lining the pore canal and orientated more-or-less parallel to the conceptacle roof, and the orientation and probable origination of the roof filaments (arrows) (scale bar = 30 µm).

Fig. 12. A close-up of the tetrasporangial conceptacle pore canal showing papillate cells (arrowheads) lining the pore canal (scale bar = 15 µm).

PL. 64

Lithophyllum onkodes f. pachydermum Foslie

Fig. 1. The habit of the type of Lithophyllum onkodes f. pachydermum Foslie.

Pl. 65

Lithophyllum onkodes f. pachydermum Foslie

Figs 2-9. The vegetation anatomy of the type of Lithophyllum onkodes f. pachydermum Foslie.

Fig. 2. The thallus surface showing relatively thin walled epithallial cells (arrowheads) with broad concave centres bearing intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing a single large pustulate trichocyte field (scale bar = 60 µm).

Fig. 4. A vertical fracture of the thallus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 5. A vertical fracture of the surface through a single large pustulate trichocyte field (scale bar = 60 µm).

Fig. 6. A vertical fracture of the margin (arrow) showing epithallial cells (arrowhead), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 75 µm).

Fig. 7. A vertical fracture of the outer thallus showing epithallial cells (arrowhead) and buried a trichocyte field (arrow) (scale bar = 30 µm).

Fig. 8. A vertical fracture of the thallus showing epithallial cells (arrowhead), cortical filaments (C), medulla filaments (M) and a buried trichocyte field (scale bar = 120 µm).

Fig. 9. A vertical fracture of the inner portion of the thallus showing plumose medullary filaments with extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Pl. 66

Lithophyllum onkodes f. pachydermum Foslie

Figs 10-14. The tetrasporangial anatomy of the type of Lithophyllum onkodes f. pachydermum Foslie.

Fig. 10. The thallus surface showing numerous flush tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 11. A close-up of a single slightly raised tetrasporangial conceptacle (arrow) (scale bar = 150 µm).

Fig. 12. A close-up of a single flush tetrasporangial conceptacle (arrow) (scale bar = 120 µm).

Fig. 13. A vertical fracture of the thallus showing numerous buried tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 14. A fracture through a single buried tetrasporangial conceptacle showing tetrasporangia (arrows) (scale bar = 60 μm).

Pl. 67

Lithophyllum onkodes f. pachydermum Foslie

Figs 15-22. The vegetative anatomy of the type of Lithophyllum onkodes f. pachydermum Foslie.

Fig. 15. A vertical section of a monomerous free margin (arrow) showing epithallial cells (arrowhead), cortical (C) and medullary filaments (M) (scale bar = 60 μm).

Fig. 16. A vertical section of a thallus sectioned at a right angle to the growing thallus showing a single large trichocyte field (arrow) at the surface and an extremely thin basal region, giving a false impression of being dimerous (arrowhead) (scale bar = 60 μm).

Fig. 17. A close-up of a monomerous free margin (arrow) showing cortical filaments (C) and plumose medullary filaments (M) (scale bar = 30 μm).

Fig. 18. A vertical section through a single trichocyte field (T) located just below the thallus surface (scale bar = 30 μm).

Fig. 19. A section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i) and first cortical cell (c) (scale bar = 15 μm).

Fig. 20. A vertical section of the thallus showing numerous buried trichocyte fields (arrows) (scale bar = 60 μm).

Fig. 21. A section of the lower portion of a monomerous thallus showing a thin plumose medullary region (M) giving rise to cortical filaments (C) bearing as single cell fusion (f) between adjacent filaments (scale bar = 15 μm).

Fig. 22. A magnified view of the thallus sectioned at a right angle to the growing thallus showing an extremely thin basal region, giving a false impression of being dimerous (arrowheads) (scale bar = 15 µm).

Pl. 68

Lithophyllum onkodes f. pachydermum Foslie

Figs 23-27. The tetrasporangial anatomy of the type of Lithophyllum onkodes f. pachydermum Foslie.

Fig. 23. A vertical section through a tetrasporangial conceptacle showing an exposed pore canal (arrow), open, un-infilled chamber (K) and a small central columella (arrow) (scale bar = 60 µm).

Fig. 24. A vertical section of the thallus showing buried tetrasporangial conceptacles (k) (scale bar = 120 µm).

Fig. 25. A close-up through a tetrasporangial conceptacle showing an exposed pore canal (arrow), open, un-infilled chamber (K) and a small central columella (arrow) (scale bar = 30 µm).

Fig. 26. A section through the chamber of a tetrasporangial conceptacle showing a central columella (arrows) and a peripheral tetrasporangium (t) (scale bar = 30 µm).

Fig. 27. A section through the pore canal (P) of a tetrasporangial conceptacle showing enlarged cells (arrows) located at the base of the pore canal (scale bar = 15 µm).

Pl. 69

Porolithon pachydermum (Foslie) Foslie (UWC: 2000/106B)

Fig. 1. The habit of Porolithon pachydermum (Foslie) Foslie from Bermuda (UWC: 2000/106B) (scale bar = 20 mm).

Pl. 70

Porolithon pachydermum (Foslie) Foslie (UWC: 2000/106B)

Figs 2-6. The vegetative anatomy of Porolithon pachydermum (Foslie) Foslie from Bermuda (UWC: 2000/106B).

Fig. 2. A vertical section of a thallus sectioned at a right angle to the growing thallus showing two large pustulate trichocyte fields (T) at the surface and an extremely thin basal region, giving a false impression of being dimerous (arrows). Note how the trichocytes end abruptly at their dorsal ends and the remains of the hairs that stain darkly still visible (arrowheads) (scale bar = 60 µm).

Fig. 3. A section of the thallus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 4. A section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and a single cell fusion (f) between two adjacent filaments (scale bar = 15 µm).

Fig. 5. A section of the inner thallus showing monomerous, plumose medullary filaments bearing cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 6. A magnified view of the thallus sectioned at a right angle to the growing thallus showing an extremely thin basal region, giving a false impression of being dimerous (arrowheads) (scale bar = 15 µm).

Pl. 71

Porolithon pachydermum (Foslie) Foslie (UWC: 2000/106B)

Figs 7-9. The tetrasprangial anatomy of Porolithon pachydermum (Foslie) Foslie from Bermuda (UWC: 2000/106B).

Fig. 7. A vertical section through a raised tetrasporangial conceptacle showing an exposed pore (arrow), open, un-infilled chamber (K) and enlarged cells (arrowheads) located at the base of the pore canal (scale bar = 60 µm).

Fig. 8. A section of a tetrasporangial conceptacle (K) crowded with tetrasporangia (arrows) (scale bar = 60 µm).

Fig. 9. A section through the pore canal of a tetrasporangial conceptacle showing enlarged cells (E) located at the base of the pore canal (scale bar = 15 µm).

Pl. 72

Lithophyllum praetextatum Foslie

Fig. 1. The habit of the type of Lithophyllum praetextatum Foslie (scale bar = 20 mm).

Pl. 73

Lithophyllum praetextatum Foslie

Figs 2-7. The vegetative anatomy of the type of Lithophyllum praetextatum Foslie.

Fig. 2. The thallus surface showing relatively thin walled epithallial cells (arrowheads) with broad, shallow concave centers bearing intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing a small pustulate trichocyte field (arrow) (scale bar = 60 µm).

Fig. 4. A vertical fracture of the outer thallus showing numerous buried trichocyte fields (arrows) (scale bar = 120 µm).

Fig. 5. A vertical fracture of the surface through a pustulate trichocyte field (arrow) (scale bar = 60 µm).

Fig. 6. A vertical fracture of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 7. A vertical fracture through the plumose medullary filaments showing numerous extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Pl. 74

Lithophyllum praetextatum Foslie

Figs 8-9. The tetrasporangial anatomy of the type of Lithophyllum praetextatum Foslie.

Fig. 8. The thallus surface showing a few flush to only slightly raised tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 9. A single flush to only slightly raised tetrasporangial conceptacle (arrow) (scale bar = 120 µm).

Pl. 75

Lithophyllum reinboldii Weber van Bosse & Foslie

Fig. 1. The typical habit of the type of Lithophyllum reinboldii Weber van Bosse & Foslie.

Pl. 76

Lithophyllum reinboldii Weber van Bosse & Foslie

Figs 2-5. The vegetative anatomy of the type of Lithophyllum reinboldii Weber van Bosse & Foslie.

Fig. 2. The thallus surface showing large convex epithallial cells bearing intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. A vertical fracture of the outer thallus showing shedding of an old epithallial cell layer (arrow), an intact single layer of epithallial cells (arrowhead), subepithallial initial (i), first erect filament cell (c) and extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Fig. 4. A fracture of the outer thallus showing a single layer of epithallial cells (arrowhead), subepithallial initial (i), first erect filament cell (c) and solitary trichocytes (T). Note the cell fusions (arrow) between adjacent subepithallial initials (scale bar = 30 µm).

Fig. 5. A vertical fracture of the inner thallus showing a single basal layer (B) of non-palisade cells giving rise to erect filaments bearing extensive cell fusions (f) (scale bar = 30 µm).

Pl. 77

Lithophyllum reinboldii Weber van Bosse & Foslie

Figs 6-10. The tetrasporangial anatomy of the type of Lithophyllum reinboldii Weber van Bosse & Foslie.

Fig. 6. A vertical fracture of the thallus showing tetrasporangial conceptacles both at the surface (arrowheads) and buried in the thallus (arrows) (scale bar = 860 µm).

Fig. 7. The thallus surface showing numerous raised tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 8. A single raised tetrasporangial conceptacle (arrow) (scale bar = 150 µm).

Fig. 9. A vertical fracture through a tetrasporangial conceptacle showing an exposed slightly sunken pore canal (arrow) and an open, un-infilled chamber (K) (scale bar = 100 µm).

Fig. 10. A fracture through the slightly sunken tetrasporangial conceptacle pore canal showing remnants of a ring of enlarged cells (arrowheads) lining the base of the pore canal (scale bar = 30 µm).

Pl. 78

Lithophyllum reinboldii Weber van Bosse & Foslie

Figs 11-17. The vegetative anatomy of the type of Lithophyllum reinboldii Weber van Bosse & Foslie.

Fig. 11. A section of the outer thallus showing solitary and paired trichocytes (T) (scale bar = 30 µm).

Fig. 12. A section of the outer thallus showing a single layer of epithallial cells (e), subepithallial initial (i), first erect filament cell (c) and a cell fusion (f) between two adjacent erect filaments (scale bar = 15 µm).

Fig. 13. A section of the thallus showing a strong horizontal arrangement of large (arrows) and small (arrowheads) cells. The large cells are in fact extensive connections of the erect filaments by broad cell fusions (scale bar = 60 µm).

Fig. 14. A section of the inner portion of a dimerous thallus along a single basal filament (B) showing primary pit connections (arrowheads) (scale bar = 30 µm).

Fig. 15. A section of the inner portion of a dimerous thallus across a series of basal filaments (B) showing a cell fusion between two adjacent basal filaments (arrow), primary pit connections (arrowheads) and cell fusions between adjacent erect filaments (f) (scale bar = 30 µm).

Fig. 16. A close-up of the dimerous thallus along a single basal filament (B) showing the locations of primary pit connections (arrows) (scale bar = 15 µm).

Fig. 17. A close-up of the dimerous thallus across a series of basal filaments (B) showing a cell fusion (f) between two adjacent basal filaments (scale bar = 15 µm).

Pl. 79

Lithophyllum reinboldii Weber van Bosse & Foslie

Figs 18-21. The tetrasporangial anatomy of the type of Lithophyllum reinboldii Weber van Bosse & Foslie.

Fig. 18. A section of the horizontally zoned thallus showing a single raised tetrasporangial conceptacle (K) at the surface, and numerous buried conceptacles (k) (scale bar = 300 µm).

Fig. Insert. A single tetrasporangium (t) (scale bar = 30 µm).

Fig. 19. A section through a raised tetrasporangial conceptacle (K) showing an exposed pore canal (arrow) (scale bar = 150 µm).

Fig. 20. A section through the pore canal and roof of a tetrasporangial conceptacle showing the slightly sunken pore (arrow), pore canal (P) and enlarged cells (arrowheads) lining the base of the pore canal (scale bar = 30 µm).

Fig. 21. A section through the slightly sunken pore canal (P) of a tetrasporangial conceptacle showing the enlarged cells (E) located at the base of the pore canal. Note the faint ring of enlarged cells (arrowheads) in the background (scale bar = 15 µm).

Pl. 80

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie

Fig. 1. The typical habit forms of Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie. A. An encrusting form (UWC: 94/1244). B. The typical rhodoliths form (UWC: 94/1264). (scale bars = 20 mm)

Pl. 81

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie

Figs 2-7. The vegetative anatomy of Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie (UWC: 94/1150).

Fig. 2. The thallus surface showing relatively thin walled epithallial cells (arrowheads) bearing broad, shallow concave centers (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing large convex epithallial cells some of which still bear intact primary pit connections (scale bar = 15 µm).

Fig. 4. The thallus surface showing numerous solitary trichocytes (arrows) (scale bar = 30 µm).

Fig. 5. A vertical fracture of the thallus showing a single epithallial cell layer (arrow) and single basal layer (arrow head) of non-palisade cells. Note the large inflated cells near the thallus surface that have resulted from extensive cell fusions between adjacent erect filaments (scale bar = 60 µm).

Fig. 6. A fracture of the outer thallus surface showing a single epithallial cell layer (arrowhead), subepithallial initial (i), first erect filament cell (c) and solitary bottle-shaped trichocytes (T) (scale bar = 30 µm).

Fig. 7. A fracture of the inner portion of the thallus showing the single basal layer (B) of non-palisade cells giving rise to erect filaments with extensive cell fusions (f) between them and large quantities of starch grains (arrowheads) in their empty cytoplasms (scale bar = 30 µm).

Pl. 82

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie

Figs 8-11. The sporangial anatomy of Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie (UWC: 94/1150).

Fig. 8. The thallus surface showing large numbers of raised sporangial conceptacles (between arrowheads) (scale bar = 860 µm).

Fig. 9. A close-up of the thallus surface showing the variable range in sizes of the sporangial conceptacles (arrows) (scale bar = 150 µm).

Fig. 10. A vertical fracture of the outer thallus showing raised sporangial conceptacles at the surface (K) and some buried within the thallus (k) (scale bar = 150 µm).

Fig. 11. A fracture through the sunken pore (arrow) and pore canal (P) of a sporangial conceptacle showing a ring of enlarged cells (arrowheads) lining the base of the pore canal (scale bar = 30 µm).

Pl. 83

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie

Figs 12-17. The vegetative anatomy of Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie (UWC: 94/1150).

Fig. 12. A vertical section of the dimerous thallus showing a single basal layer (B) of non-palisade cells, a single epithallial cell layer (arrowhead) and subepithallial initial (i) with a cell fusion between two adjacent subepithallial initials (arrow) (scale bar = 30 µm).

Fig. 13. A section of the thallus showing a strong horizontal arrangement of large (arrows) and small (arrowheads) cells. The large cells are in fact extensive connections of the erect filaments by broad cell fusions (scale bar = 60 µm).

Fig. 14. A section of the outer thallus showing a solitary bottle-shaped trichocyte, a single epithallial cell layer (e), subepithallial initial (i) and a cell fusion between two, first erect filament cells (cf) (scale bar = 15 µm).

Fig. 15. A close-up of the thallus showing the strong horizontal arrangement of large (arrows) and small (arrowheads) cells. The large cells are in fact extensive connections of the erect filaments by broad cell fusions (scale bar = 30 µm).

Fig. 16. A section through the inner thallus along a single basal filament (B) showing the location of primary pit connections (arrows) (scale bar = 15 µm).

Fig. 17. A section through the inner thallus across a series of basal filaments (B) showing cell fusions (f) between adjacent basal filaments (scale bar = 15 µm).

Pl. 84

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie

Figs 18-21. The sporangial anatomy of Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie.

Fig. 18. A section of the thallus showing the epithallial cell layer (arrow), erect filaments (C) and buried sporangial conceptacles (k) (scale bar = 300 µm). (UWC: 94/1150)

Fig. 19. A section through a raised sporangial conceptacle (K) (scale bar = 60 µm). (UWC: 94/1382)

Fig. Insert. A single bisporangium (b) (scale bar = 30 µm). (UWC: 94/1382)

Fig. 20. A section through a tetrasporangial conceptacle showing its sunken pore (arrow) and a single large tetrasporangium (t) completely filling the conceptacle chamber (scale bar = 60 µm). (UWC: 94/1041)

Fig. 21. A section through the sunken pore (arrow) and pore canal (P) of a sporangial conceptacle showing a single enlarged cell (E) located at the base of the pore canal (scale bar = 15 µm). (UWC: 94/1041)

Pl. 85

Lithothamnion onkodes Heydrich

Fig. 1. The habit of the type of Lithothamnion onkodes Heydrich. A. Slides and specimen fragments. B. Type specimen packaging. (scale bars = 20 mm).

Pl. 86

Lithothamnion onkodes Heydrich

Figs 2-7. The vegetative anatomy of the type of Lithothamnion onkodes Heydrich.

Fig. 2. The thallus surface showing variably thin to thick walled epithallial cells (arrowheads) with variably shallow to deep concave centers (arrows), a few of which still bear intact primary pit connections (scale bar = 15 µm).

Fig. 3. The thallus surface showing a number of pustulate trichocyte fields (arrows) (scale bar = 200 µm).

Fig. 4. A vertical fracture of a monomerous thallus showing epithallial cells (arrow), cortical (C) and medullary filaments (M) (scale bar = 200 µm).

Fig. 5. A close-up of a single large pustulate trichocyte field (T) (scale bar = 60 µm).

Fig. 6. A vertical fracture of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 7. A vertical fracture of the plumose medullary filaments showing extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Pl. 87

Lithothamnion onkodes Heydrich

Figs 8-11. The vegetative and tetrasporangial anatomy of the type of Lithothamnion onkodes Heydrich.

Fig. 8. A vertical fracture of the thallus surface showing buried trichocyte fields just below the surface and deeper in the thallus (arrows) (scale bar = 60 µm).

Fig. 9. A vertical fracture of the thallus showing trichocyte fields (arrows) buried deeply in the thallus (scale bar = 120 µm).

Fig. 10. A vertical fracture of the thallus showing a buried trichocyte field and a single buried, open, un-infilled tetrasporangial conceptacle (K) (scale bar = 120 µm).

Fig. 11. A fracture through the pore canal of a buried tetrasporangial conceptacle showing the remnants of a ring of enlarged cells (arrowheads) lining the base of the pore canal (scale bar = 30 µm).

Pl. 88

Lithothamnion onkodes Heydrich

Figs 12-15. The vegetative anatomy of the type of Lithothamnion onkodes Heydrich.

Fig. 12. A section of the outer thallus through a single large trichocyte field (arrow) (scale bar = 30 µm).

Fig. 13. A section of the outer thallus showing an old layer of epithallial cells being shed (arrow), an intact multiple layer of epithallial cells (arrowheads), a subepithallial initial (i), and a first cortical cell (c) (scale bar = 15 µm).

Fig. 14. A section of the thallus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 15. A section of the inner thallus showing a plumose medullary region terminating in elongate to domed inner epithallial cells (arrowheads) and bearing extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Pl. 89

Lithothamnion onkodes Heydrich

Figs 16-19. The tetrasporangial anatomy of the type of Lithothamnion onkodes Heydrich.

Fig. 16. A section of the thallus showing buried, open, un-infilled tetrasporangial conceptacles (K) (scale bar = 150 µm).

Fig. 17. A section of the outer thallus showing a single flush tetrasporangial conceptacle (K) with shedding epithallial layer (arrow) and exposed pore canal (P) (scale bar = 60 µm).

Fig. 18. A section through the pore (P) and roof of a tetrasporangial conceptacle showing the approximate location (arrow) of the enlarged cells which in this case are missing (scale bar = 30 µm).

Fig. 19. A section through the pore canal of a sunken tetrasporangial conceptacle showing the existence of a ring of enlarged cells (E) located at the base of the pore canal (scale bar = 15 µm).

Pl. 90

Hydrolithon onkodes (Heydrich) Penrose & Woelkerling

Fig. 1. The differential habits of Hydrolithon onkodes (Heydrich) Penrose & Woelkerling. A. Epilithic and encrusting. B. Encrusting on a fishing line. C. A three-dimensional honey-combed form in which upright lobes are produced, at the bases of which are found the tubular burrows of the chiton Cryptoplax larvaeformis.

Pl. 91

Hydrolithon onkodes (Heydrich) Penrose & Woelkerling

Figs 2-7. The vegetative anatomy of Hydrolithon onkodes (Heydrich) Penrose & Woelkerling (UWC: 99/114).

Fig. 2. The thallus surface showing variably thick walled epithallial cells (arrowheads) bearing shallow to deep concave centers and intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing numerous scattered pustulate trichocyte fields (arrows) (scale bar = 300 µm).

Fig. 4. A vertical fracture of the thallus showing cortical filaments (C), plumose medullary filaments (M) and buried trichocyte fields (arrow) (scale bar = 150 μm).

Fig. 5. The thallus surface showing a single large pustulate trichocyte field (T) (scale bar = 60 μm).

Fig. 6. A vertical fracture of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c), buried trichocyte field (T) and a cell fusion (f) between two cortical filaments (scale bar = 30 μm).

Fig. 7. A vertical fracture of the plumose medullary filaments showing cell fusions (f) between adjacent filaments (scale bar = 30 μm).

Pl. 92

Hydrolithon onkodes (Heydrich) Penrose & Woelkerling

Figs 8-11. The tetrasporangial anatomy of Hydrolithon onkodes (Heydrich) Penrose & Woelkerling (UWC: 99/114).

Fig. 8. The thallus surface showing numerous flush to only slightly raised tetrasporangial conceptacles (arrows) (scale bar = 860 μm).

Fig. 9. A close-up of a single slightly raised tetrasporangial conceptacle (arrow) and a trichocyte field (T) (scale bar = 90 μm).

Fig. 10. A vertical fracture of the outer thallus through a tetrasporangial conceptacle (K) (scale bar = 60 μm).

Fig. 11. A fracture through the tetrasporangial conceptacle pore (arrow) and pore canal showing remnants of the enlarged cells (arrowheads) lining the base of the pore canal (scale bar = 15 μm).

Pl. 93

Hydrolithon onkodes (Heydrich) Penrose & Woelkerling

Figs 12-16. The vegetative and tetrasporangial anatomy of *Hydrolithon onkodes* (Heydrich) Penrose & Woelkerling.

Fig. 12. A vertical section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i) and first cortical cell (scale bar = 15 µm) (UWC: 94/1175).

Fig. 13. A vertical section of the outer thallus showing a single large pustulate trichocyte field (arrows) (scale bar = 30 µm) (UWC: 94/ 1269).

Fig. 14. A vertical section of inner thallus showing plumose medullary filaments (scale bar = 30 µm) (UWC: 94/1175).

Fig. 15. A vertical section through a buried tetrasporangial conceptacle showing an extensive central fusion cell (arrow) and peripheral tetrasporangia (t) (scale bar = 30 µm). (UWC: 94/1175)

Fig. 16. A section through the pore canal of a buried tetrasporangial conceptacle showing the enlarged cells (E) that typically line the base of the pore canal (scale bar = 15 µm) (UWC: 94/ 1269).

Pl. 94

Hydrolithon onkodes (Heydrich) Penrose & Woelkerling

Figs 17-19. The gametangial anatomy of *Hydrolithon onkodes* (Heydrich) Penrose & Woelkerling.

Fig. 17. A vertical section of the thallus showing open, un-infilled (K) and infilled (arrows) spermatangial conceptacles (scale bar = 120 µm) (UWC: COR/122).

Fig. 18. A vertical section of a monoecious thallus showing buried spermatangial (S) and carposporangial (C) conceptacles (scale bar = 60 µm) (UWC: 94/ 1269).

Fig. 19. A section through a spermatangial conceptacle showing simple spermatangia restricted to the conceptacle floor (arrows) (scale bar = 15 µm) (UWC: COR/122).

Pl. 95

Hydrolithon onkodes (Heydrich) Penrose & Woelkerling

Figs 20-23. The female gametangial anatomy of Hydrolithon onkodes (Heydrich) Penrose & Woelkerling (UWC: COR/122).

Fig. 20. A section through a carpogonial conceptacle (arrow) (scale bar = 60 µm).

Fig. 21. A section through the chamber of a carpogonial conceptacle showing carpogonial branches across the conceptacle floor bearing terminal trichogynes (t) and subtended by a carpogonium (c) and a support cell (s) (scale bar = 15 µm).

Fig. 22. A section through a carposporangial conceptacle showing peripherally located gonimoblast filaments ending in terminal carpospores (C) (scale bar = 30 µm).

Fig. 23. A section through the periphery of a carposporangial chamber showing a continuous fusion cell (arrow), and a gonimoblast filament bearing 9 cells and a terminal carpospore (C) (scale bar = 30 µm).

Pl. 96

Porolithon castellum Dawson

Fig. 1. The habit of the type of Porolithon castellum Dawson (scale bar = 20 mm).

Pl. 97

Porolithon castellum Dawson

Figs 2-9. The vegetative anatomy of the type of Porolithon castellum Dawson.

Fig. 2. The thallus surface showing relatively thick walled epithallial cells (arrowheads) with relatively narrow shallow to deep concave centers bearing intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing numerous scattered pustulate trichocyte fields (arrows) (scale bar = 200 µm).

Fig. 4. A fracture of the outer thallus showing a single pustulate trichocyte field at the surface and two more trichocyte fields buried within the thallus (arrows) (scale bar = 60 µm).

Fig. 5. The thallus surface showing a single large pustulate trichocyte field (scale bar = 60 µm).

Fig. 6. A vertical fracture of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 7. A vertical fracture of a free margin (arrow) showing epithallial cells (arrowhead), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 120 µm).

Fig. 8. A fracture through the inner portion of the thallus showing plumose medullary filaments bearing extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Fig. 9. A fracture through the inner portion of the thallus showing plumose medullary filaments terminating in elongate to domed inner epithallial cells (arrowheads) (scale bar = 30 µm).

Pl. 98

Porolithon castellum Dawson

Figs 10-15. The tetrasporangial conceptacle anatomy of the type of Porolithon castellum Dawson.

Fig. 10. The thallus surface showing numerous flush to slightly sunken tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 11. A close-up of a single slightly sunken tetrasporangial conceptacle (arrow) and a few trichocyte fields (arrowheads) (scale bar = 120 µm).

Fig. 12. A vertical fracture through a tetrasporangial conceptacle (K) showing an exposed pore canal (arrowhead) and a small central columella (arrow) (scale bar = 100 µm).

Fig. 13. A fracture through the chamber of a tetrasporangial conceptacle showing incompletely divided tetrasporangia (arrows) (scale bar = 30 µm).

Fig. 14. A X/S of a protuberance showing numerous buried tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 15. A fracture through the tetrasporangial conceptacle pore canal showing papillate cells (arrowheads) lining and tilted slightly into the pore canal, and subtended by the remnants of a ring of somewhat smaller enlarged cells (arrows) lining the base of the pore canal (scale bar = 30 µm).

Pl. 99

Porolithon castellum Dawson

Figs 16-21. The vegetative anatomy of the type of Porolithon castellum Dawson.

Fig. 16. A vertical section of the thallus showing epithallial cells (arrow), cortical (C) and medullary filaments (M) (scale bar = 120 µm).

Fig. 17. A section of the outer thallus through a single large pustulate trichocyte field at the surface (T) and one buried in the thallus (arrow) (scale bar = 30 µm).

Fig. 18. A vertical section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and cell fusions (f) between adjacent cortical filaments (scale bar = 15 µm).

Fig. 19. A vertical section through a single pustulate trichocyte field (T). Note how the trichocytes end abruptly at their dorsal ends and the remains of the hairs that stain darkly still visible (arrowheads) (scale bar = 15 µm).

Fig. 20. A section though the plumose medullary filaments showing a number of cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 21. A vertical section of the thallus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Pl. 100

Porolithon castellum Dawson

Figs 22-27. The tetrasporangial anatomy of the type of Porolithon castellum Dawson.

Fig. 22. A section of the outer thallus through a flush tetrasporangial conceptacle (K) showing an occluded pore canal (P). Note the buried trichocyte field (arrow) below the conceptacle (scale bar = 60 µm).

Fig. 23. A section of the thallus showing a number of buried tetrasporangial conceptacles (k) (scale bar = 120 µm).

Fig. 24. A section through the chamber of a tetrasporangial conceptacle showing a number of completely divided (arrowheads) and undifferentiated tetrasporangia (arrows) (scale bar = 30 µm).

Fig. 25. A section through a tetrasporangial conceptacle (K) bearing a small central columella (arrow) (scale bar = 60 µm).

Fig. 26. A fracture through the tetrasporangial conceptacle pore canal (P) and roof showing papillate cells (arrows) lining and tilted slightly into the pore canal, and a smaller enlarged cell (E) located at the base of the pore canal (scale bar = 15 µm).

Fig. 27. A fracture through the tetrasporangial conceptacle pore canal (P) and roof showing papillate cells (arrows) lining and tilted slightly into the pore canal, and an almost insignificant cell (arrowhead) located at the base of the pore canal (scale bar = 15 µm).

Pl. 101

Porolithon cocosicum Lemoine (BM slide 5369 ~ UWC: 94/10BM)

Figs 1-4. The vegetative anatomy of the type of Porolithon cocosicum Lemoine (BM slide 5369 ~ UWC: 94/10BM).

Fig. 1. A section through a single large pustulate trichocyte field (T) (scale bar = 30 µm).

Fig. 2. A section of the thallus showing a buried trichocyte field (arrow) (scale bar = 30 µm).

Fig. 3. A section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and cell fusions (f) between adjacent cortical filaments (scale bar = 15 µm).

Fig. 4. A section of the plumose medullary filaments showing cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Pl. 102

Porolithon cocosicum Lemoine (BM slide 5369 ~ UWC: 94/10BM)

Figs 5-8. The female gametangial anatomy of the type of Porolithon cocosicum Lemoine (BM slide 5369 ~ UWC: 94/10BM).

Fig. 5. A section of a monoecious thallus showing a buried spermatangial (S) and carposporangial (Cs) conceptacle side-by-side (scale bar = 60 µm).

Fig. 6. A section through a spermatangial conceptacle showing simple spermatangia restricted to the conceptacle floor (arrows) (scale bar = 15 µm).

Fig. 7. A section through a carposporangial conceptacle chamber showing a continuous fusion cell (arrow) bearing unfertilized carpogonial branches (arrowheads) at its centre (scale bar = 15 µm).

Fig. 8. A section through a carposporangial conceptacle showing a thin, narrow, continuous central fusion cell (arrows) bearing peripheral gonimoblast filaments. The gonimoblast filaments may comprise up to 11 cells excluding a terminal carpospore (C) (scale bar = 15 µm).

Pl. 103

Porolithon cocosicum Lemoine (PC holotype fragment)

Figs 1-3. The vegetative anatomy of the type of Porolithon cocosicum Lemoine (PC holotype fragment).

Fig. 1. The thallus surface showing relatively thick walled epithallial cells (arrowheads) with deeply concave centers (scale bar = 15 µm).

Fig. 2. The thallus surface showing a single large pustulate trichocyte field (scale bar = 30 µm).

Fig. 3. A vertical fracture of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Pl. 104

Porolithon cocosicum Lemoine (PC holotype fragment)

Figs 4-9. The tetrasporangial conceptacle anatomy of the type of Porolithon cocosicum Lemoine (PC holotype fragment).

Fig. 4. The thallus surface showing a number of flush to sunken tetrasporangial conceptacles (arrows). Note the vertical fractures (arrowheads) through two conceptacles (scale bar = 860 µm).

Fig. 5. The thallus surface showing a single slightly sunken tetrasporangial conceptacle (arrow) (scale bar = 150 µm).

Fig. 6. A vertical fracture of the thallus showing tetrasporangial conceptacles both at the surface (K) and buried (k) in the thallus (scale bar = 200 µm).

Fig. 7. A vertical fracture of the outer thallus through a slightly sunken tetrasporangial conceptacle (K) showing an exposed pore canal (arrow) (scale bar = 120 µm).

Fig. 8. A fracture through the periphery of a tetrasporangial conceptacle chamber showing a tetrasporangium (t) (scale bar = 30 µm).

Fig. 9. A fracture through the pore canal of a tetrasporangial conceptacle showing remnants of a ring of enlarged cells (arrowheads) lining the base of the pore canal (scale bar = 30 µm).

Pl. 105

Porolithon cocosicum Lemoine (PC holotype fragment)

Figs 10-13. The vegetative anatomy of the type of Porolithon cocosicum Lemoine (PC holotype fragment).

Fig. 10. A section of the outer thallus through a pustulate trichocyte field (T). Note the remains of the hairs that stain darkly still visible (arrowheads) (scale bar = 30 µm).

Fig. 11. A section of the thallus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 12. A section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and cell fusions (f) between adjacent cortical filaments (scale bar = 15 µm).

Fig. 13. A section through the plumose medullary filaments bearing cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Pl. 106

Porolithon cocosicum Lemoine (PC holotype fragment)

Figs 14-17. The tetrasporangial anatomy of the type of Porolithon cocosicum Lemoine (PC holotype fragment).

Fig. 14. A vertical section of the outer thallus showing a trichocyte field (arrow) and two tetrasporangial conceptacles, one at the surface (K) and one buried in the thallus (k) (scale bar = 60 µm).

Fig. 15. A section of the thallus showing tetrasporangial conceptacles both at the surface (K) and buried in the thallus (k). Note that infilling (arrows) of the thallus also occurs (scale bar = 120 µm).

Fig. 16. A section through a sunken tetrasporangial conceptacle showing apparently viable tetrasporangia (arrows) (scale bar = 30 µm).

Fig. 17. A section through the pore (P) and pore canal of a tetrasporangial conceptacle showing a ring of enlarged cells (arrows) located at the base of the pore canal (scale bar = 15 µm).

Pl. 107

Porolithon marshallense W.R. Taylor ("marshallensis") (BM isotype)

Fig. 1. The habit of the type of Porolithon marshallense W.R. Taylor ("marshallensis") (BM isotype). A. Dorsal view. B. Lateral view.

Pl. 108

Porolithon marshallense W.R. Taylor ("marshallensis") (BM isotype)

Figs 2-9. The vegetative anatomy of the type of Porolithon marshallense W.R. Taylor ("marshallensis") (BM isotype).

Fig. 2. The thallus surface showing variably thin to thick walled epithallial cells (arrowheads) with broad to narrow and shallow concave centers. Primary pit connections (arrow) are also often visible (scale bar = 15 µm).

Fig. 3. The thallus surface showing a single large pustulate trichocyte field (arrow) (scale bar = 60 µm).

Fig. 4. The thallus surface showing variably thin to thick walled epithallial cells with shallow to somewhat deeper, broad to narrow concave centers bearing intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 5. A vertical fracture of the thallus showing a number of buried trichocyte fields (arrows) (scale bar = 150 µm).

Fig. 6. A vertical fracture of a free margin (arrow) showing the epithallial cells (arrowhead), cortical (C) and medullary filaments (M) (scale bar = 120 µm).

Fig. 7. A vertical fracture through the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and abundant cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 8. A fracture through the plumose medullary filaments showing extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Fig. 9. A fracture through the inner thallus showing only a few plumose medullary filament (M) giving rise to cortical filaments (C) and terminating toward the inner portion in elongate to domed inner epithallial cells (arrows) (scale bar = 30 µm).

Pl. 109

Porolithon marshallense W.R. Taylor ("marshallensis") (BM isotype)

Figs 10-11. The tetrasporangial anatomy of the type of Porolithon marshallense W.R. Taylor ("marshallensis") (BM isotype).

Fig. 10. The thallus surface showing numerous slightly raised tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 11. The thallus surface showing a single raised tetrasporangial conceptacle (arrow) (scale bar = 120 µm).

Pl. 110

Porolithon marshallense W.R. Taylor ("marshallensis") (BM isotype)

Figs 12-14. The vegetative anatomy of the type of Porolithon marshallense W.R. Taylor ("marshallensis") (BM isotype).

Fig. 12. A vertical section of the outer thallus through a single large pustulate trichocyte field (T). Note how the trichocytes end abruptly at their dorsal ends and the remains of the hairs that stain darker still visible (arrowheads) (scale bar = 30 µm).

Fig. 13. A vertical section of the outer thallus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 14. A section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initials (i) and first cortical cell (c) (scale bar = 15 µm).

Pl. 111

Porolithon marshallense W.R. Taylor ("marshallensis") (BM isotype)

Figs 15-18. The tetrasporangial anatomy of the type of Porolithon marshallense W.R. Taylor ("marshallensis") (BM isotype).

Fig. 15. A section of the thallus showing a tetrasporangial conceptacle (K) with exposed pore canal (P) and buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 16. A section of the thallus showing buried tetrasporangial conceptacles (K) with central columellas (arrows) (scale bar = 120 µm).

Fig. 17. A section of the thallus showing a tetrasporangial conceptacle bearing tetrasporangia (arrows) and buried trichocyte fields (arrowheads) (scale bar = 60 µm).

Fig. 18. A section through the pore canal (P) of a tetrasporangial conceptacle showing a single intact enlarged cell (arrow) located at the base of the pore canal (scale bar = 15 µm).

Pl. 112

Porolithon marshallense W.R. Taylor ("marshallensis") (PC isotype)

Figs 1-5. The vegetative anatomy of the type of Porolithon marshallense W.R. Taylor ("marshallensis") (PC isotype).

Fig. 1. The thallus surface showing relatively thick walled epithallial cells (arrowheads) with shallow to deep concave centers bearing intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 2. The thallus surface showing numerous pustulate trichocyte fields (arrows) (scale bar = 600 µm).

Fig. 3. The thallus surface showing a single large pustulate trichocyte field (scale bar = 60 µm).

Fig. 4. A vertical fracture of the thallus showing numerous buried trichocyte fields (arrows) (scale bar = 300 µm).

Fig. 5. A fracture through the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c), a portion of a trichocyte field (T) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Pl. 113

Porolithon marshallense W.R. Taylor ("marshallensis") (PC isotype)

Figs 6-10. The tetrasporangial anatomy of the type of Porolithon marshallense W.R. Taylor ("marshallensis") (PC isotype).

Fig. 6. The thallus surface showing numerous slightly raised tetrasporangial conceptacles (arrows) (scale bar = 300 µm).

Fig. 7. The thallus surface showing a single raised tetrasporangial conceptacle (arrow) and a few trichocyte fields (arrowheads) (scale bar = 120 µm).

Fig. 8. A vertical fracture of the thallus showing a slightly sunken tetrasporangial conceptacle (K) bearing a central columella (arrowhead), and buried trichocyte fields (arrows) (scale bar = 120 µm).

Fig. 9. A vertical fracture of the thallus showing a buried tetrasporangial conceptacle (K), and trichocyte fields both at the surface (arrowhead) and buried in the thallus (arrows) (scale bar = 100 µm).

Fig. 10. A fracture through the tetrasporangial conceptacle pore canal showing the remnants of a ring of enlarged cells (arrowheads) located at the base of the pore canal (scale bar = 30 µm).

Pl. 114

Porolithon marshallense W.R. Taylor ("marshallensis") (PC isotype)

Figs 11-15. The vegetative and tetrasporangial anatomy of the type of Porolithon marshallense W.R. Taylor ("marshallensis") (PC isotype).

Fig. 11. A section of the outer thallus showing multiple epithallial cell layers (arrowheads), subepithallial initial (i), first cortical cell (c) and a cell fusion (f) between adjacent cortical

filaments. Note the different sized subepithallial initials (i) indicating a recent division (scale bar = 15 µm).

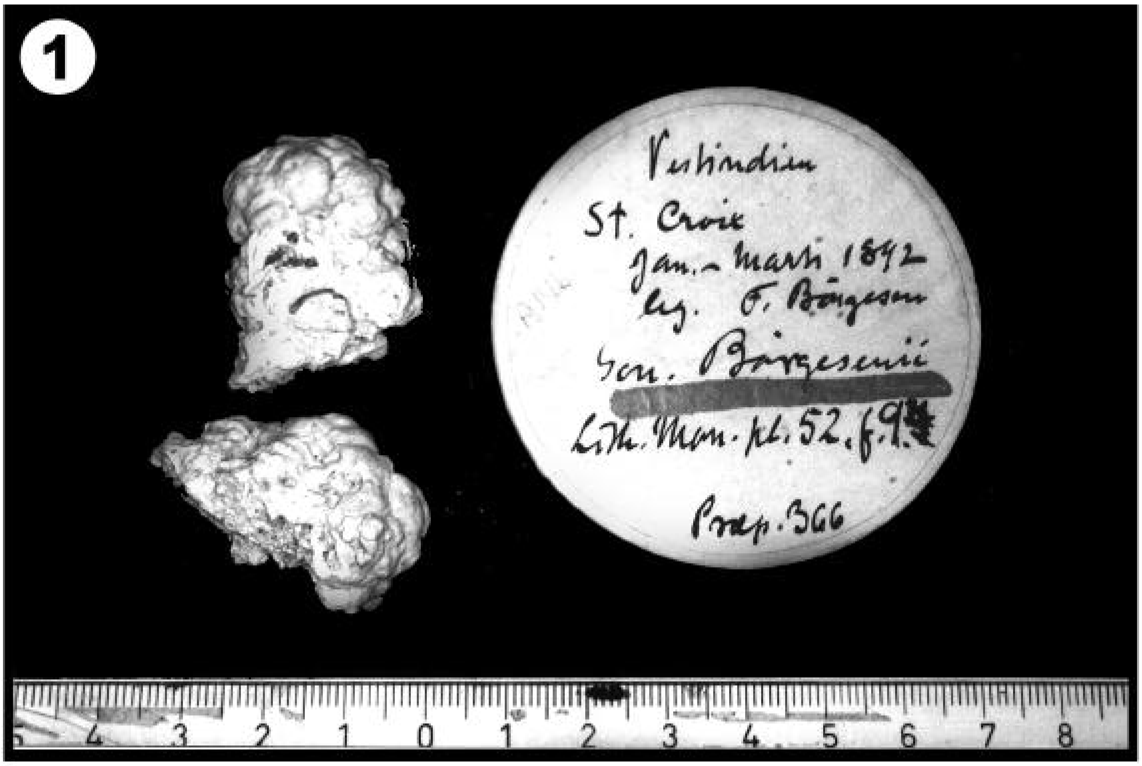
Fig. 12. A section of the outer thallus showing a trichocyte field (T) with some trichocytes still bearing their hairs (arrows) (scale bar = 30 µm).

Fig. 13. A section of the thalus showing buried trichocyte fields (arrows) (scale bar = 60 µm).

Fig. 14. A section through a slightly raised tetrasporangial conceptacle (K) showing an exposed pore canal (P) (scale bar = 60 µm).

Fig. 15. A section through a tetrasporangial conceptacle pore canal (P) showing enlarged cells (arrows) located at the base of the pore canal (scale bar = 15 µm).

Plate 1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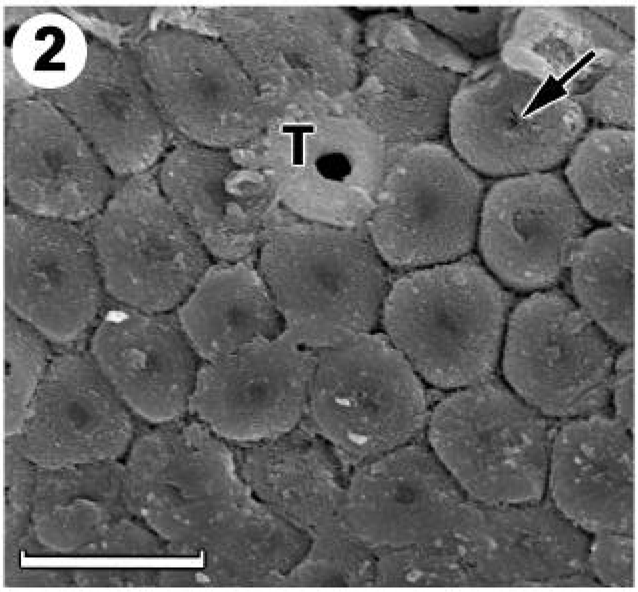

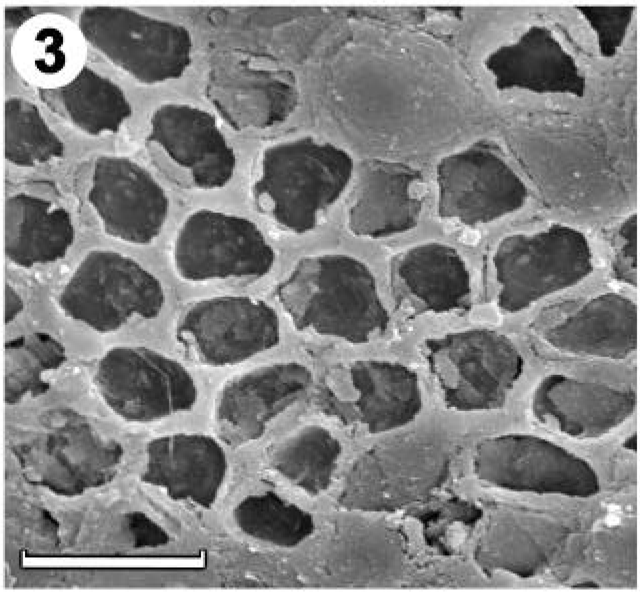

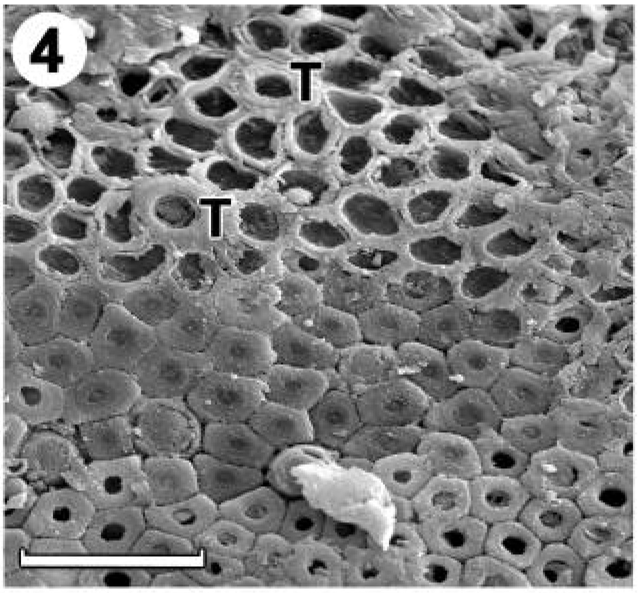

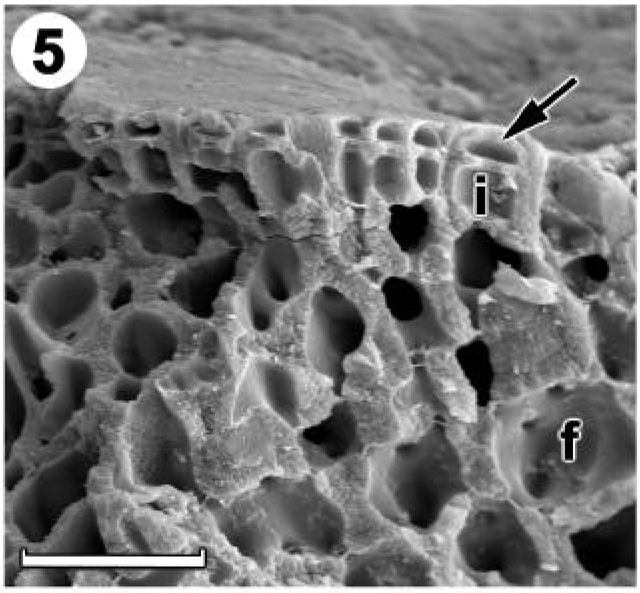

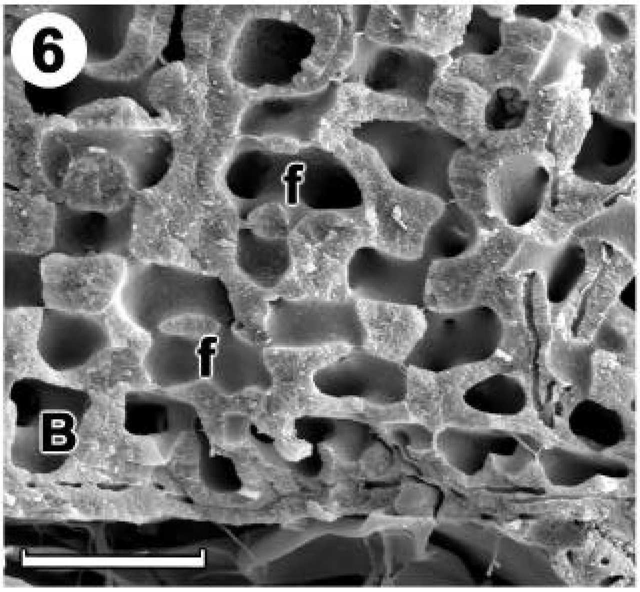

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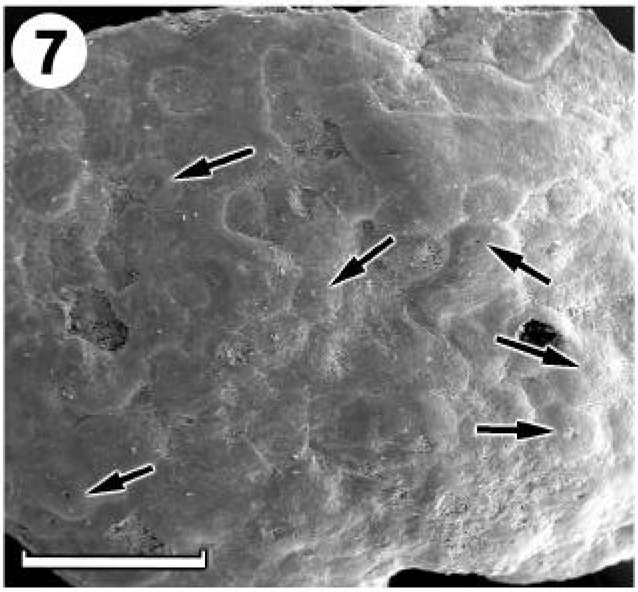

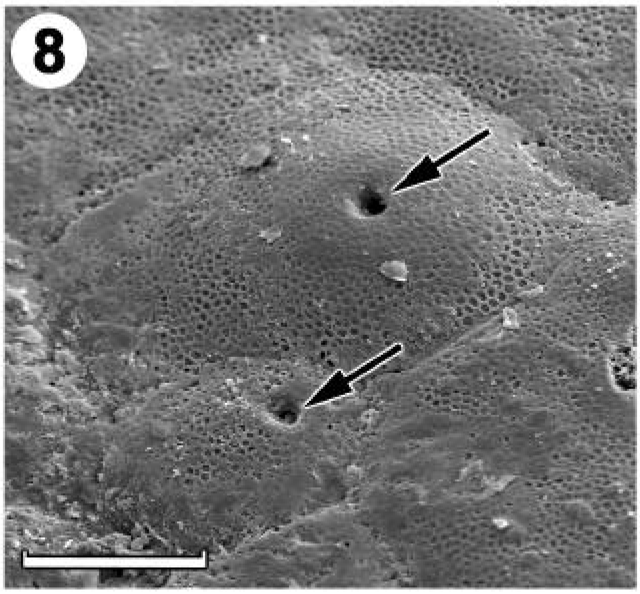

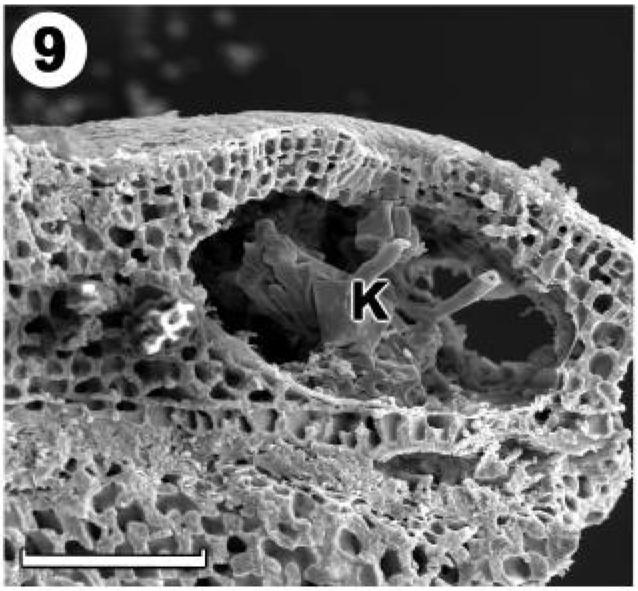

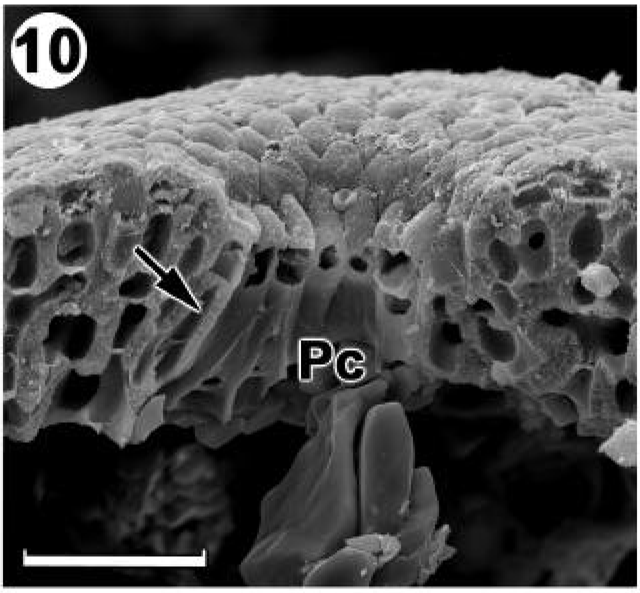

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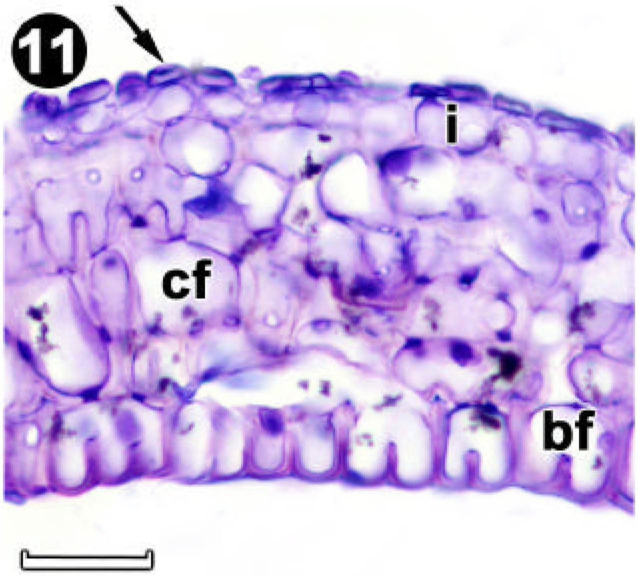

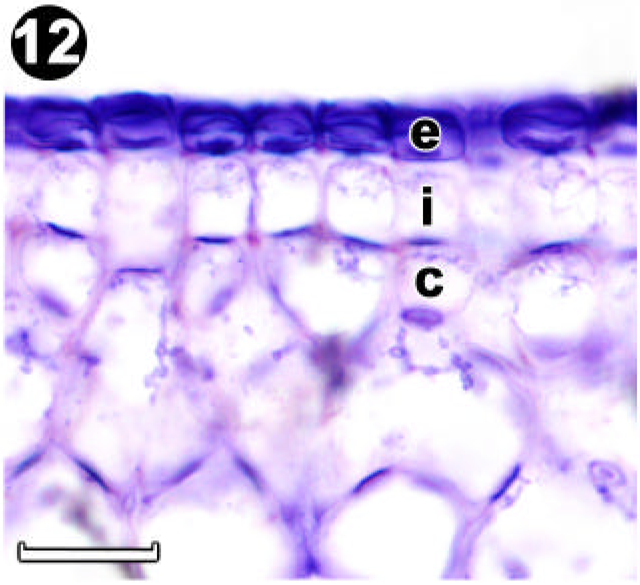

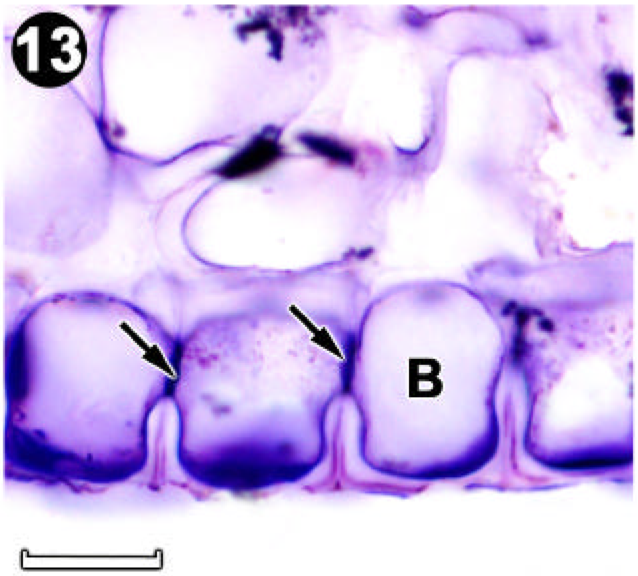

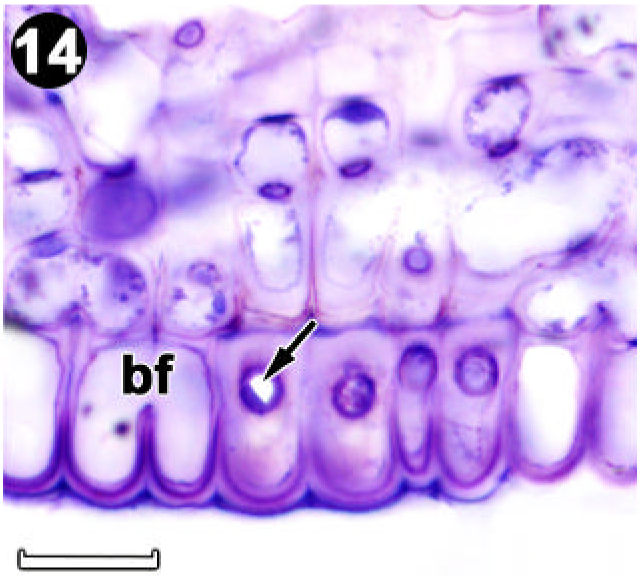

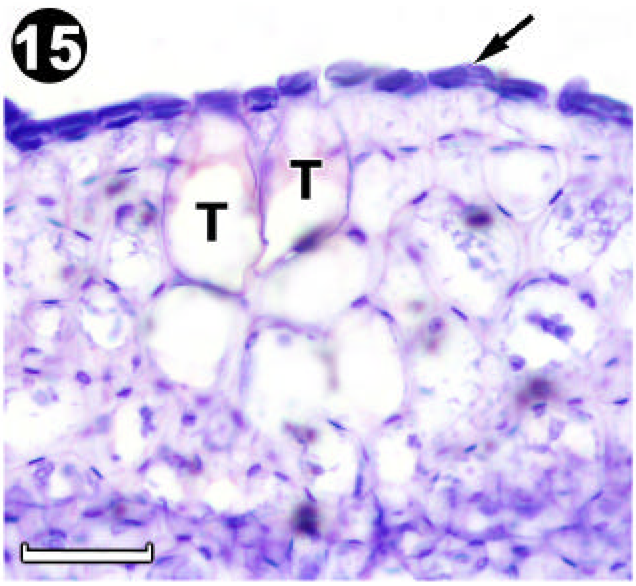

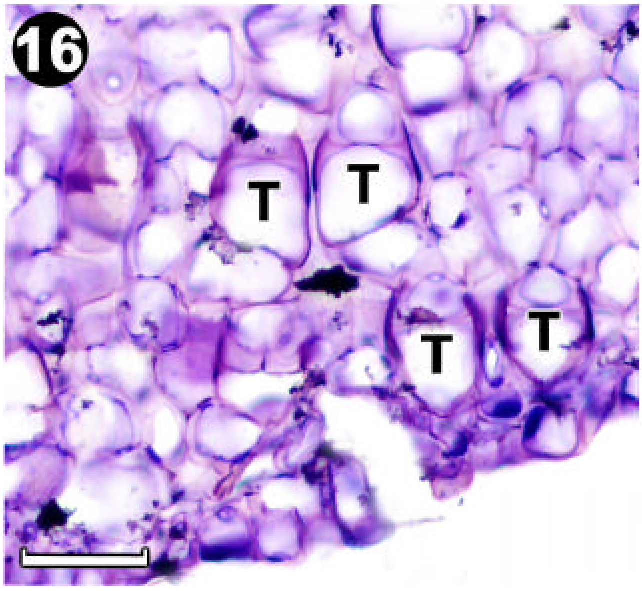

Plate 5

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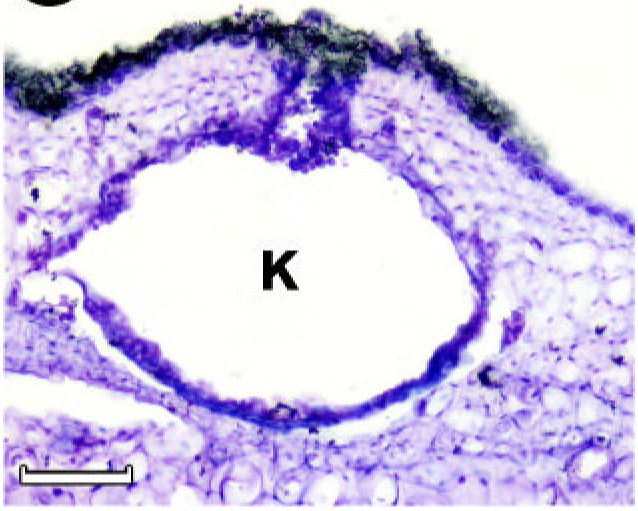

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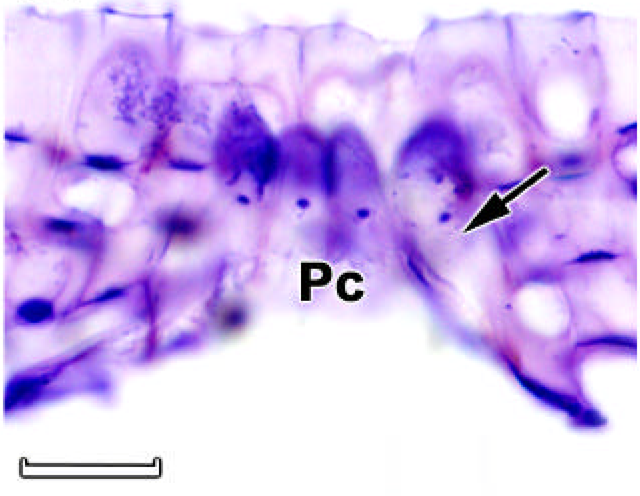

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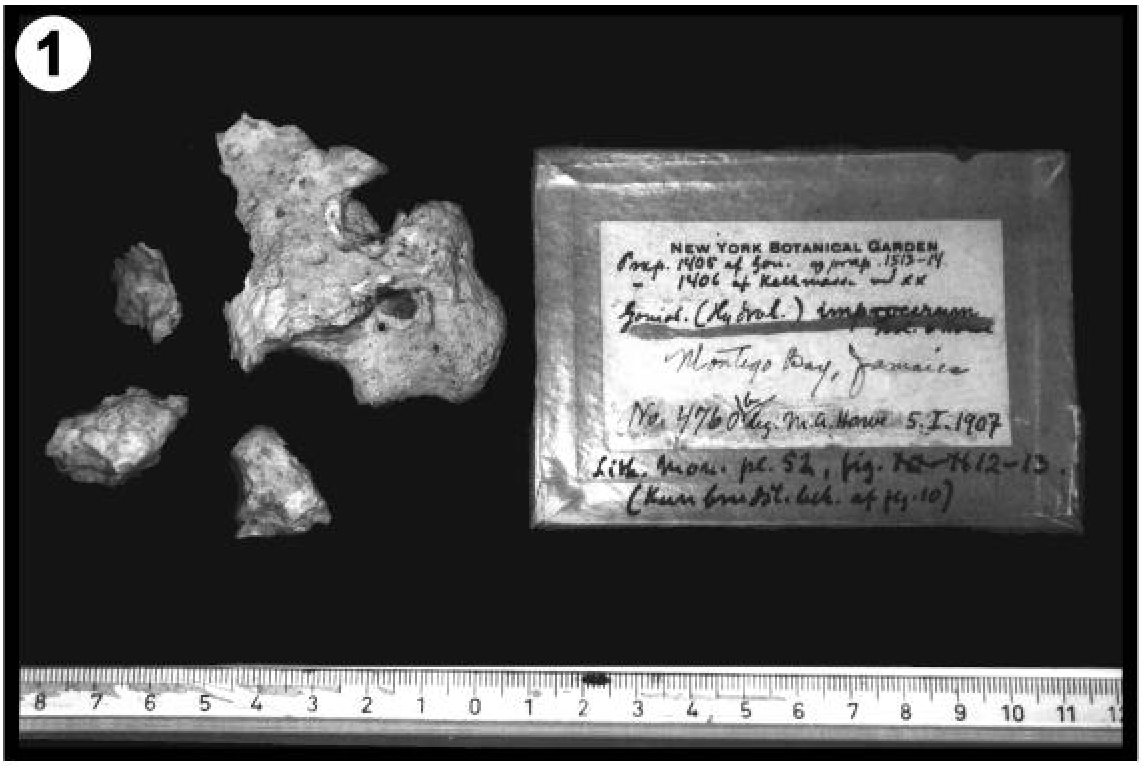
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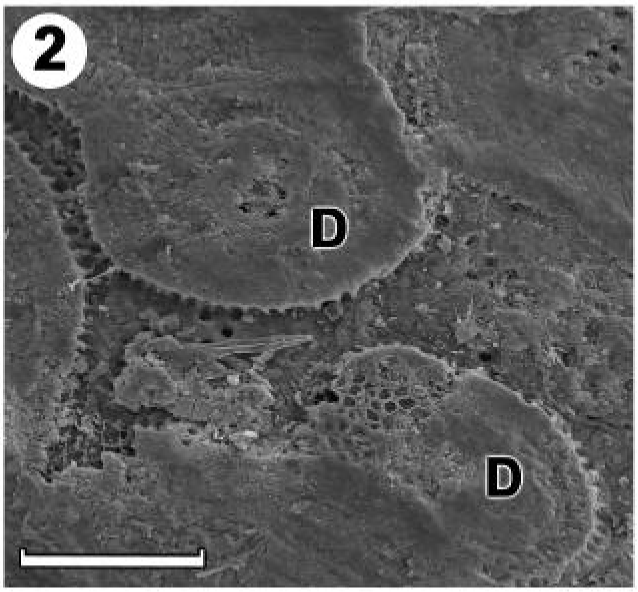
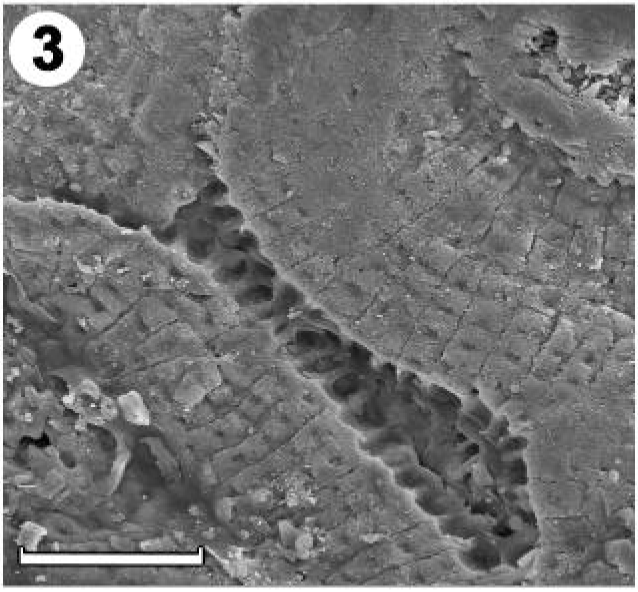
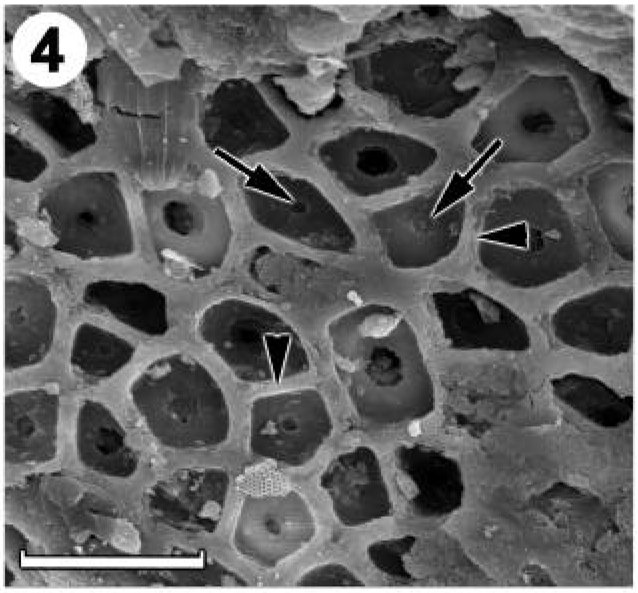
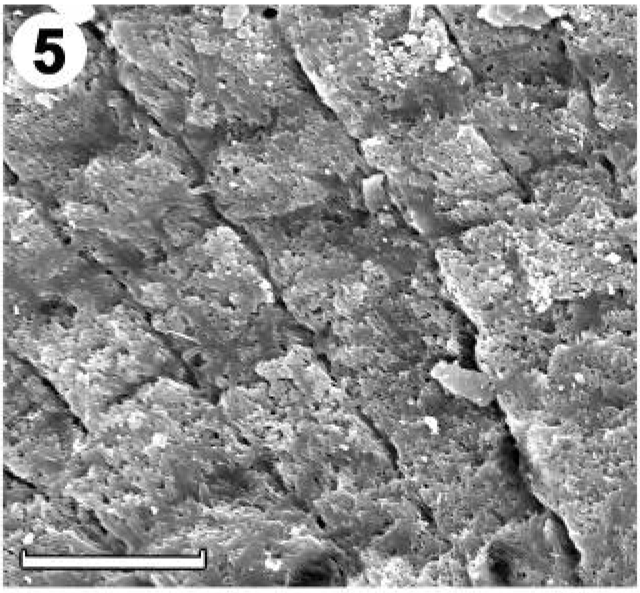
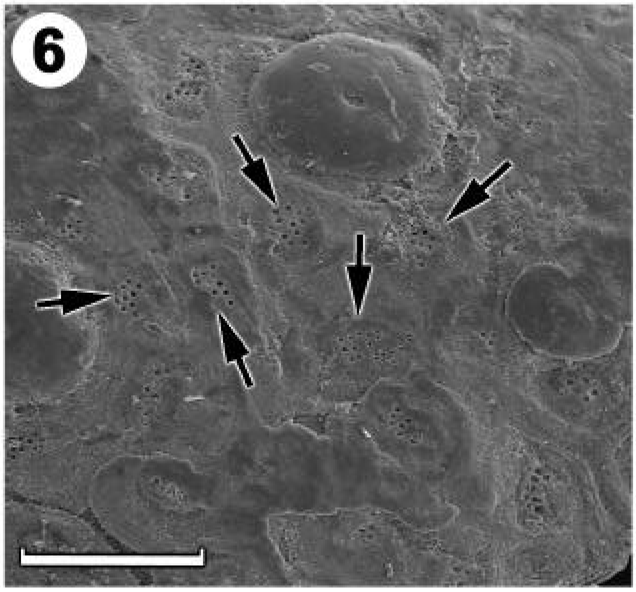
Plate 7











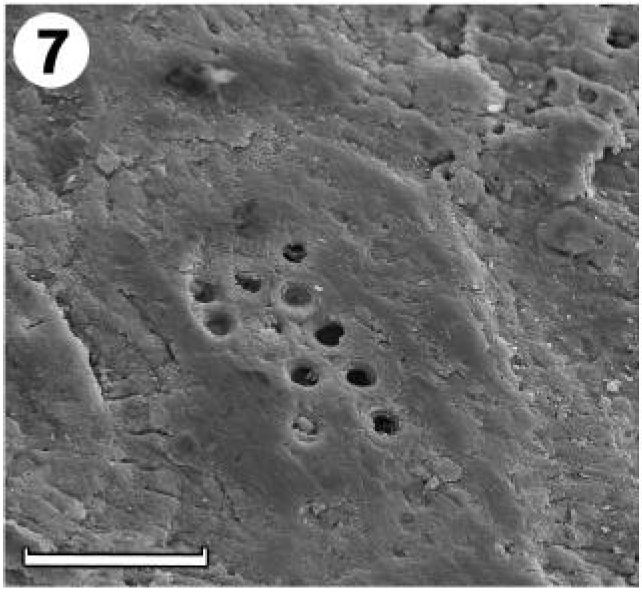
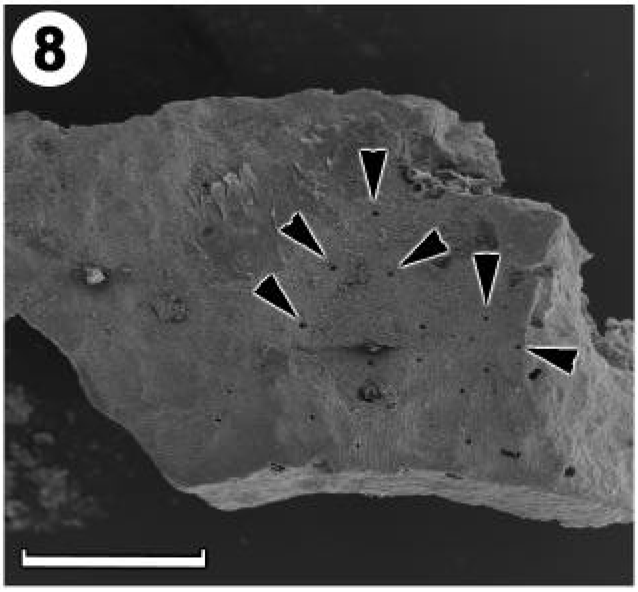
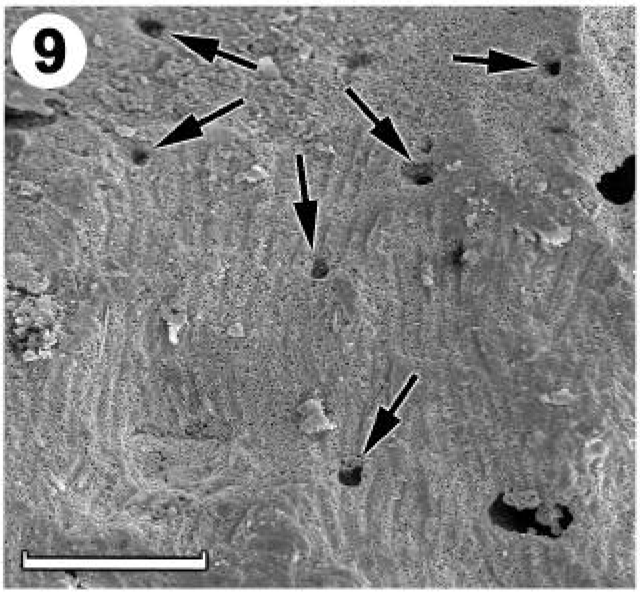
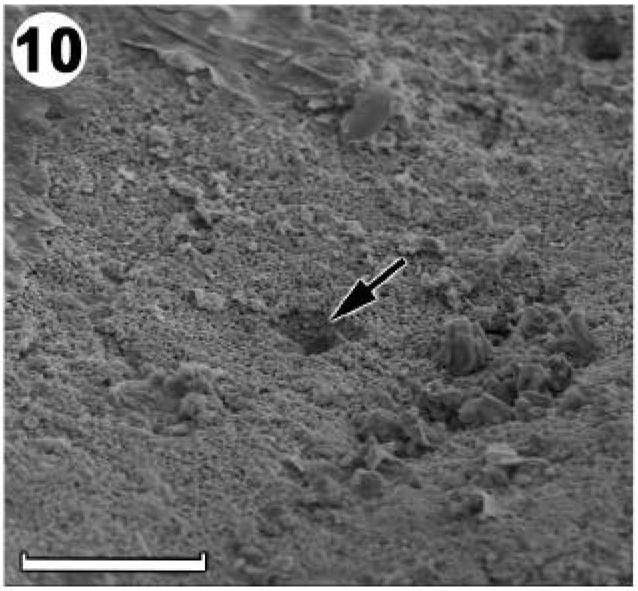
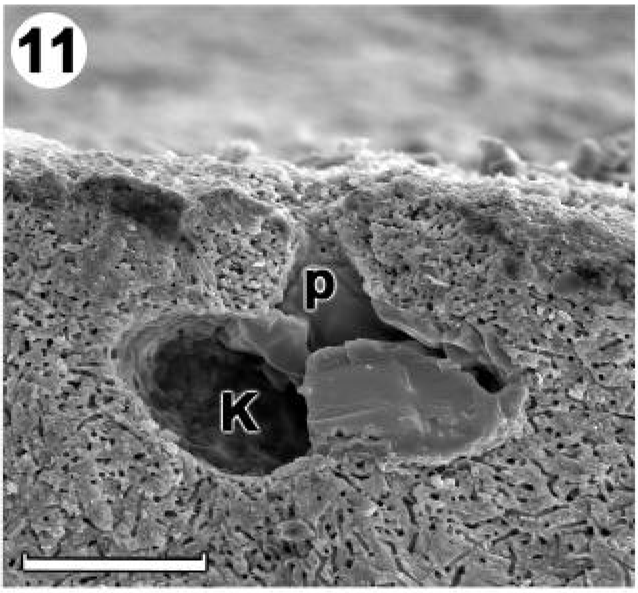


Plate 8









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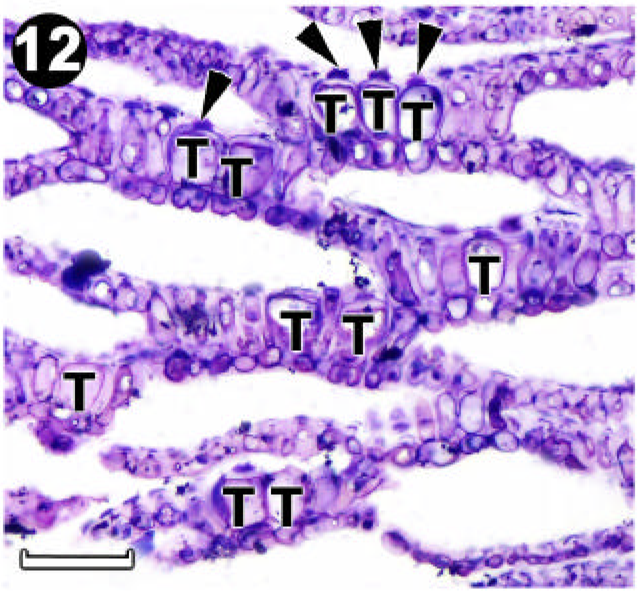

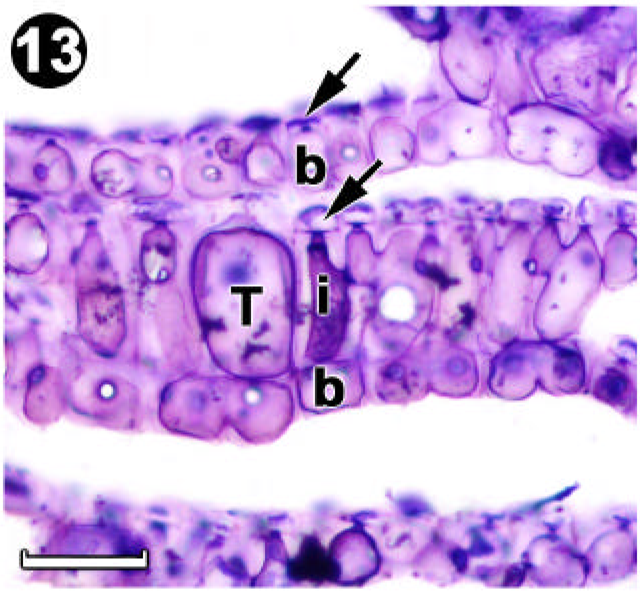

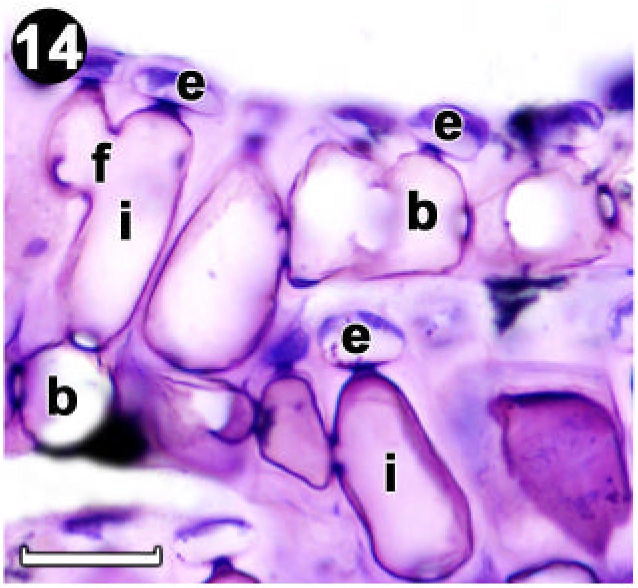

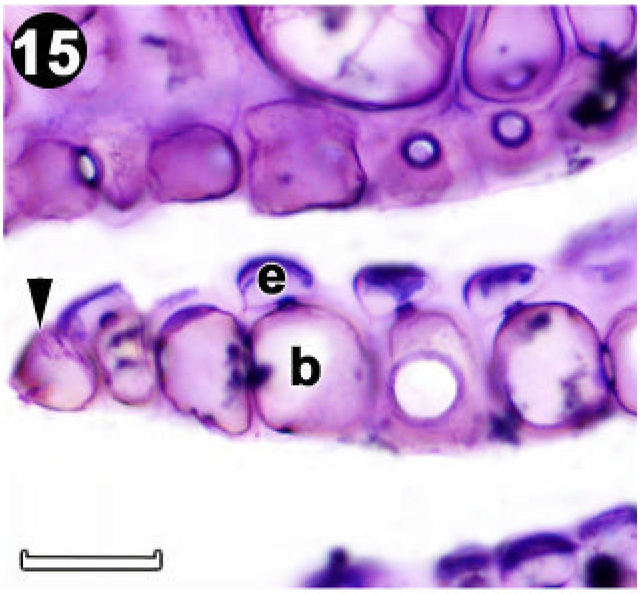

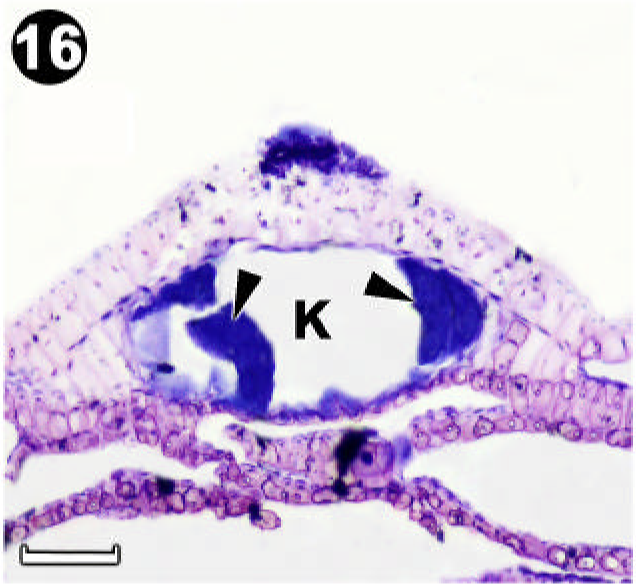

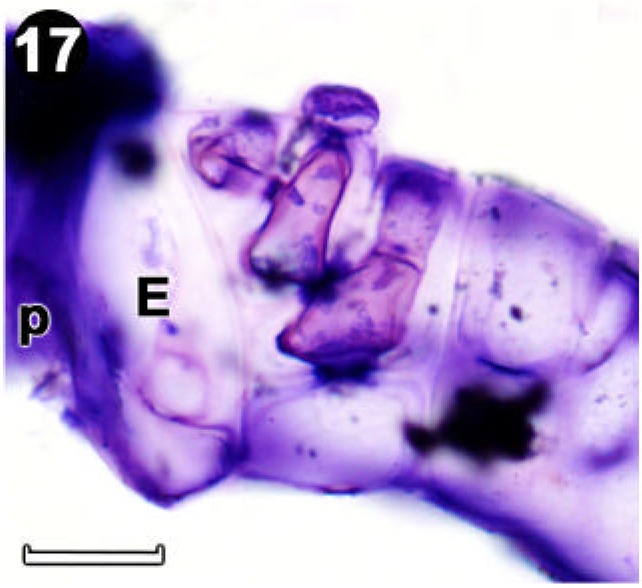

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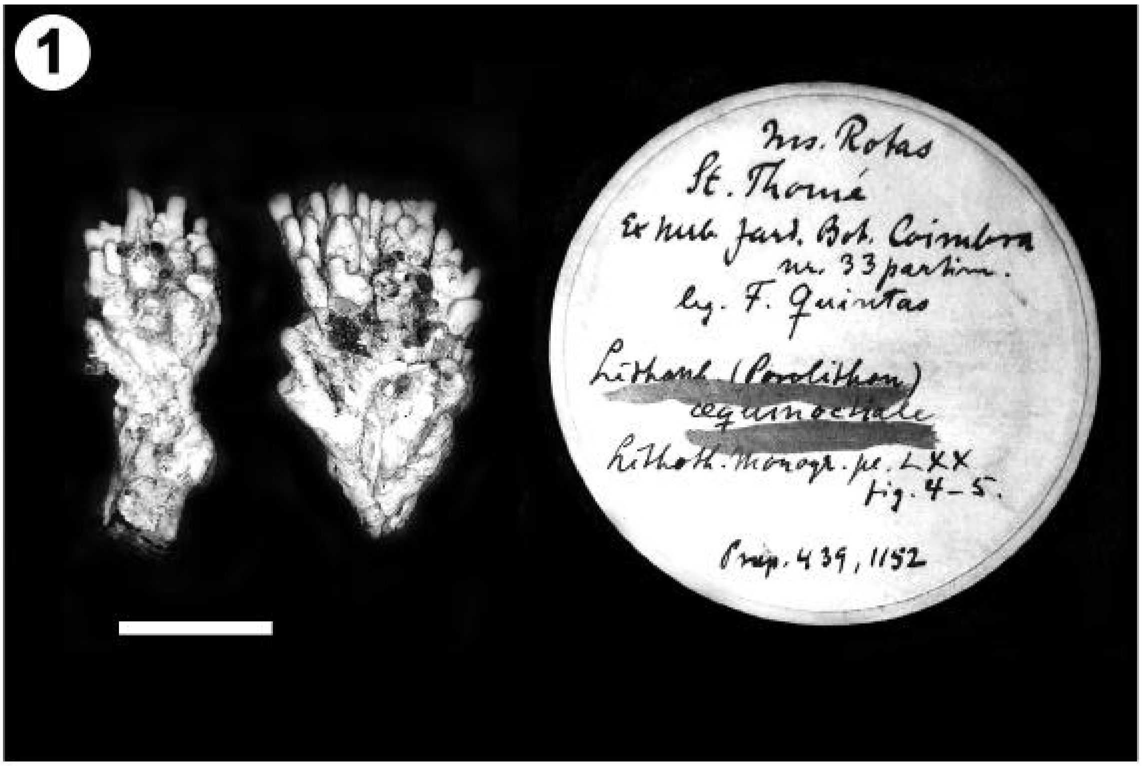
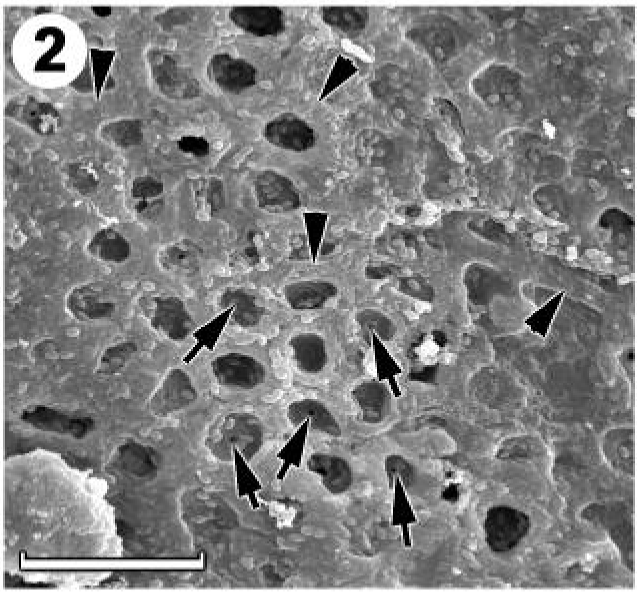


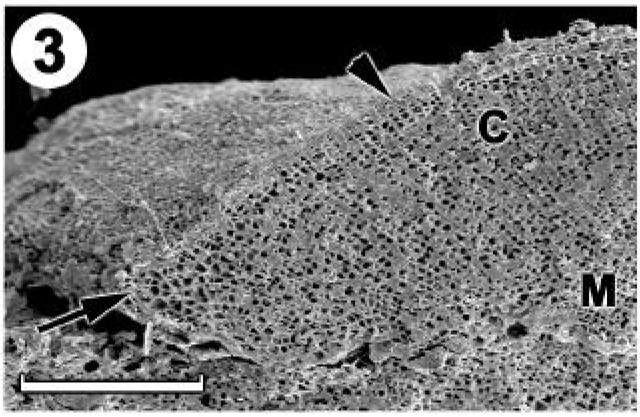
Ins. Rolas
St. Thomé
Ex herb. Jard. Bot. Coimbra
nr. 33 partim.
leg. F. Quintas

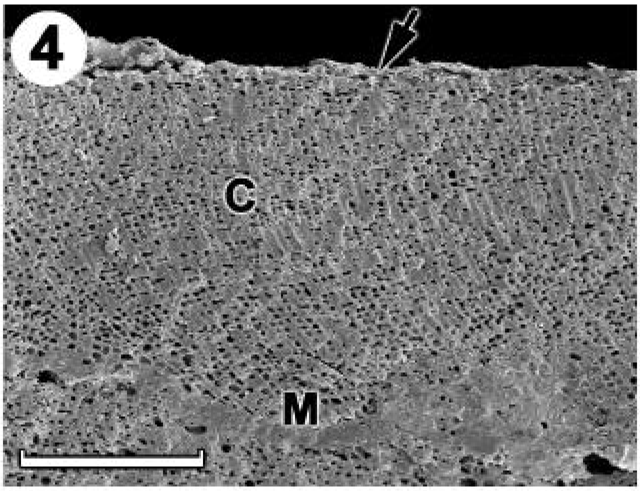
Lithoth. (Porolithon)
æquinoctiale
Lithoth. Monogr. pl. LXX
fig. 4–5.

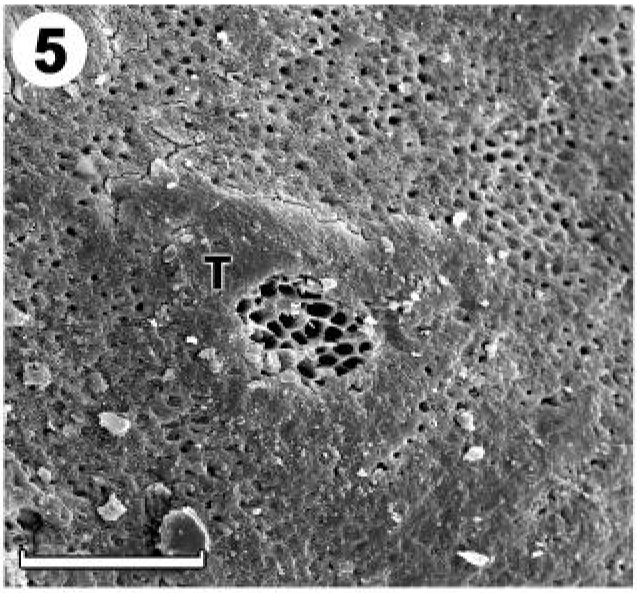
Prep. 439, 1152

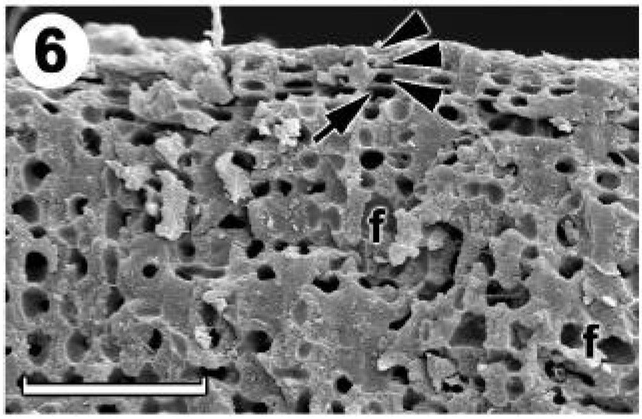
Plate 11

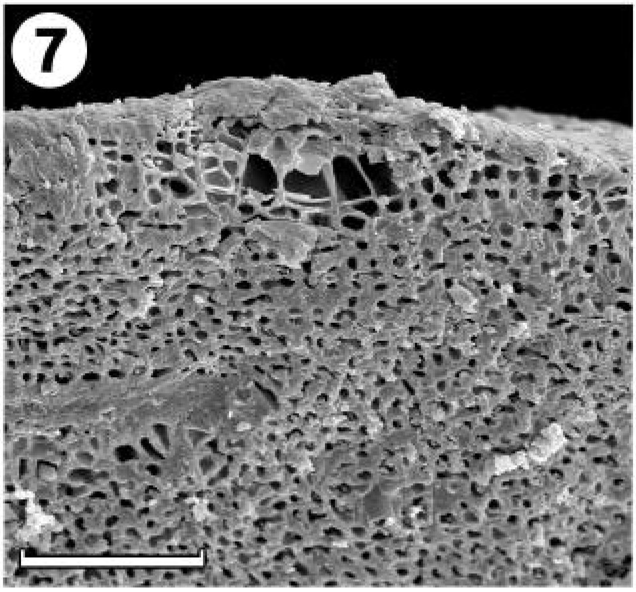


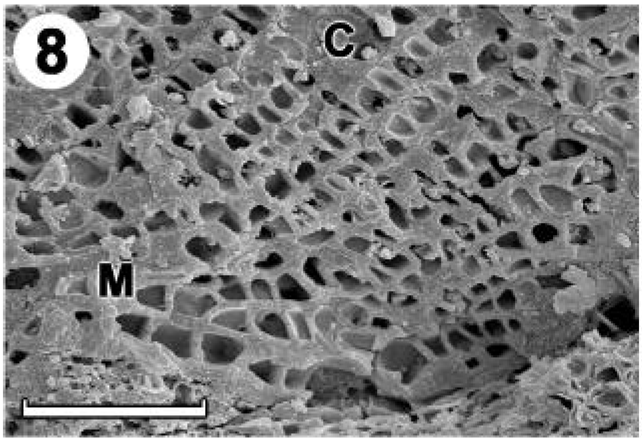












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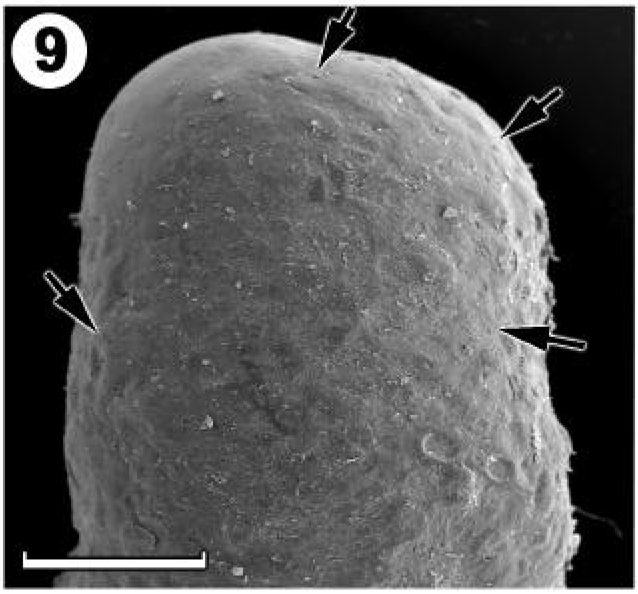


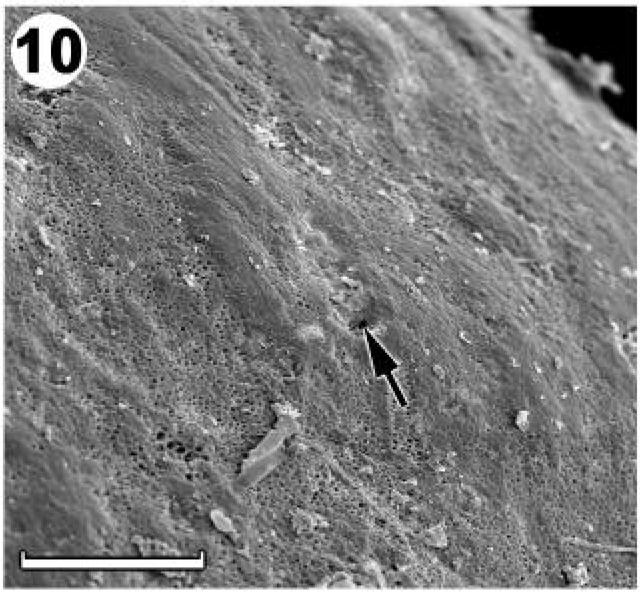
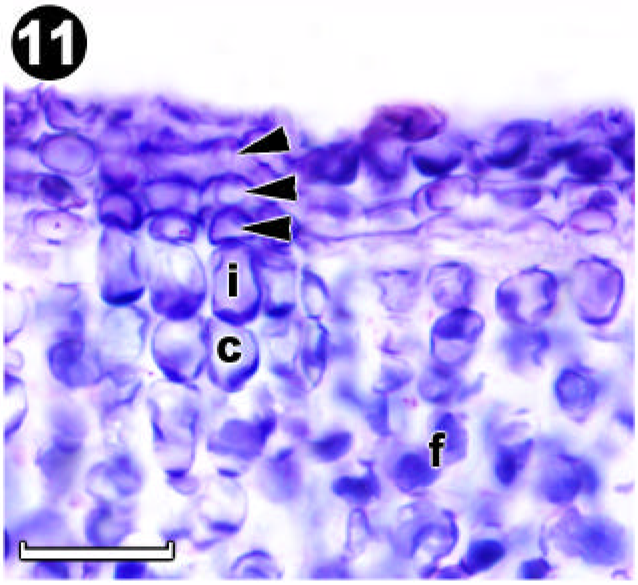
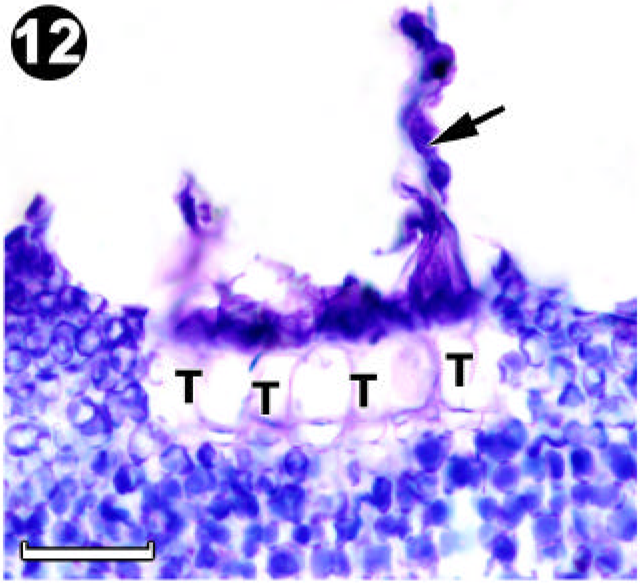
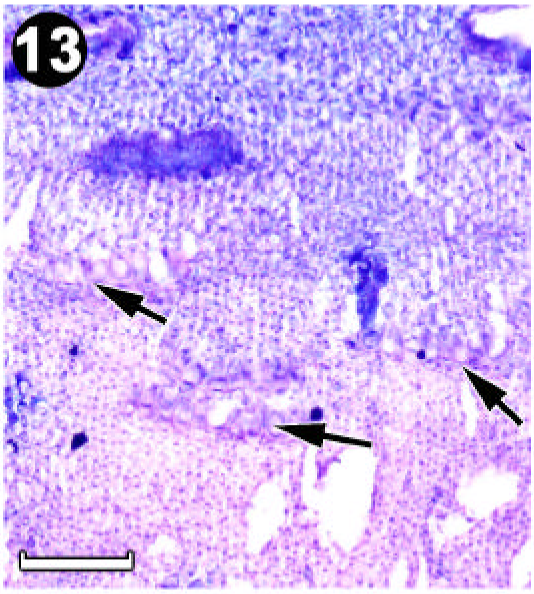
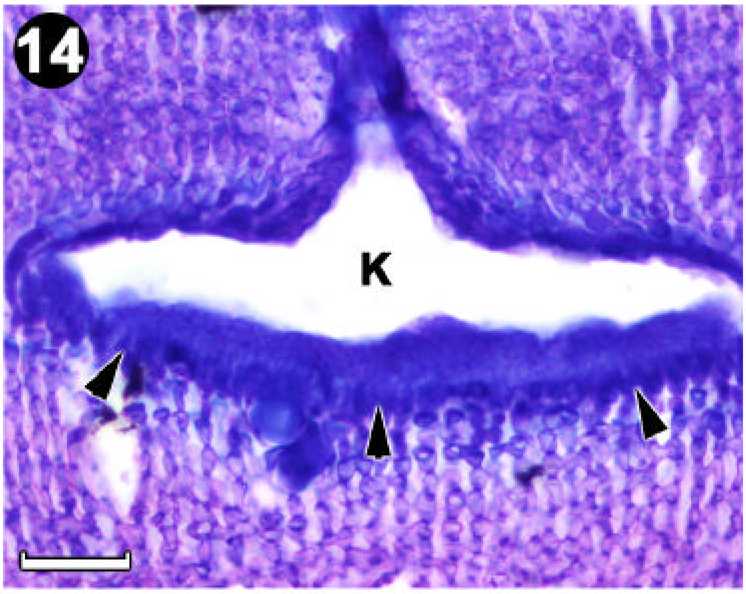


Plate 13









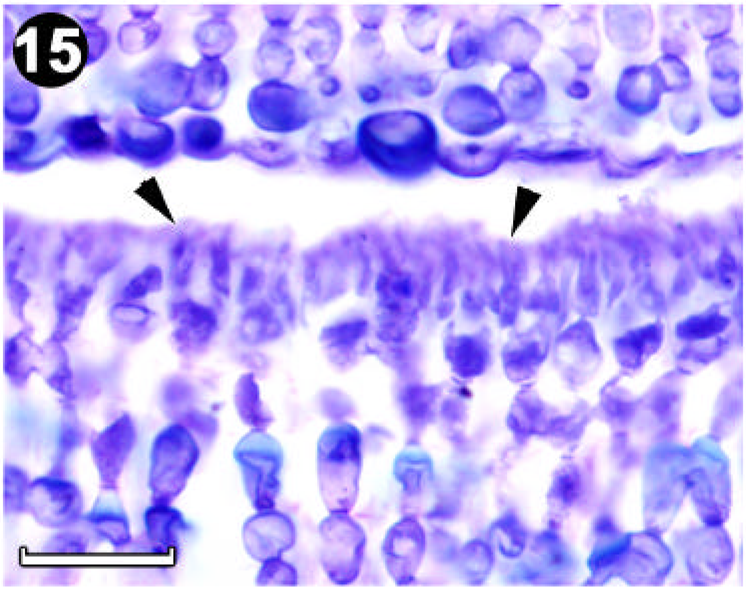
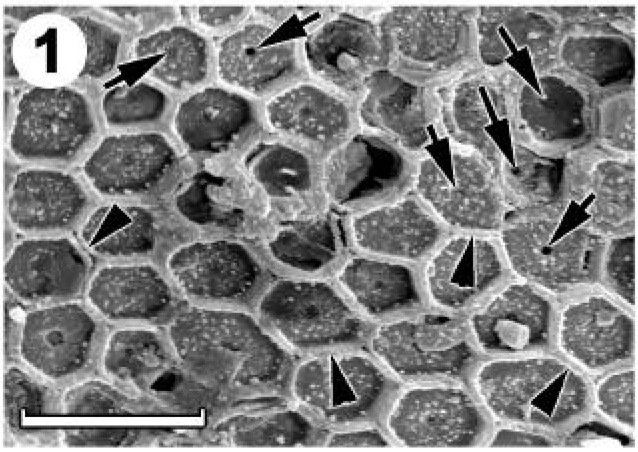
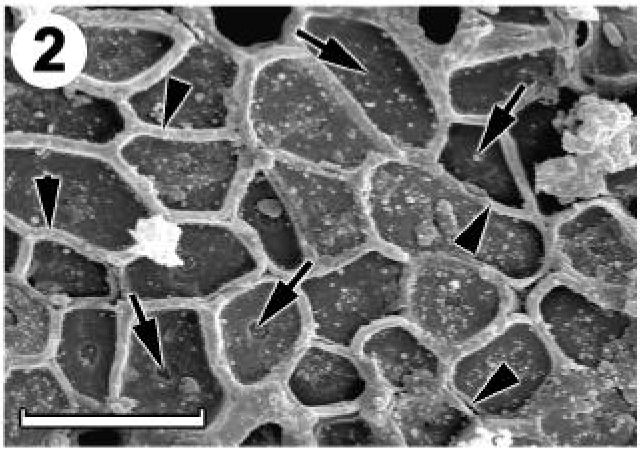
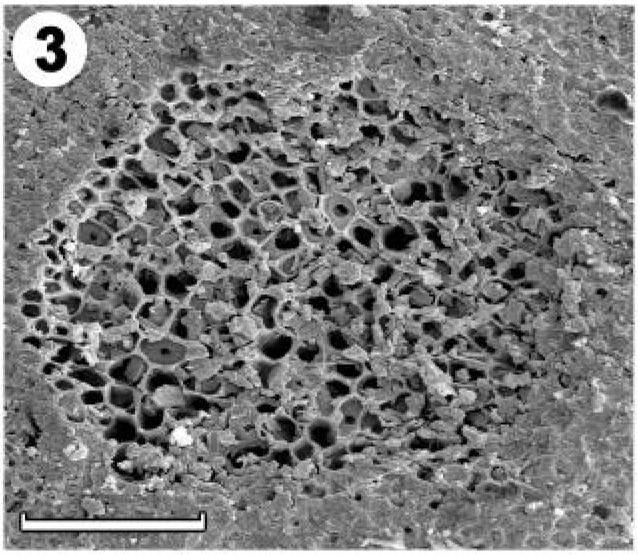
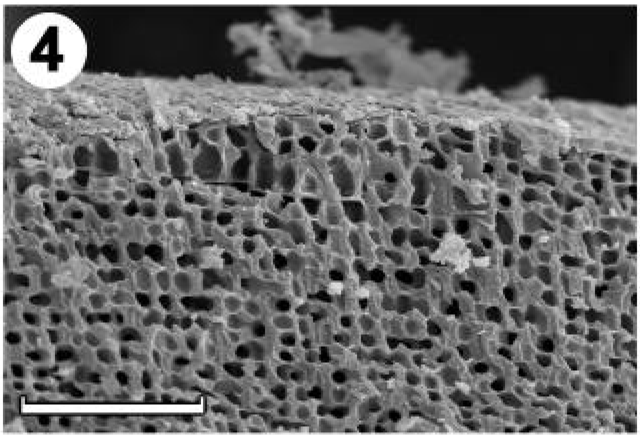


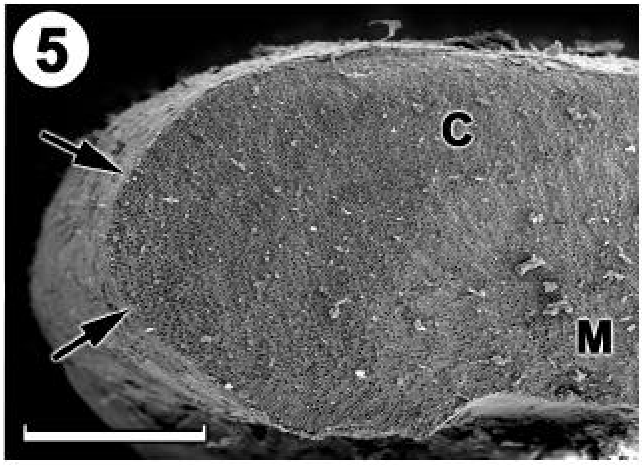
Plate 14

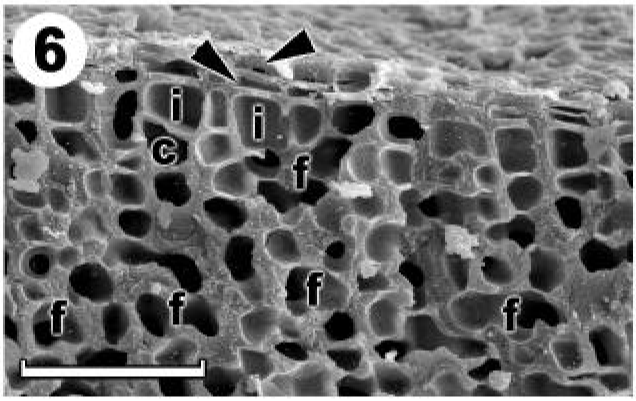


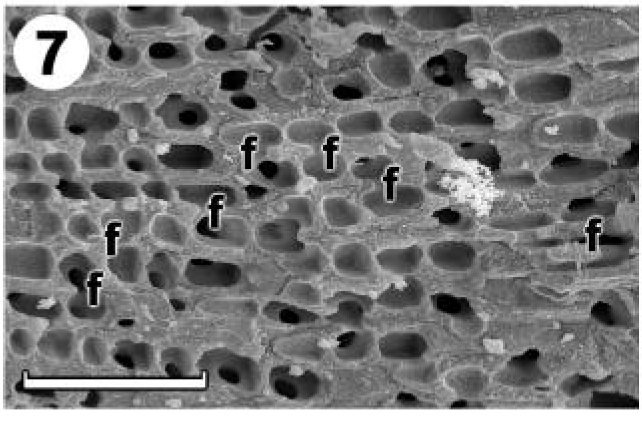


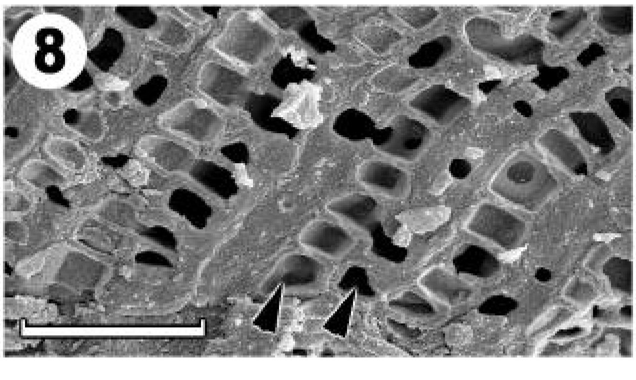












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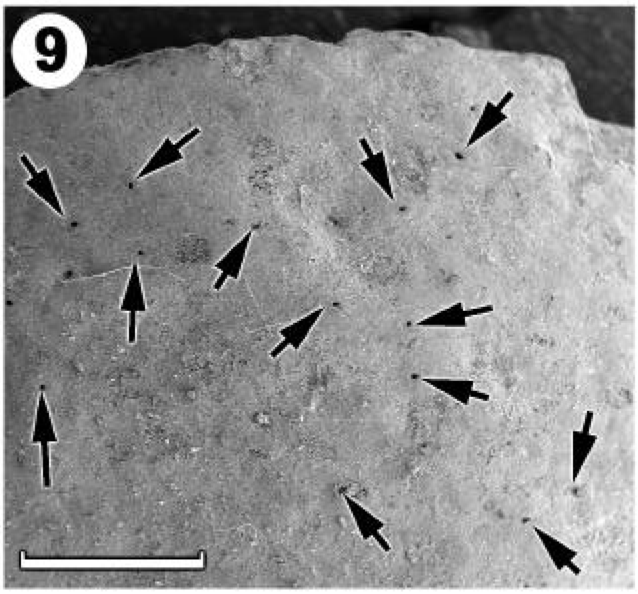
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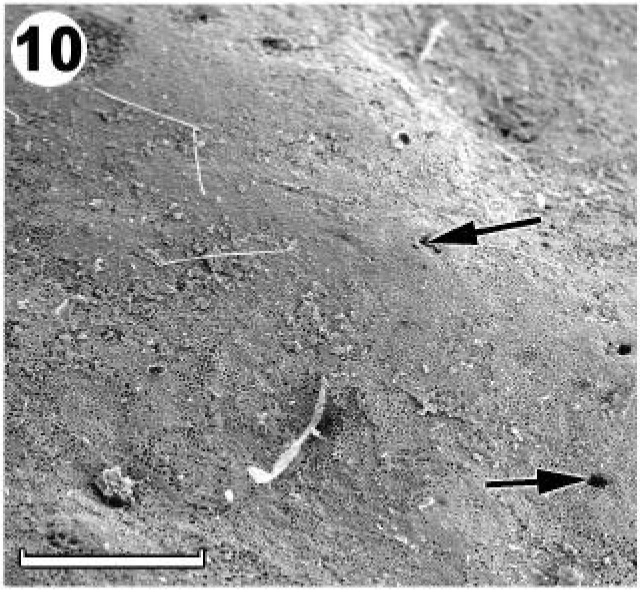
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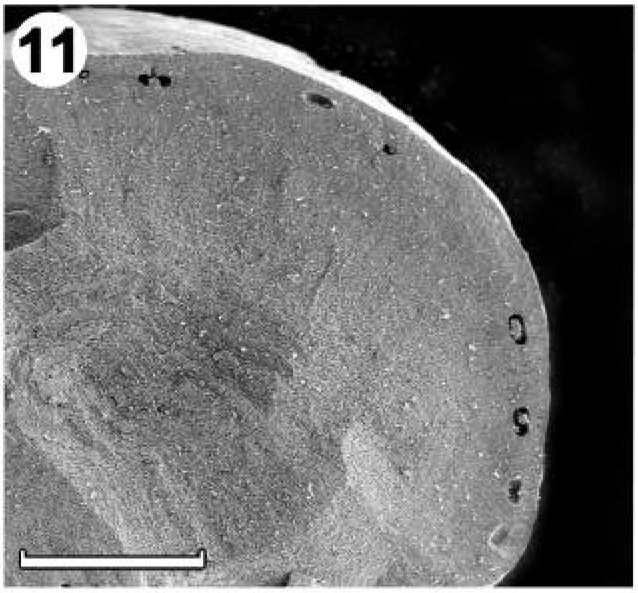
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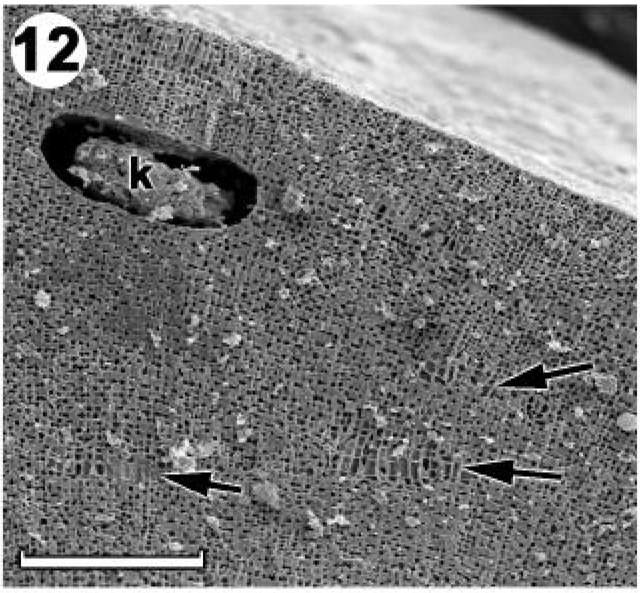
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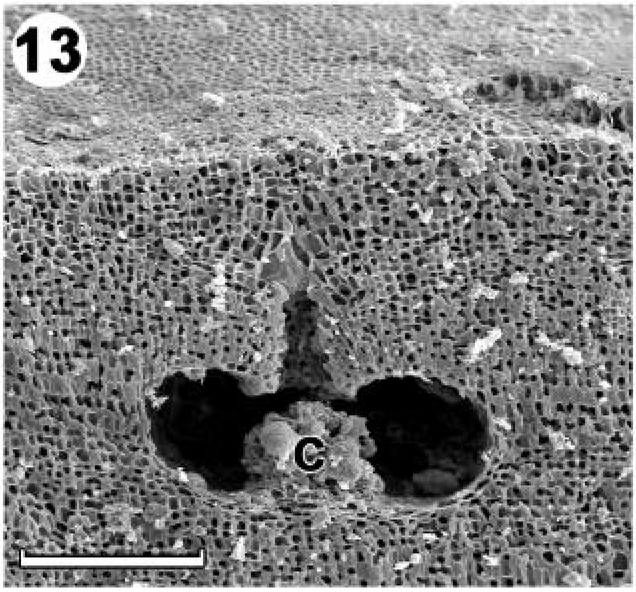
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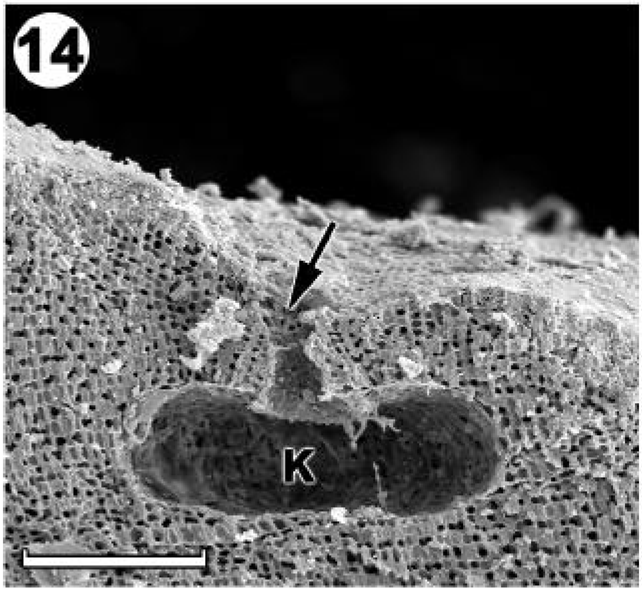
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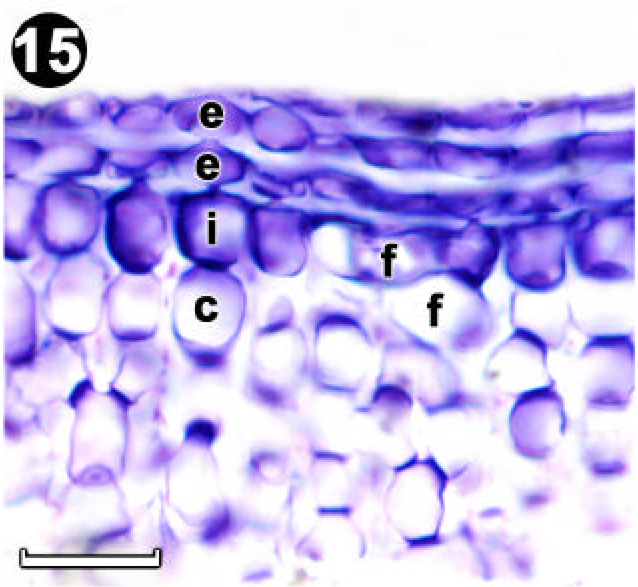
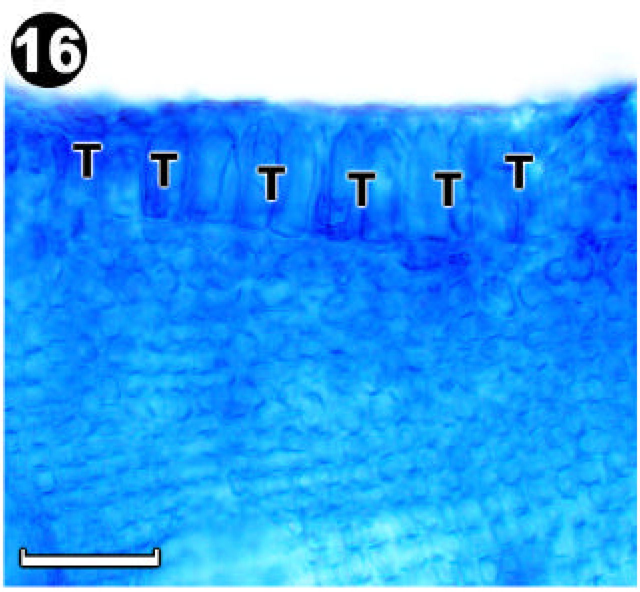
Plate 16





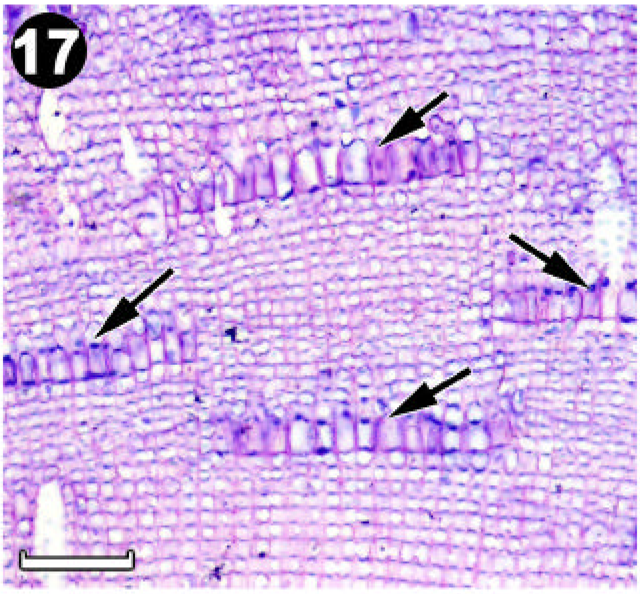
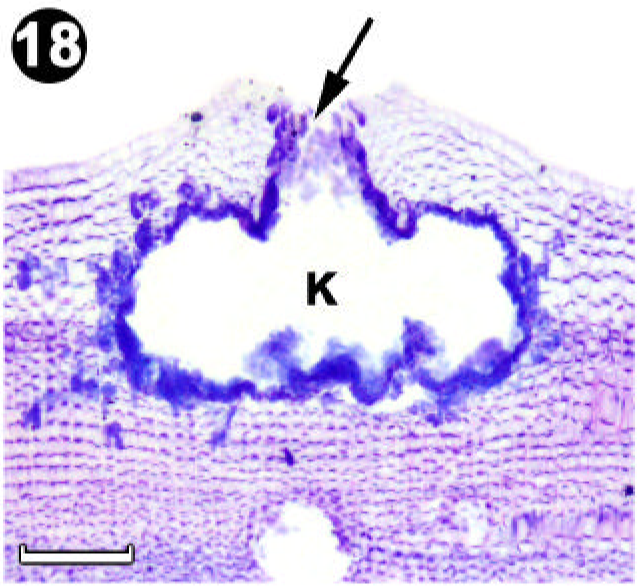
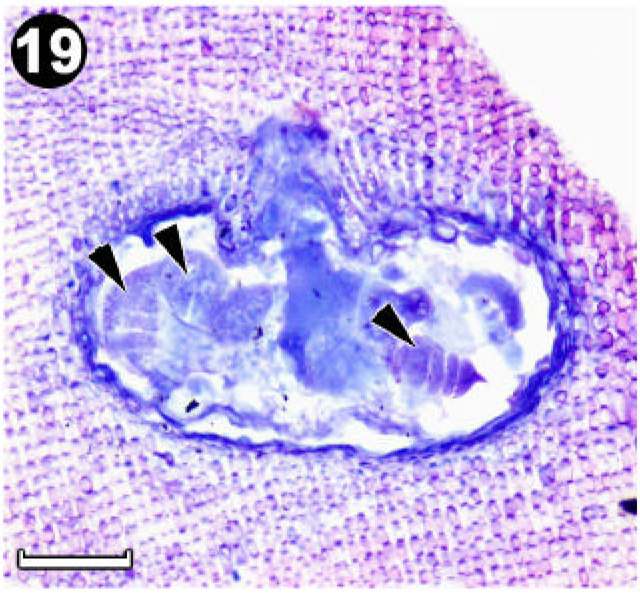
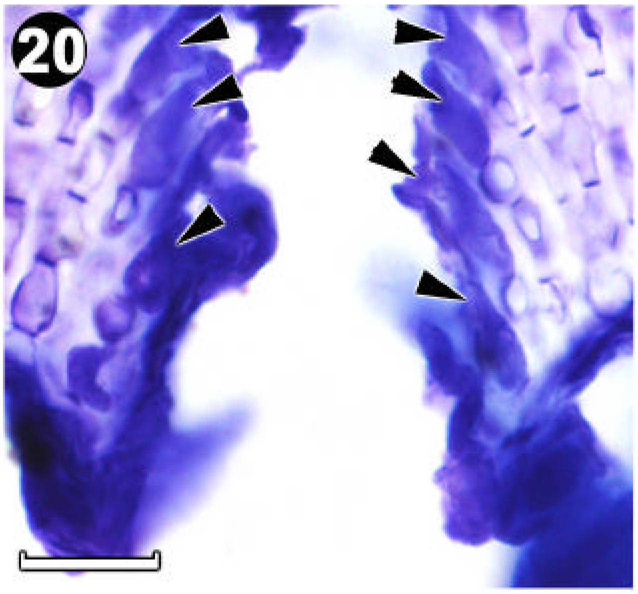
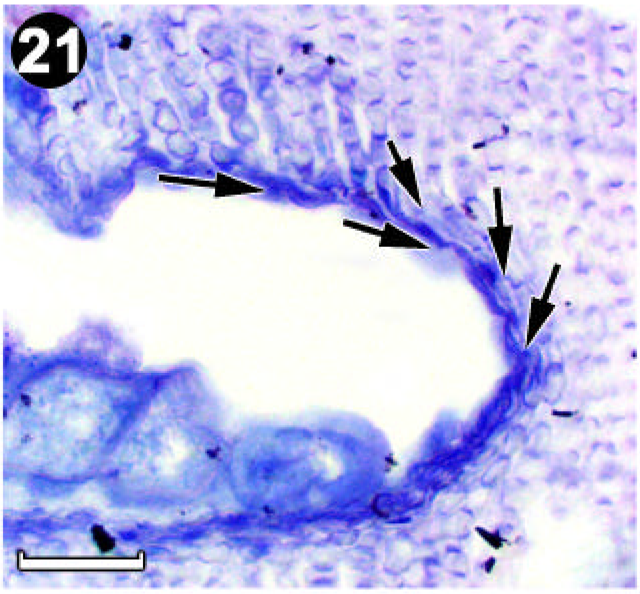


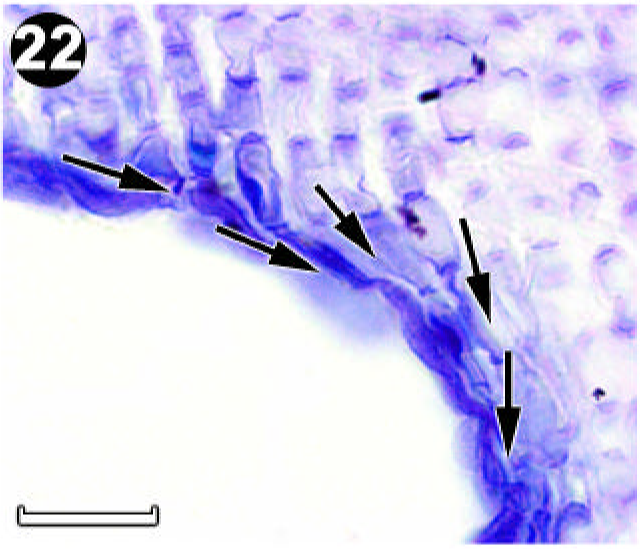
Plate 17











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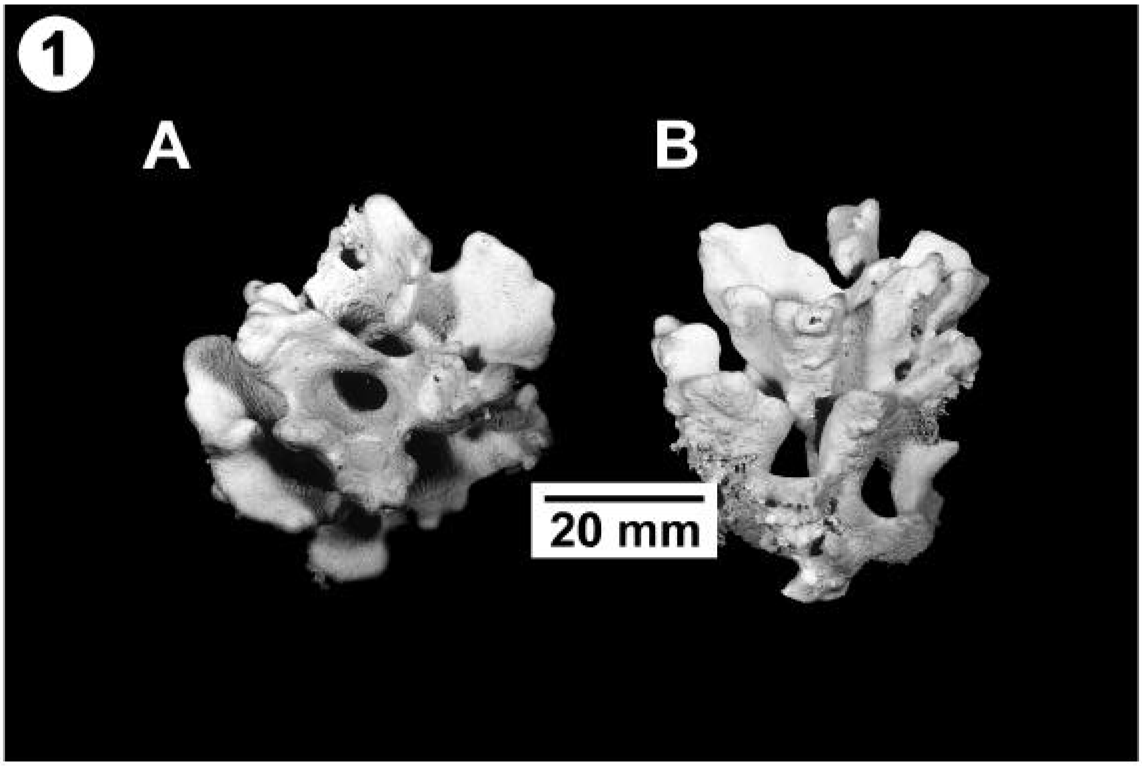
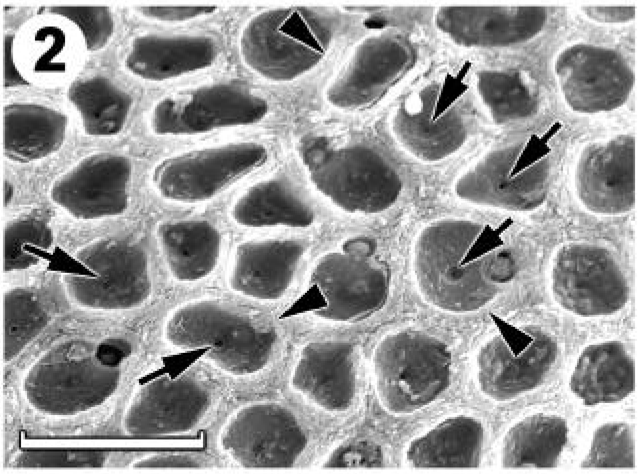
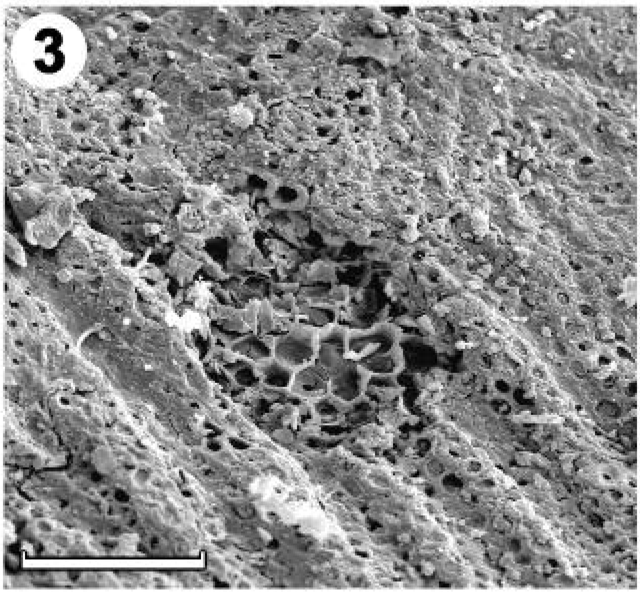
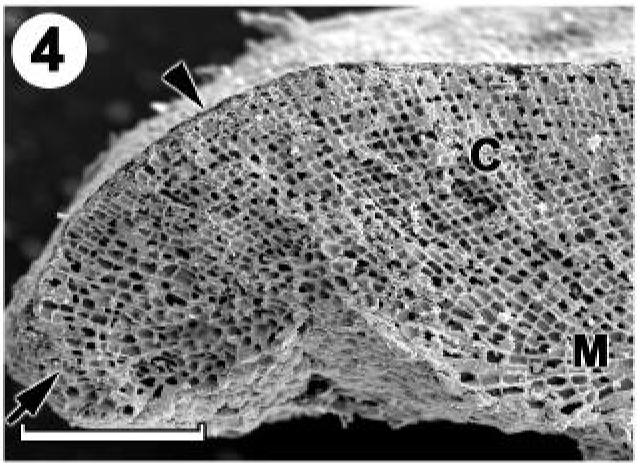
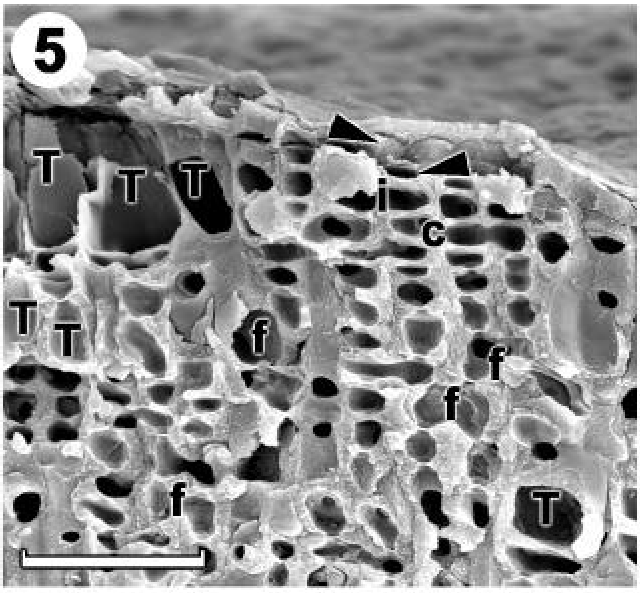


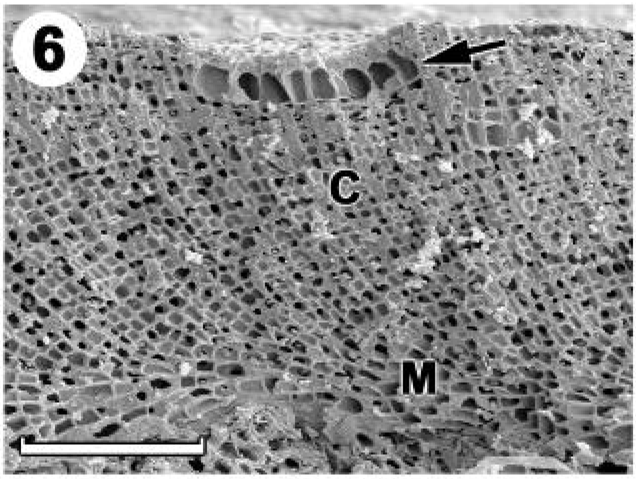
Plate 19

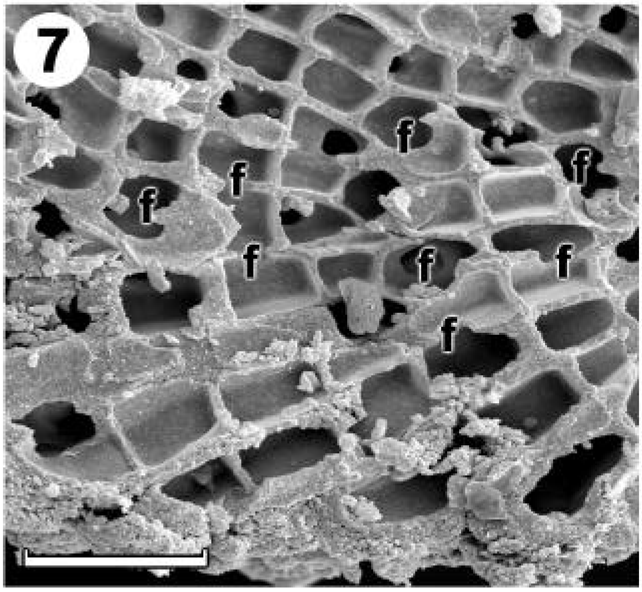


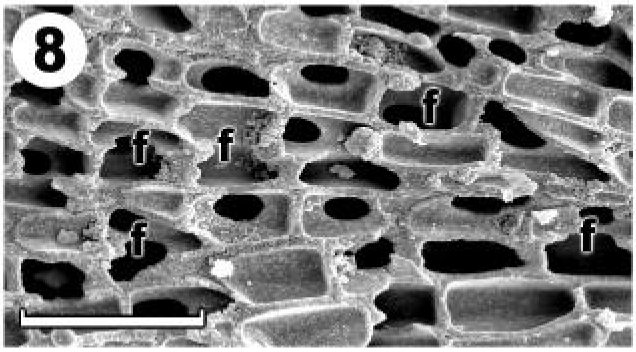












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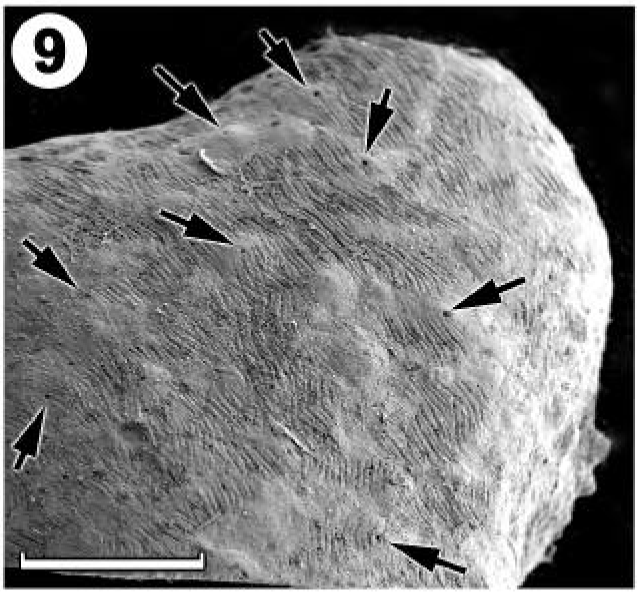
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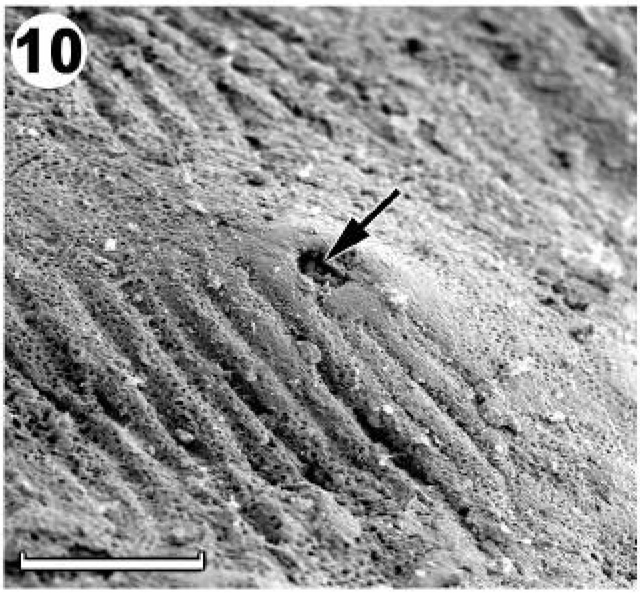
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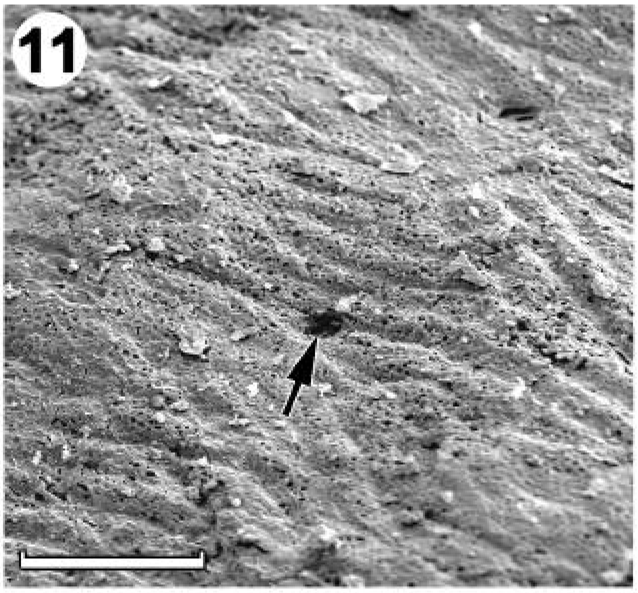
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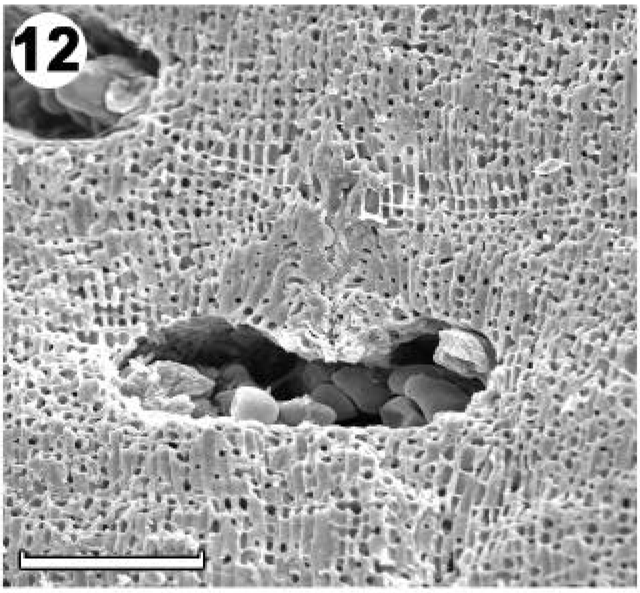
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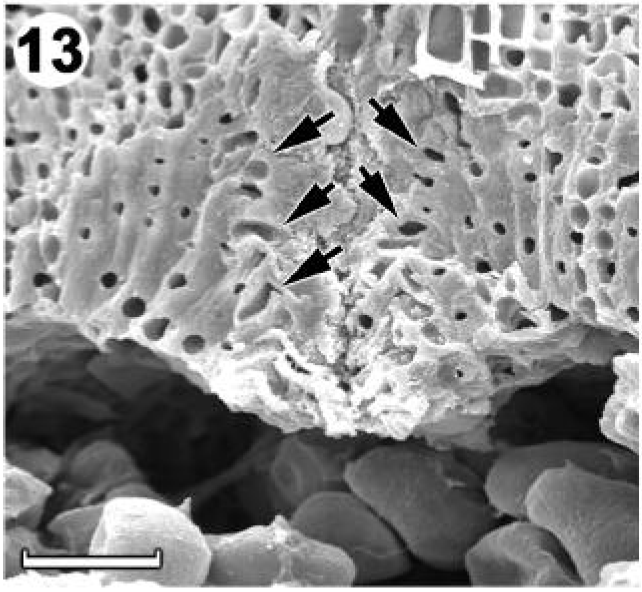
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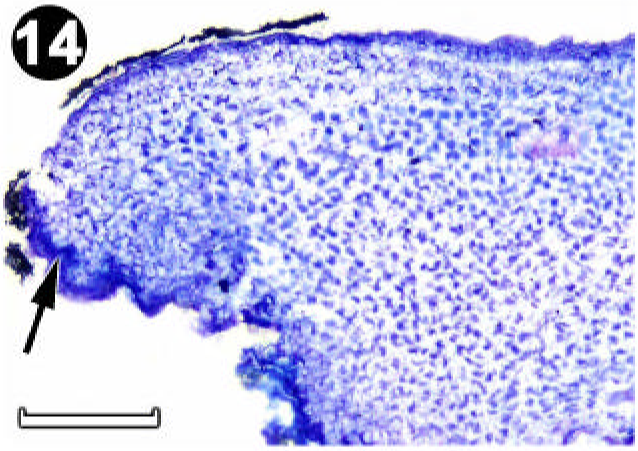
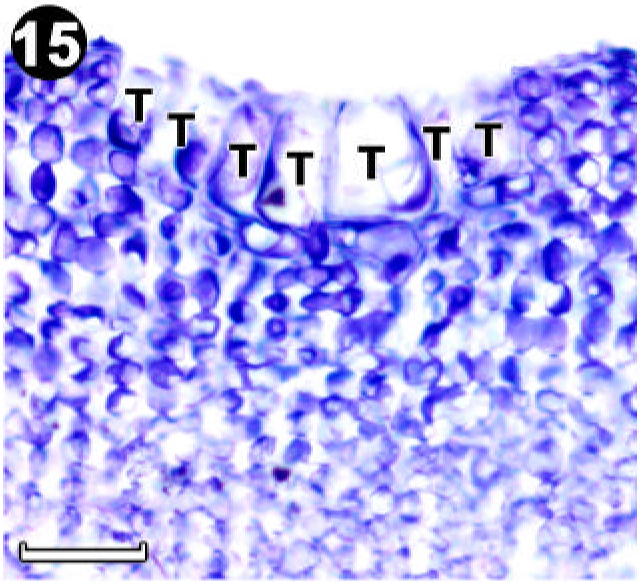
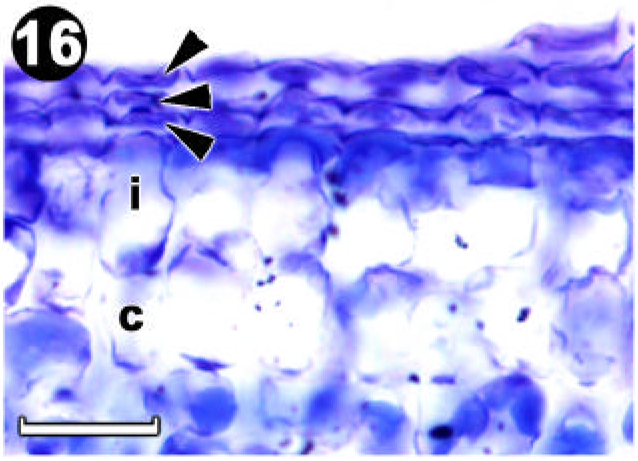
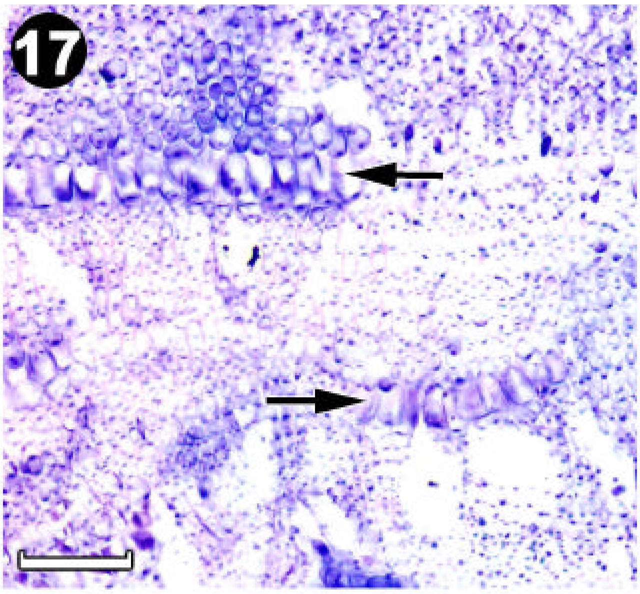
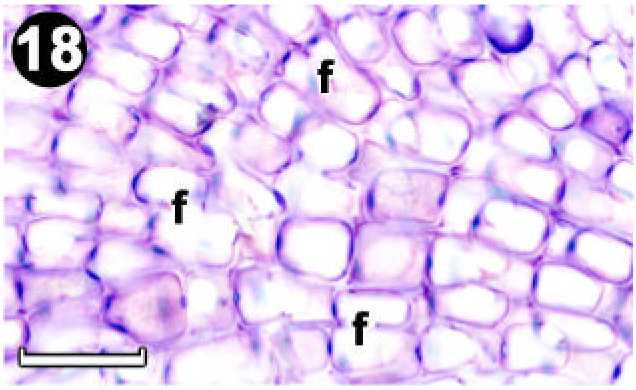
Plate 21

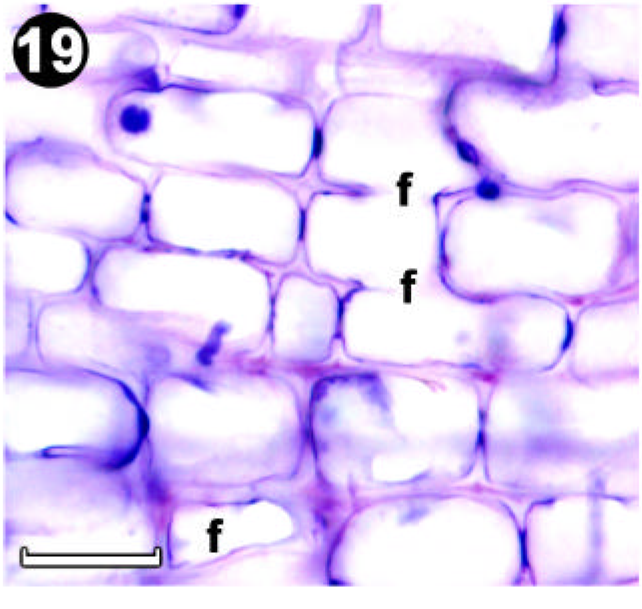












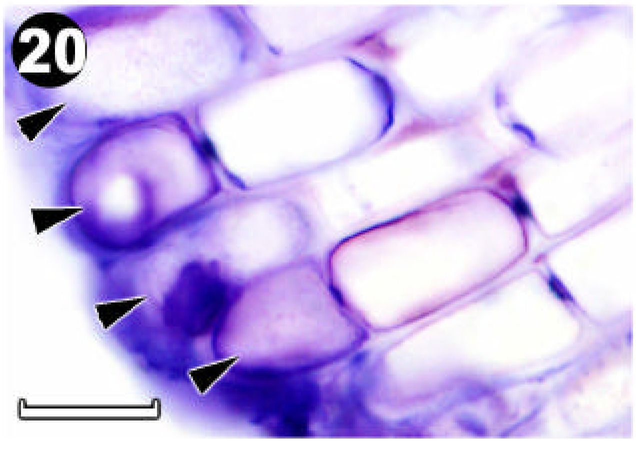


Plate 22

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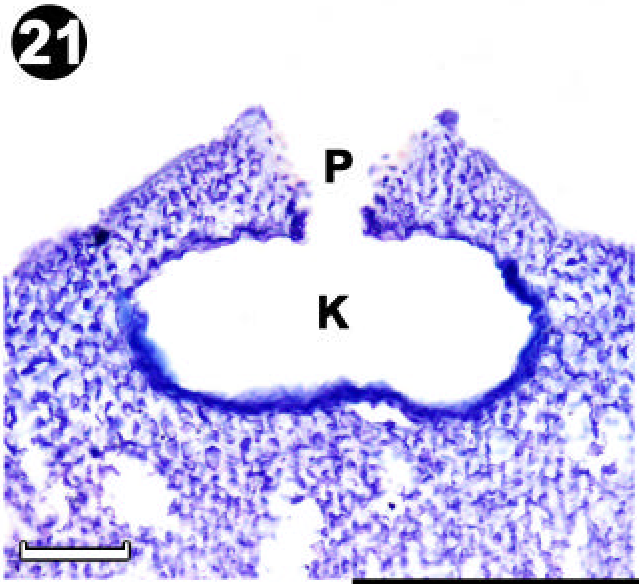

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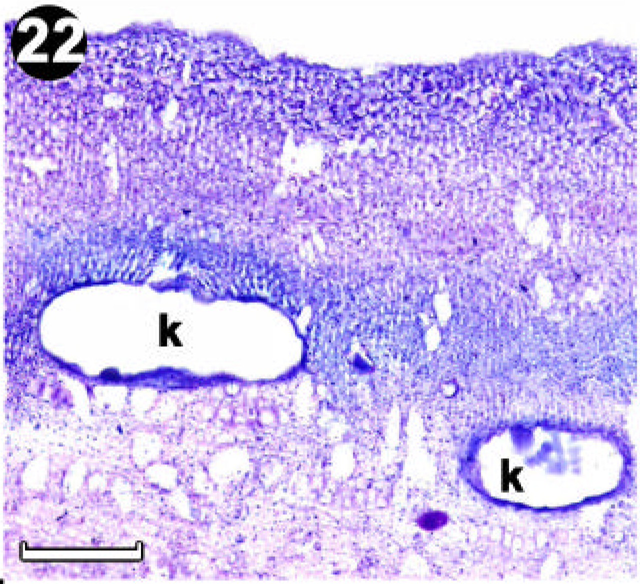

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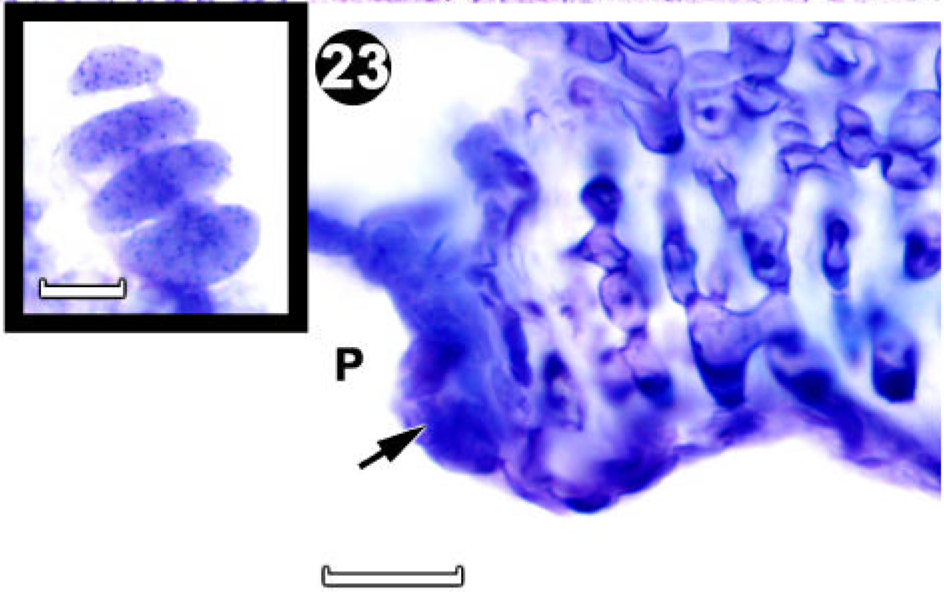

Plate 23

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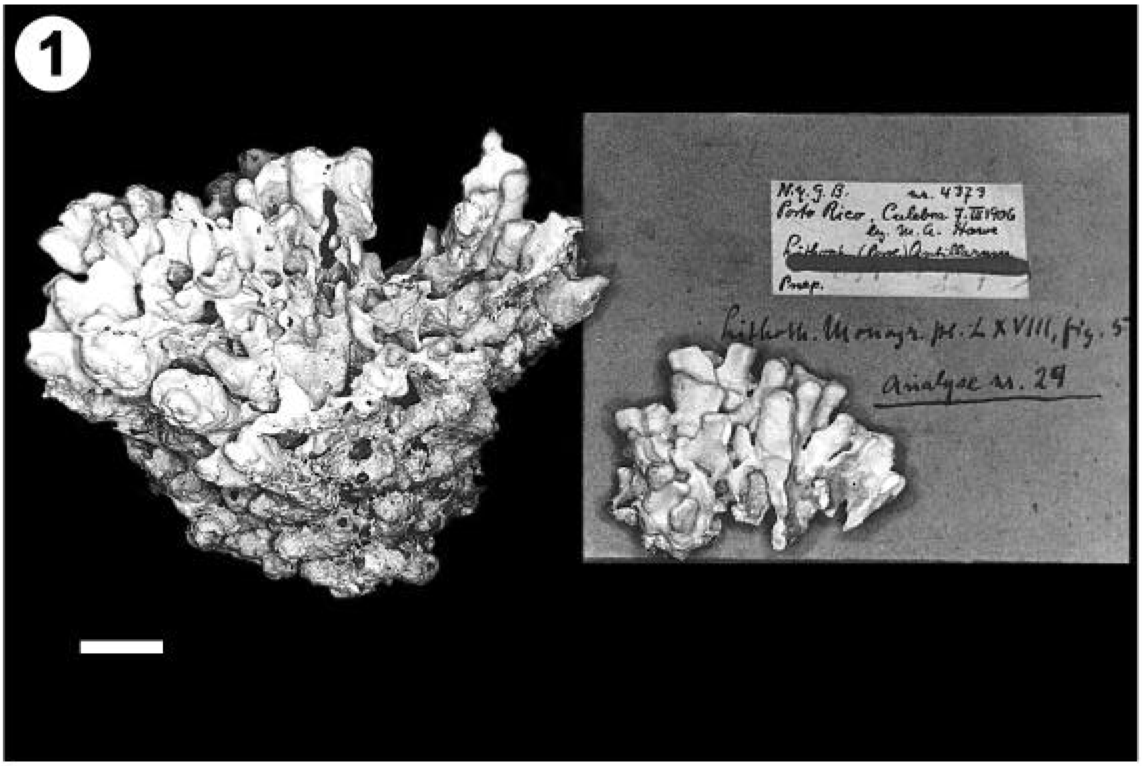
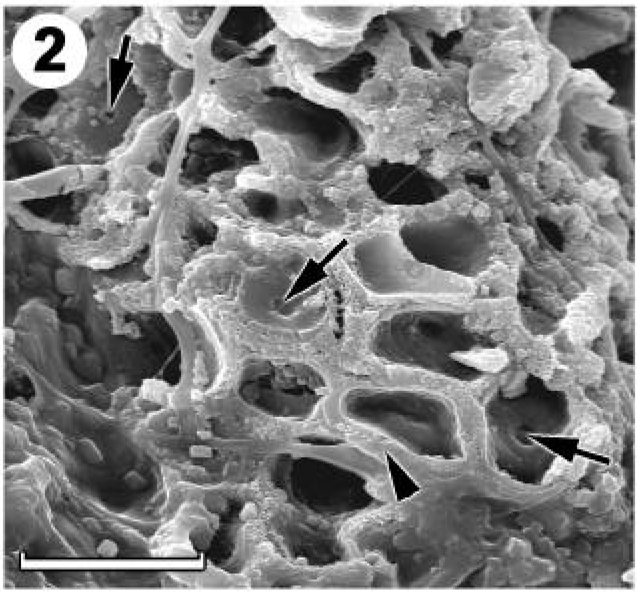
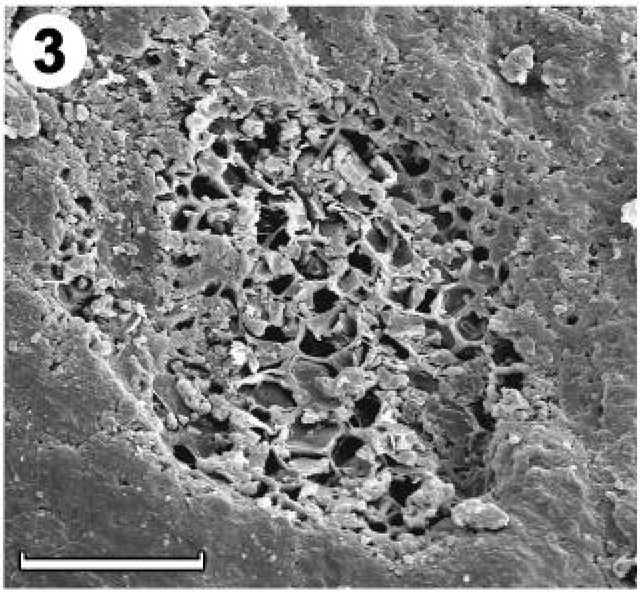
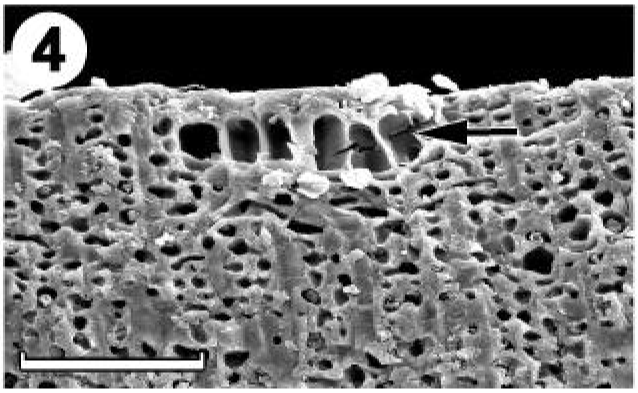
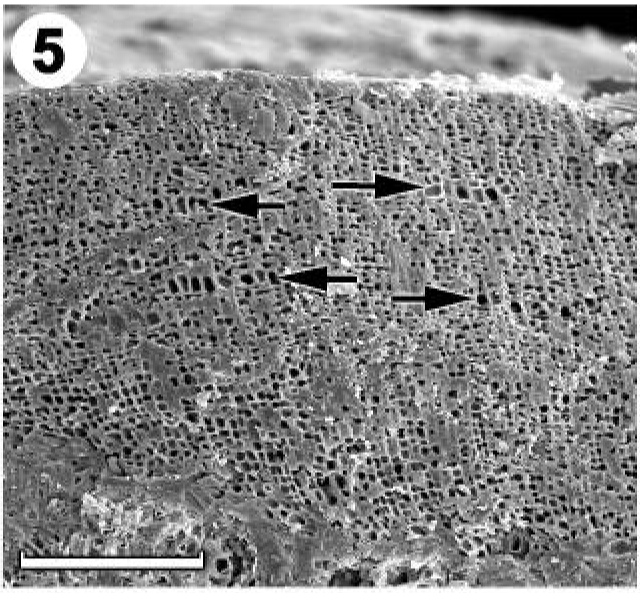

N.Y.G.B. nr. 4373
Porto Rico, Culebra 7.III.1906
by M. A. Howe
Lithoth. (Poro.) Antillarum
Prep.
Lithoth. Monogr. pl. LXVIII, fig. 5
Analyse nr. 29

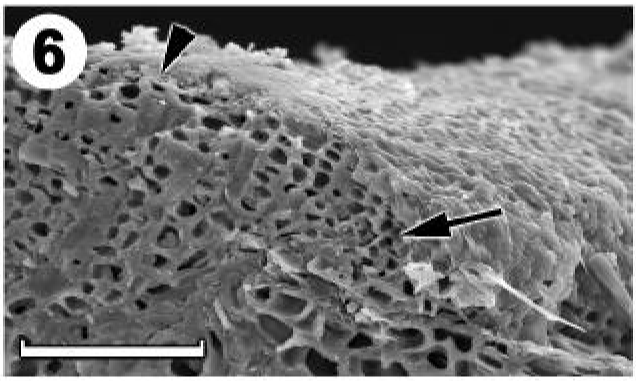
Plate 24

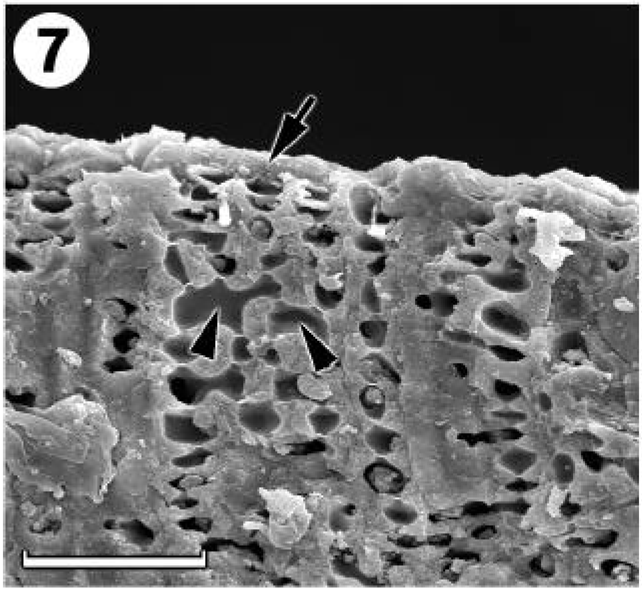












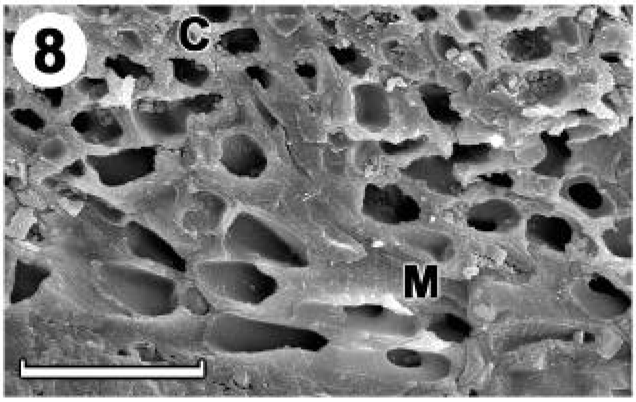
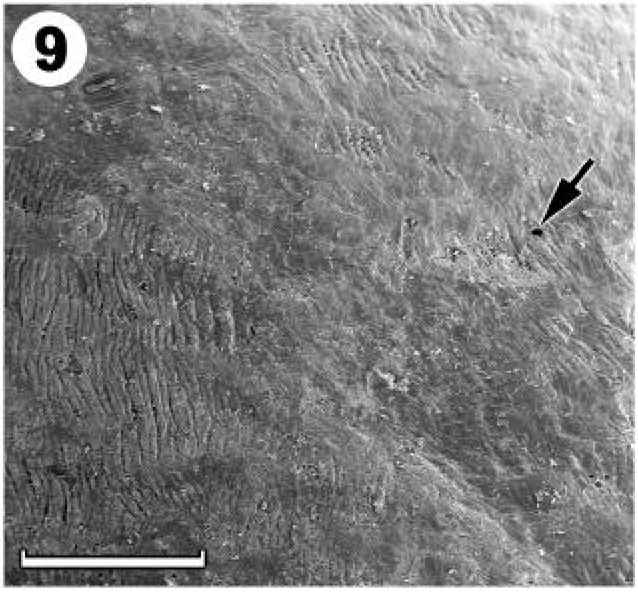
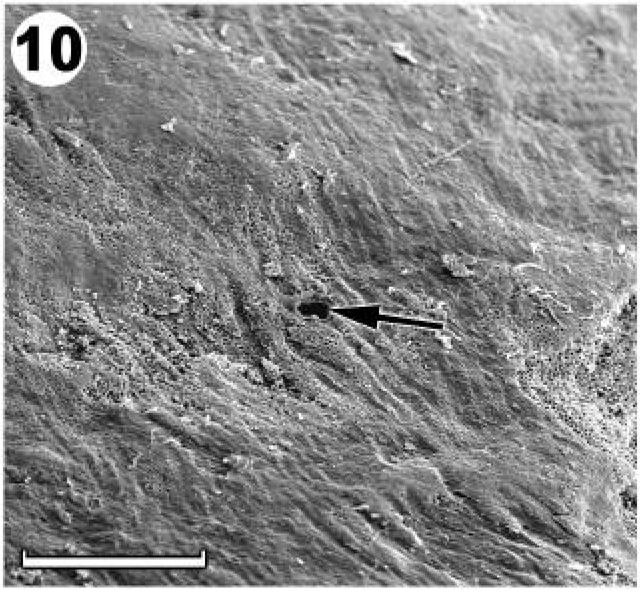
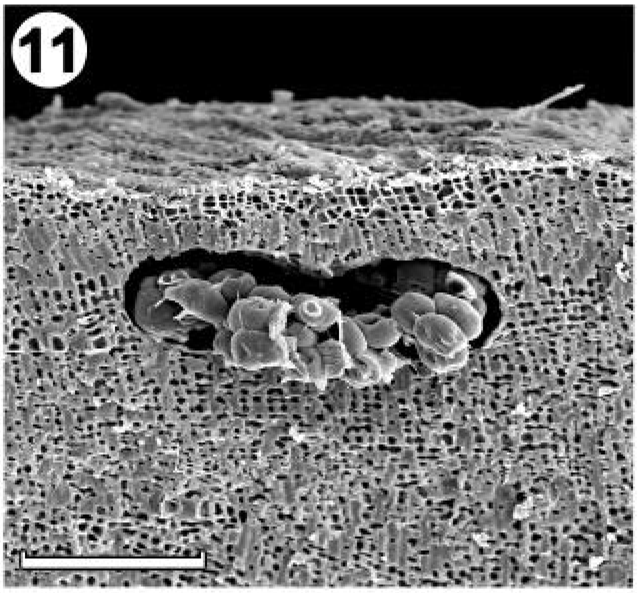


Plate 25







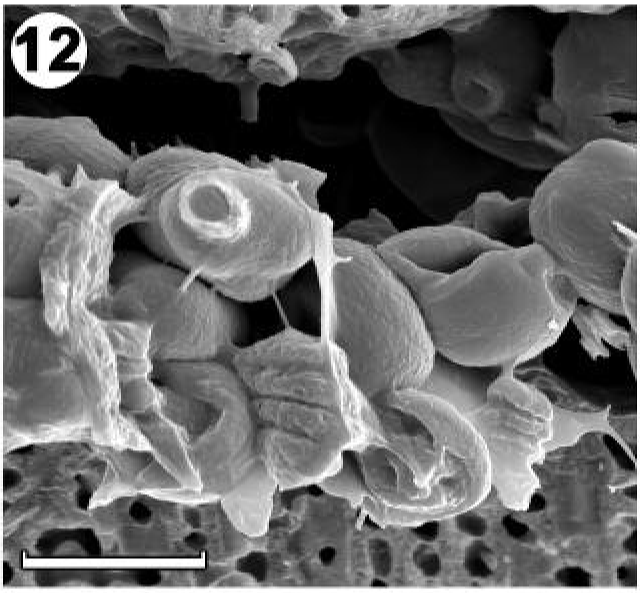
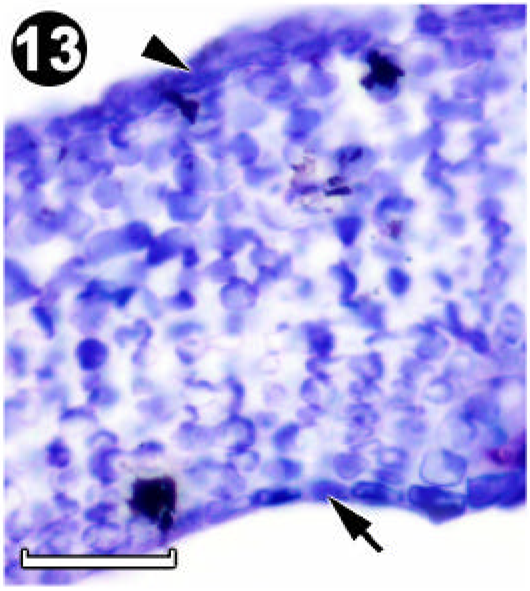
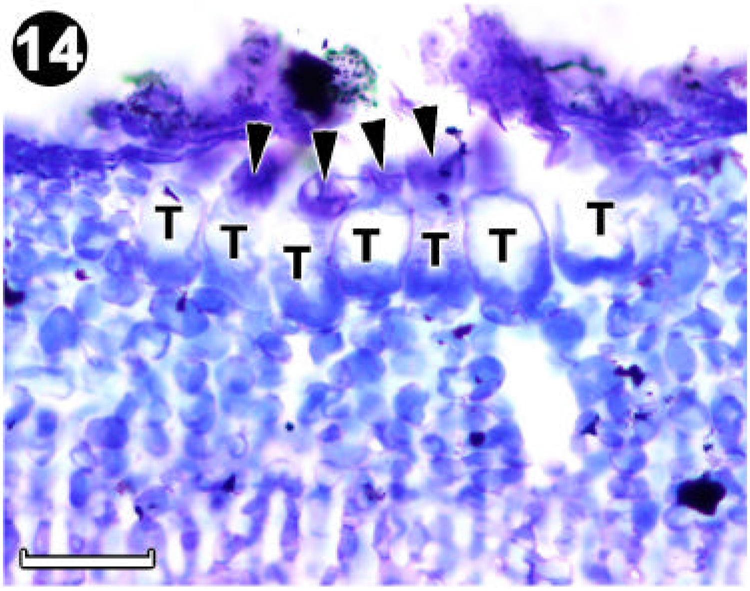
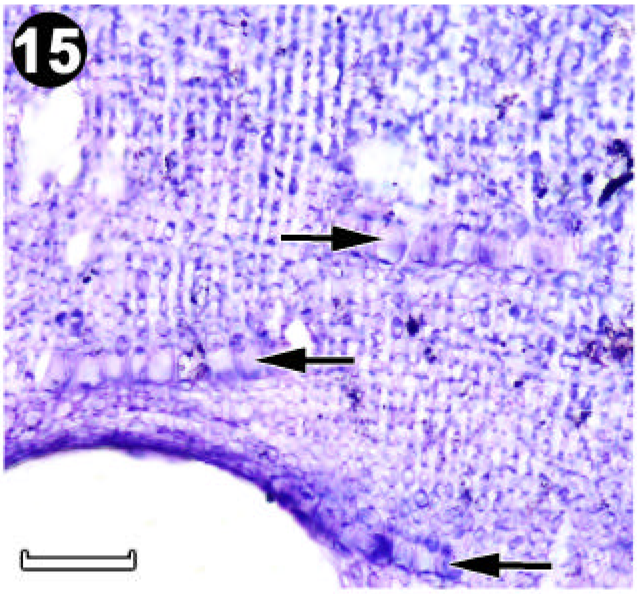
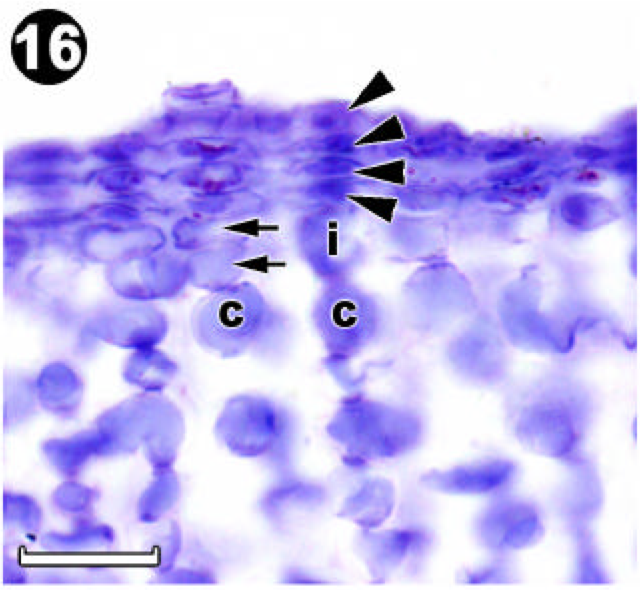


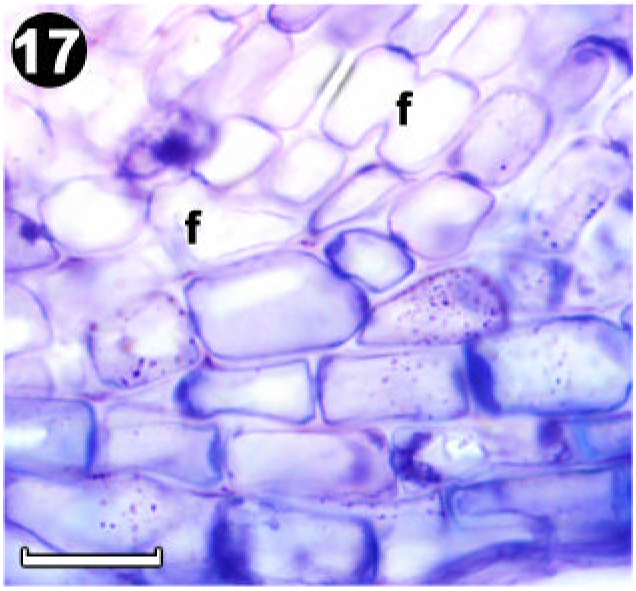
Plate 26











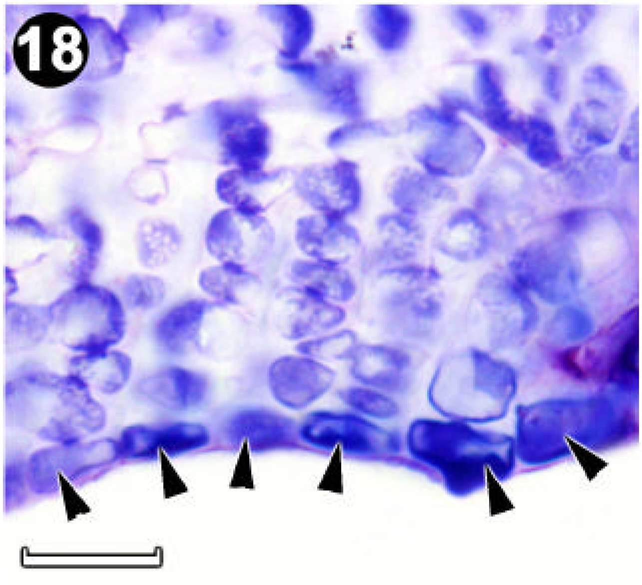


Plate 27

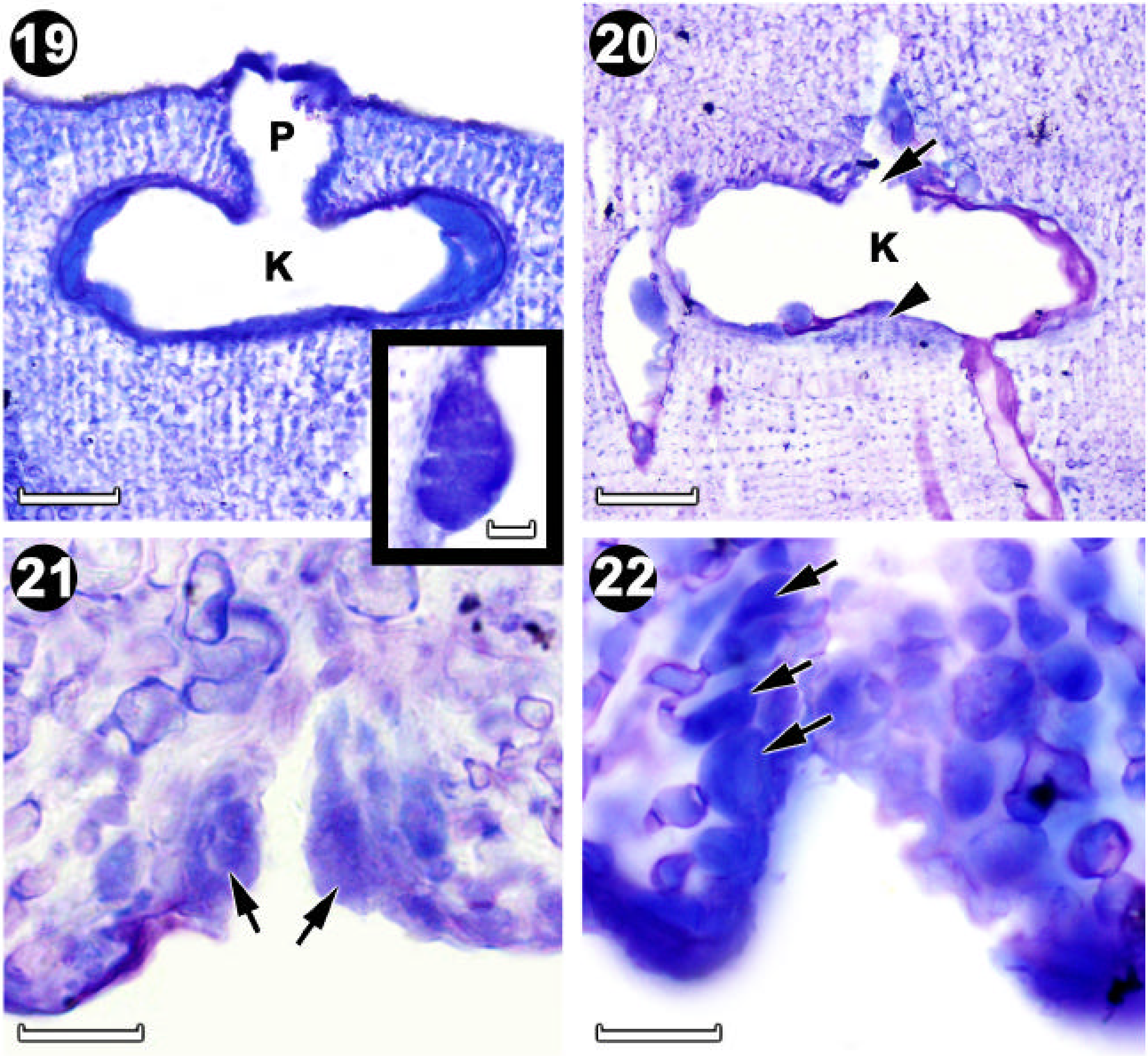


Plate 28


1
Prep. 286, 288, 1429
Cocos isl. Keeling-öarne
Josephine. sp. (?). 11°50'S.
96°51'O
Lithoph. (Porolithon)
coarctatum
f. typica
Lithoth. Monogr. pl. LXX
fig. 2.

Plate 29

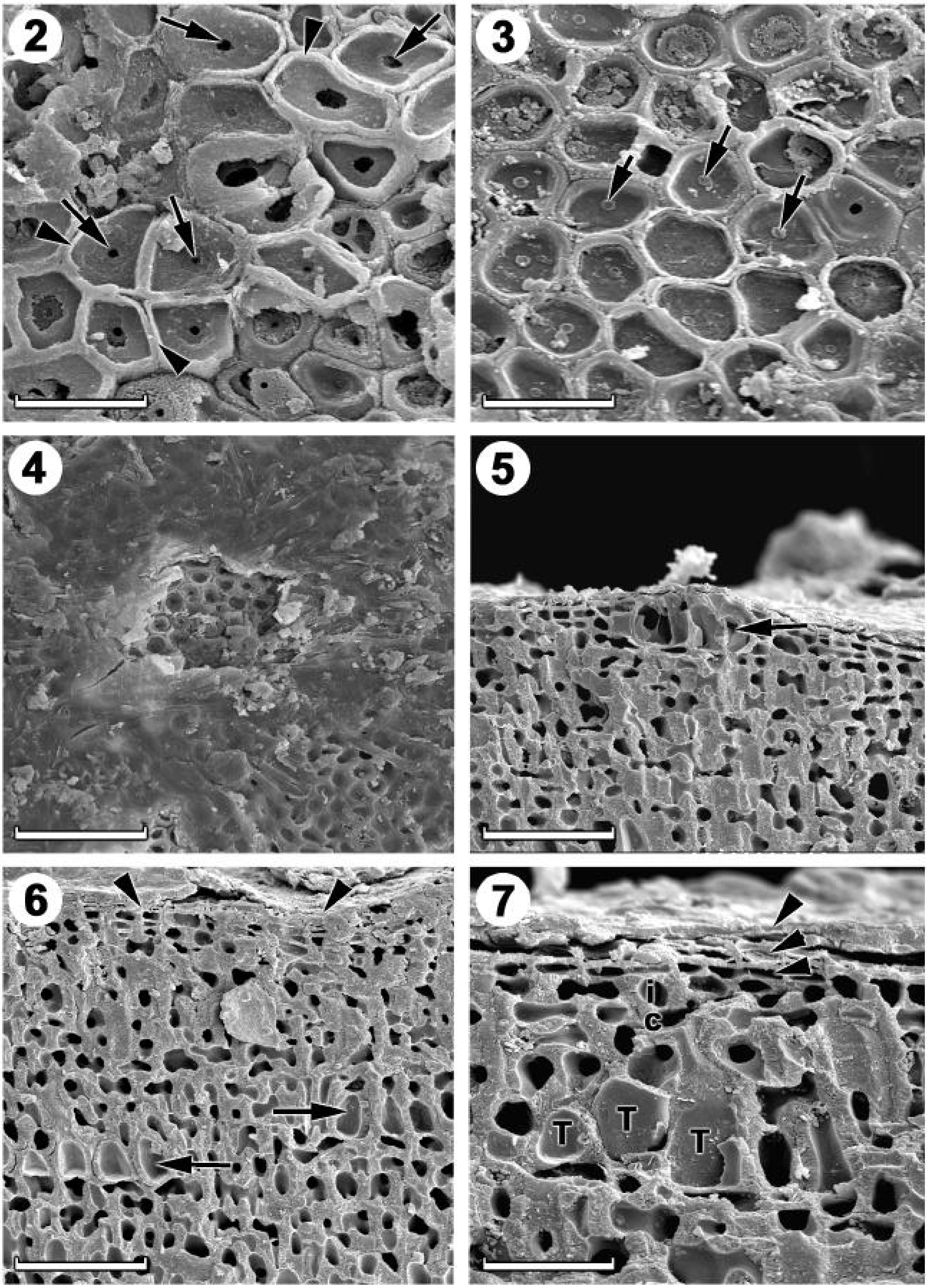
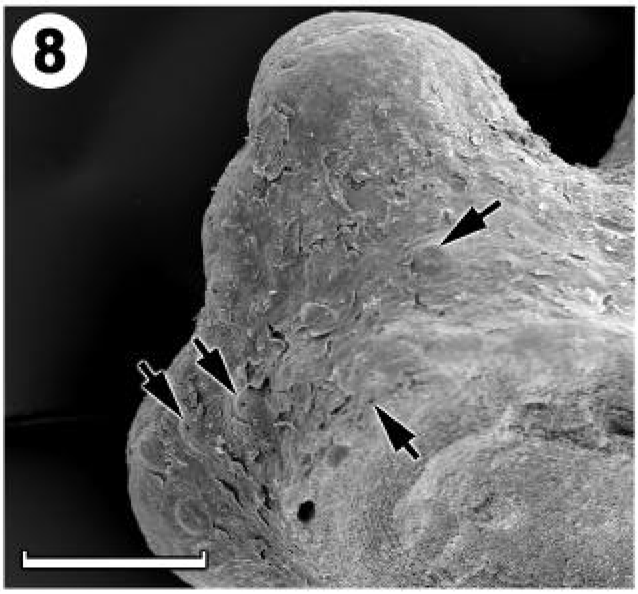
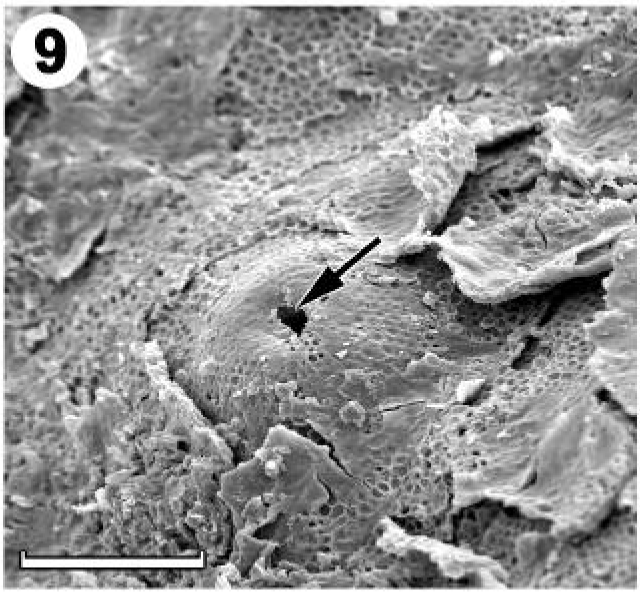
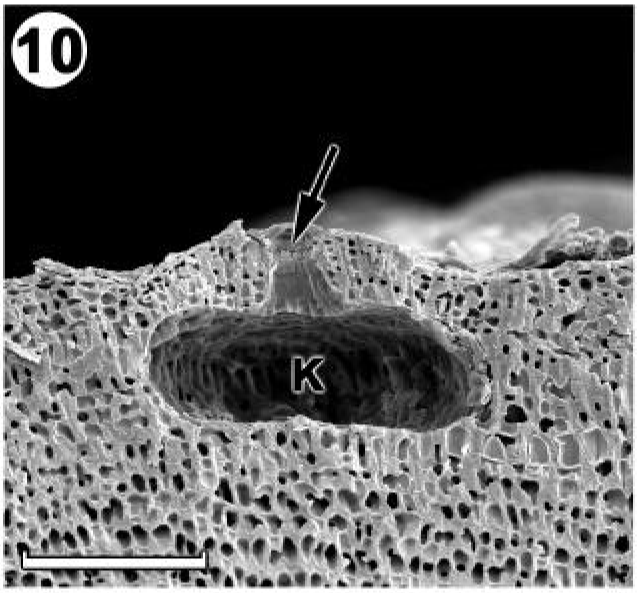
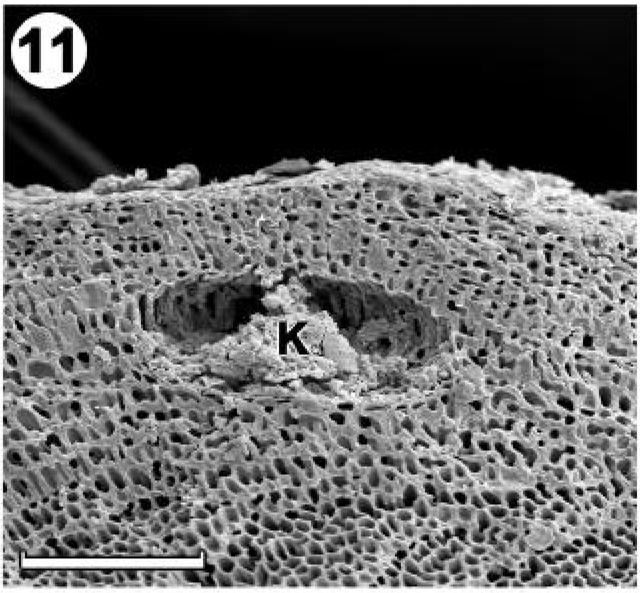


Plate 30









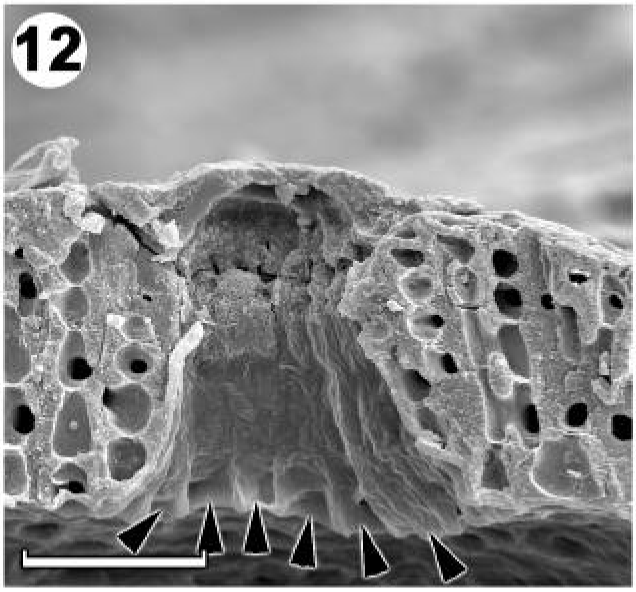
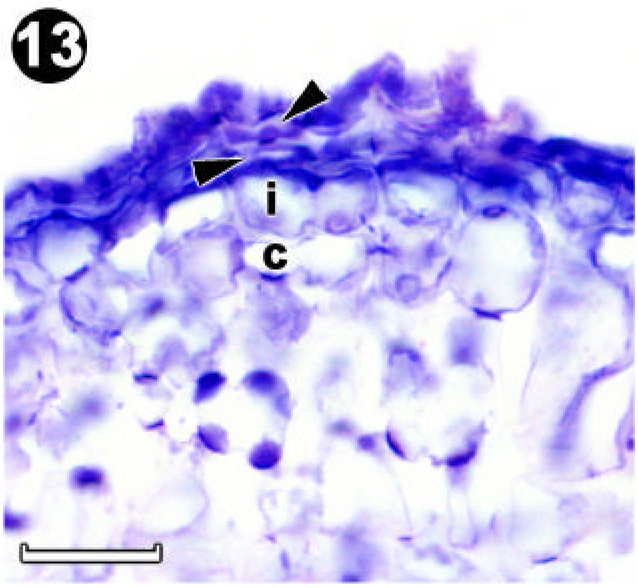
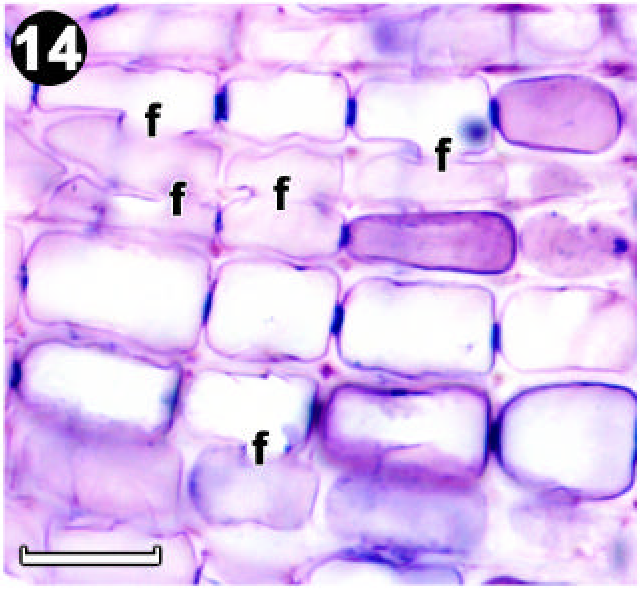
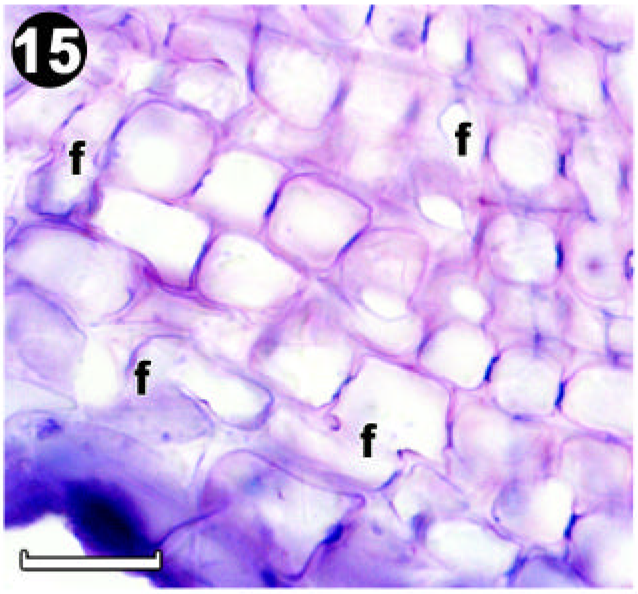


Plate 31







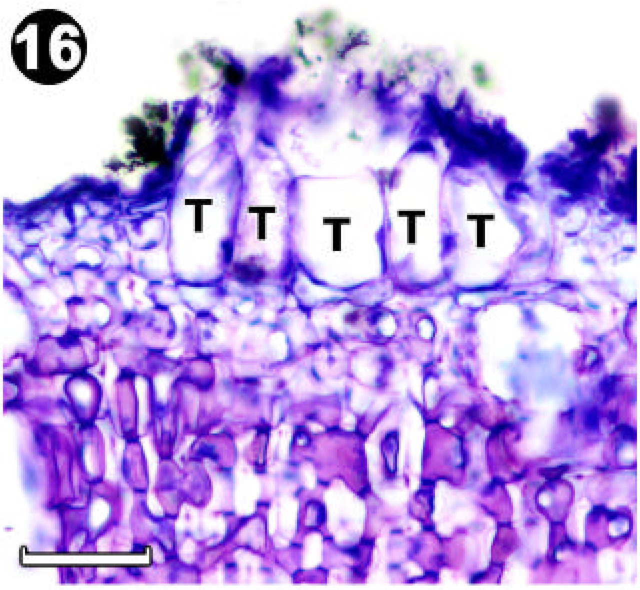
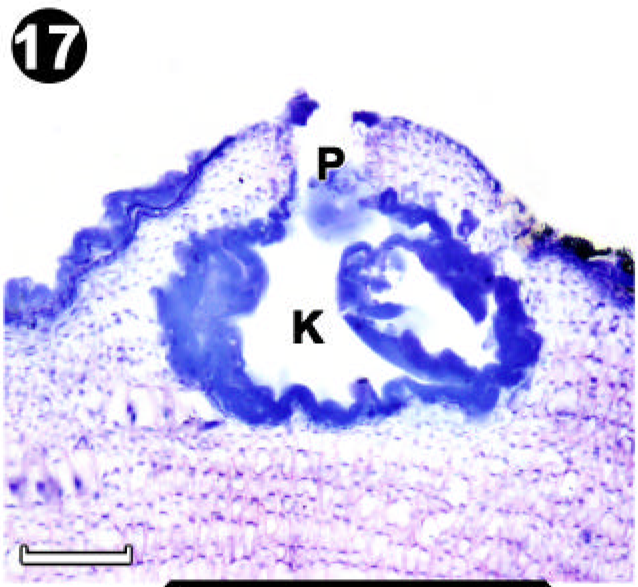
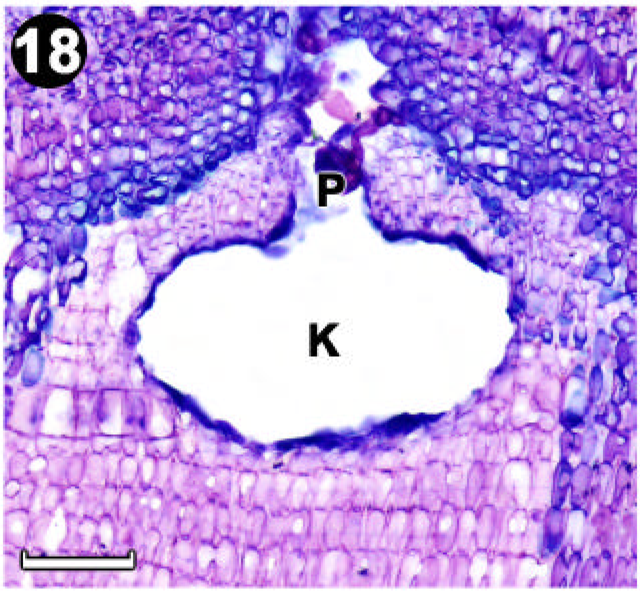


Plate 32





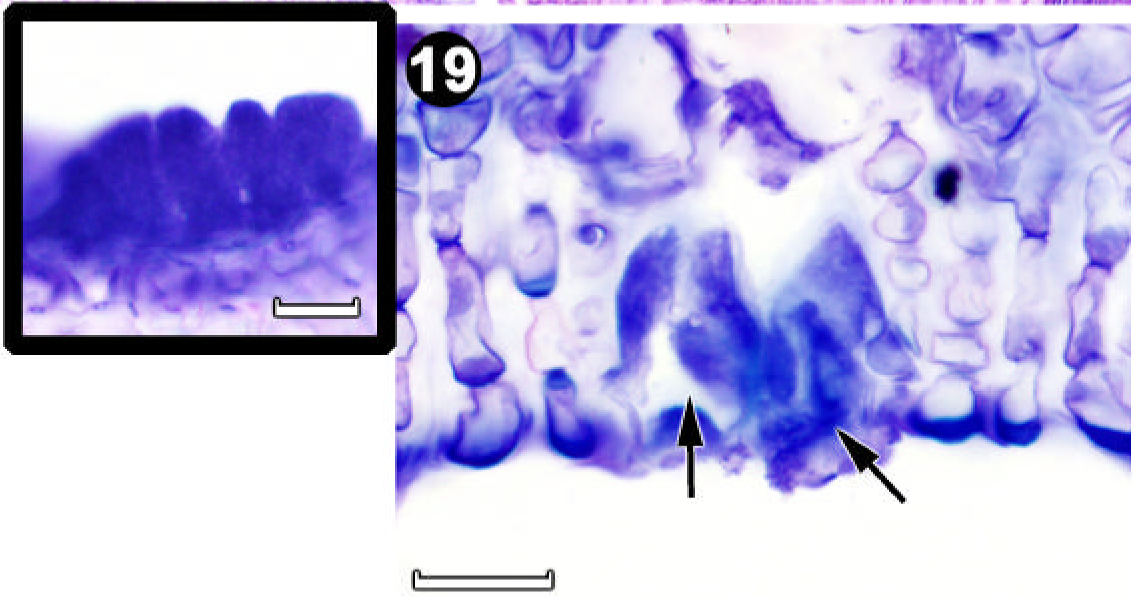


Plate 33

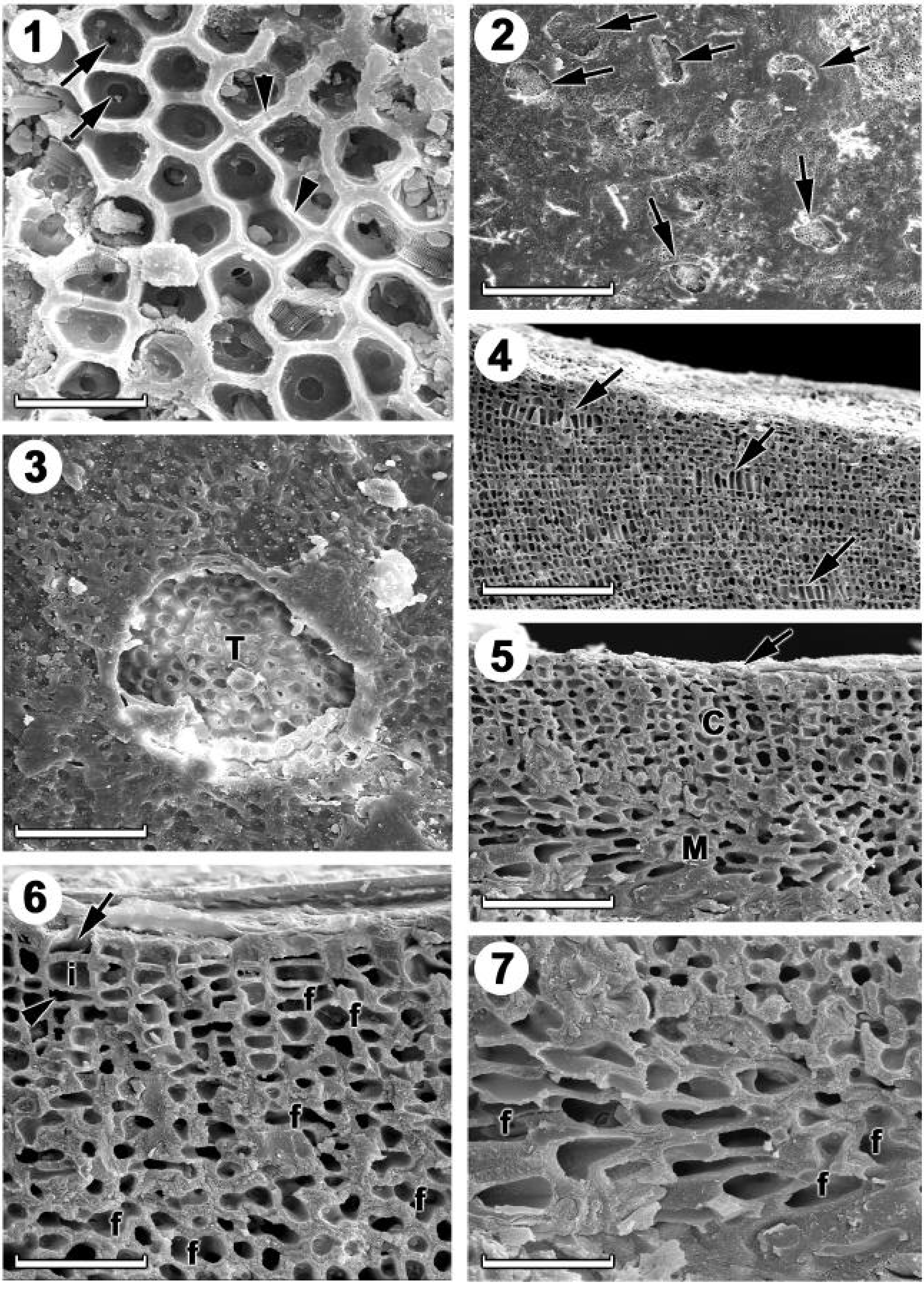
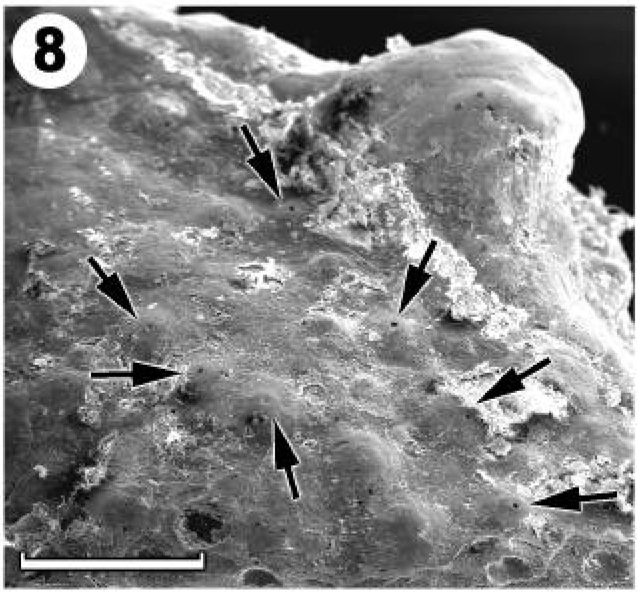
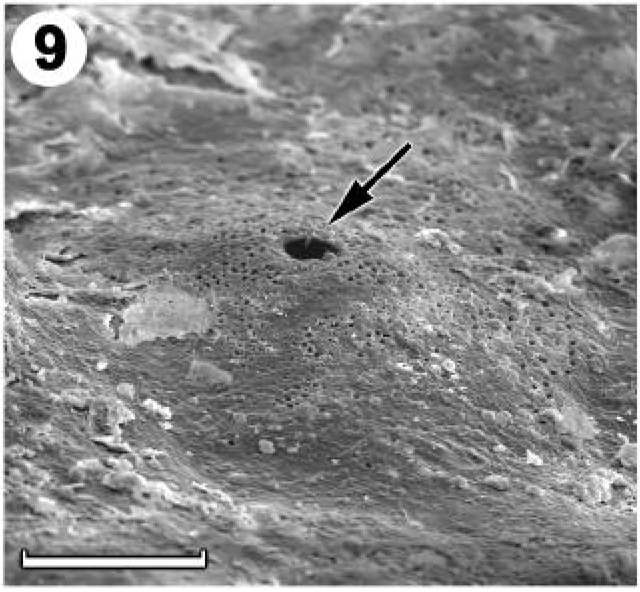
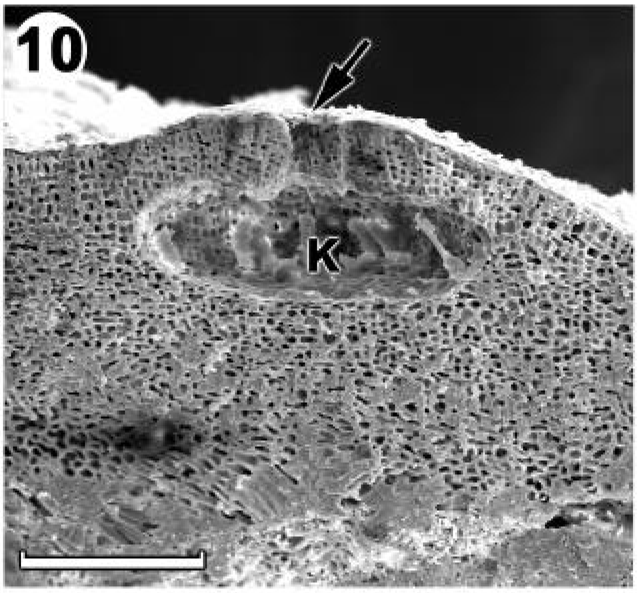
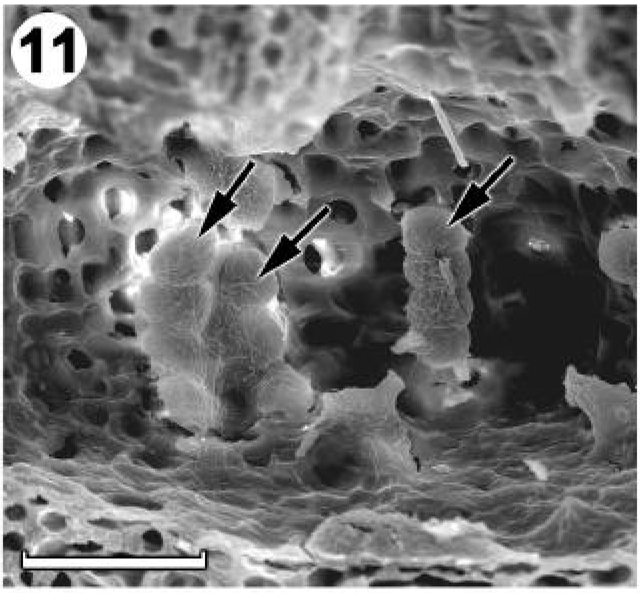


Plate 34









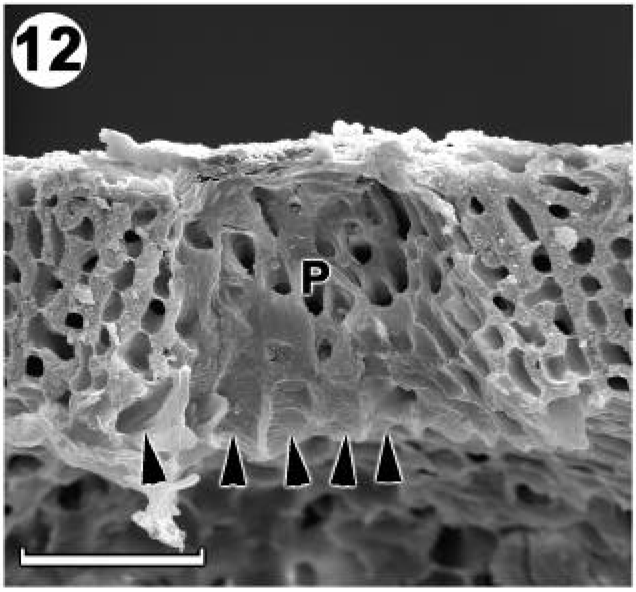
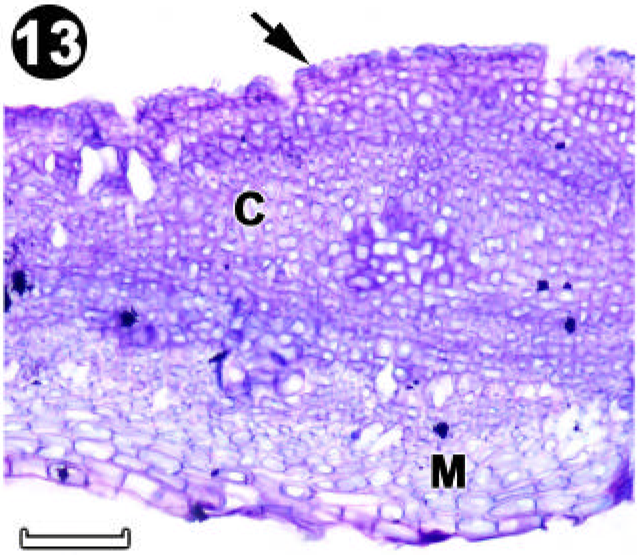
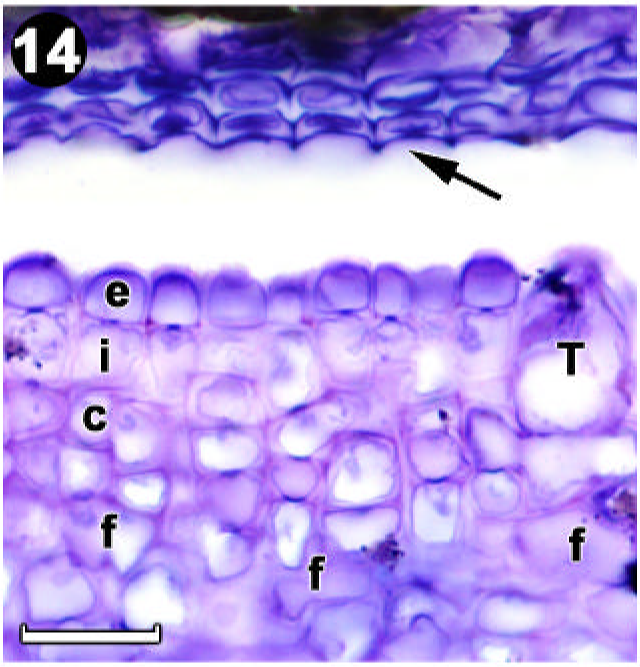
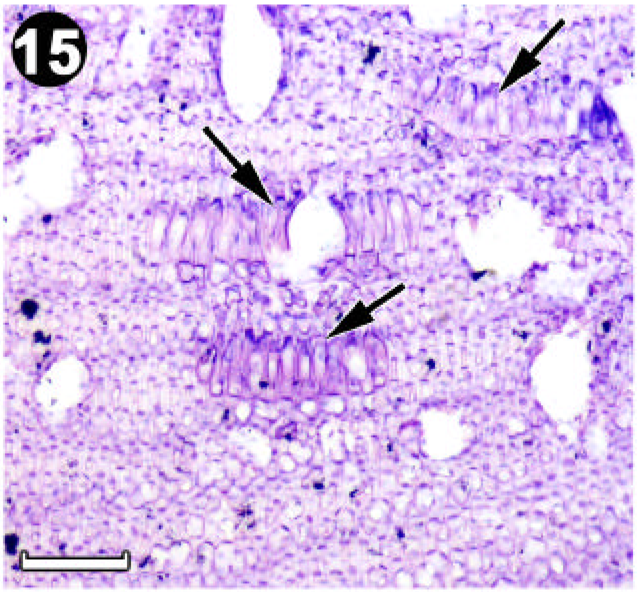


Plate 35







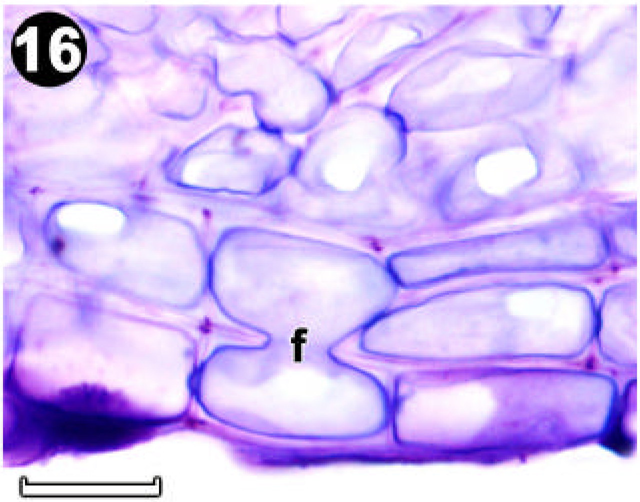


Plate 36

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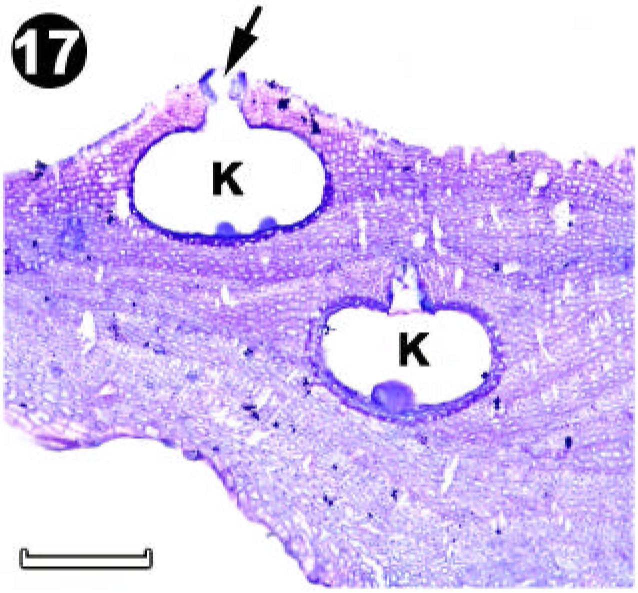

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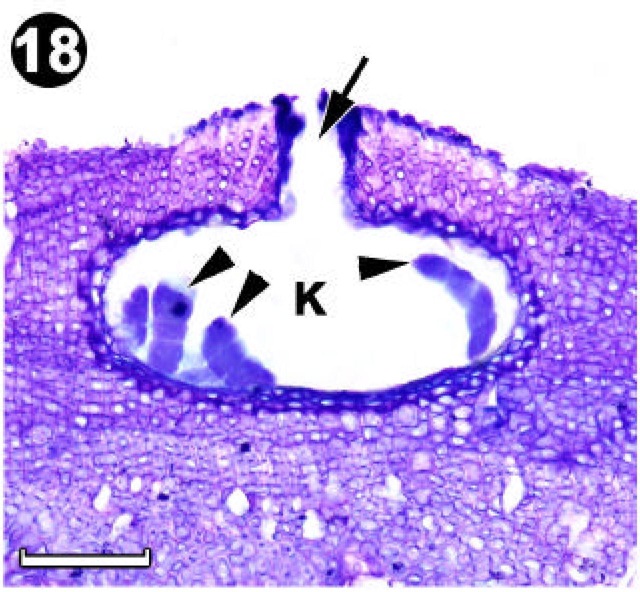

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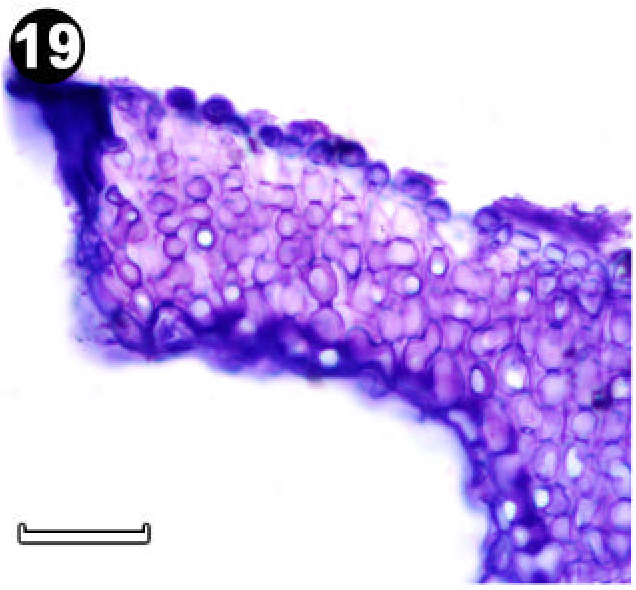

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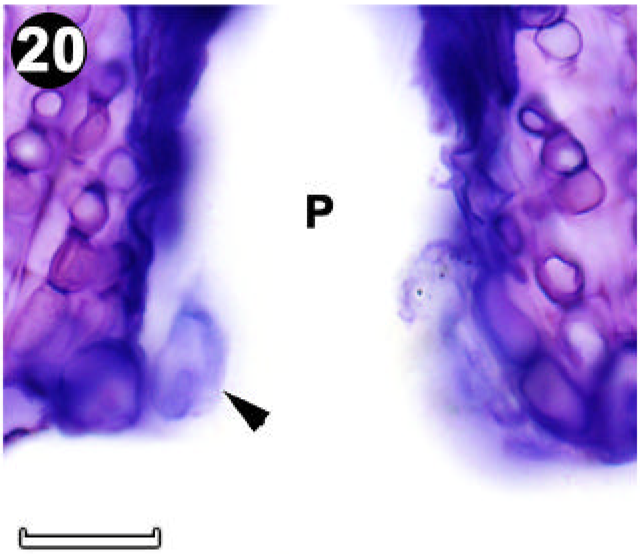

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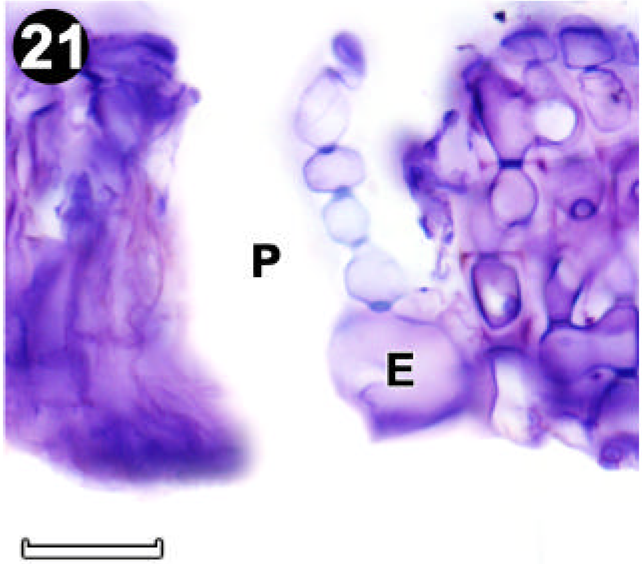
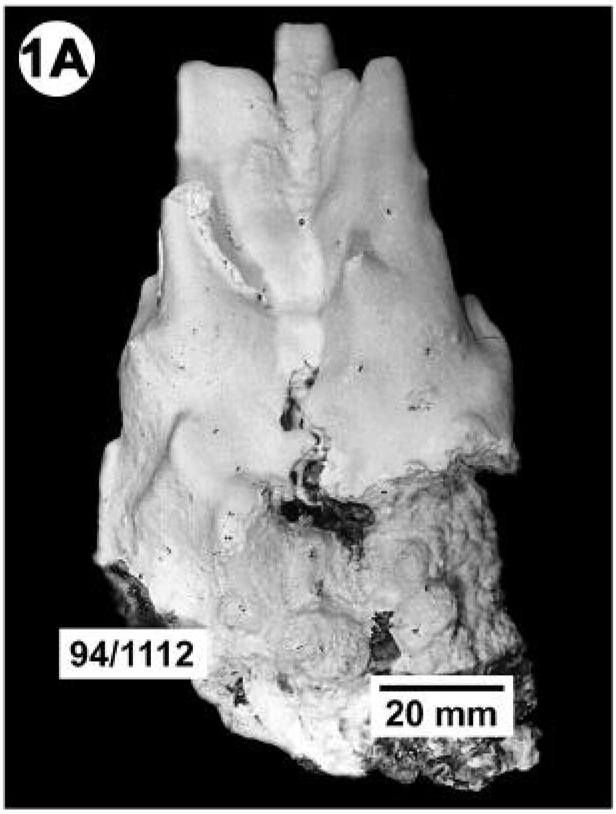


Plate 37



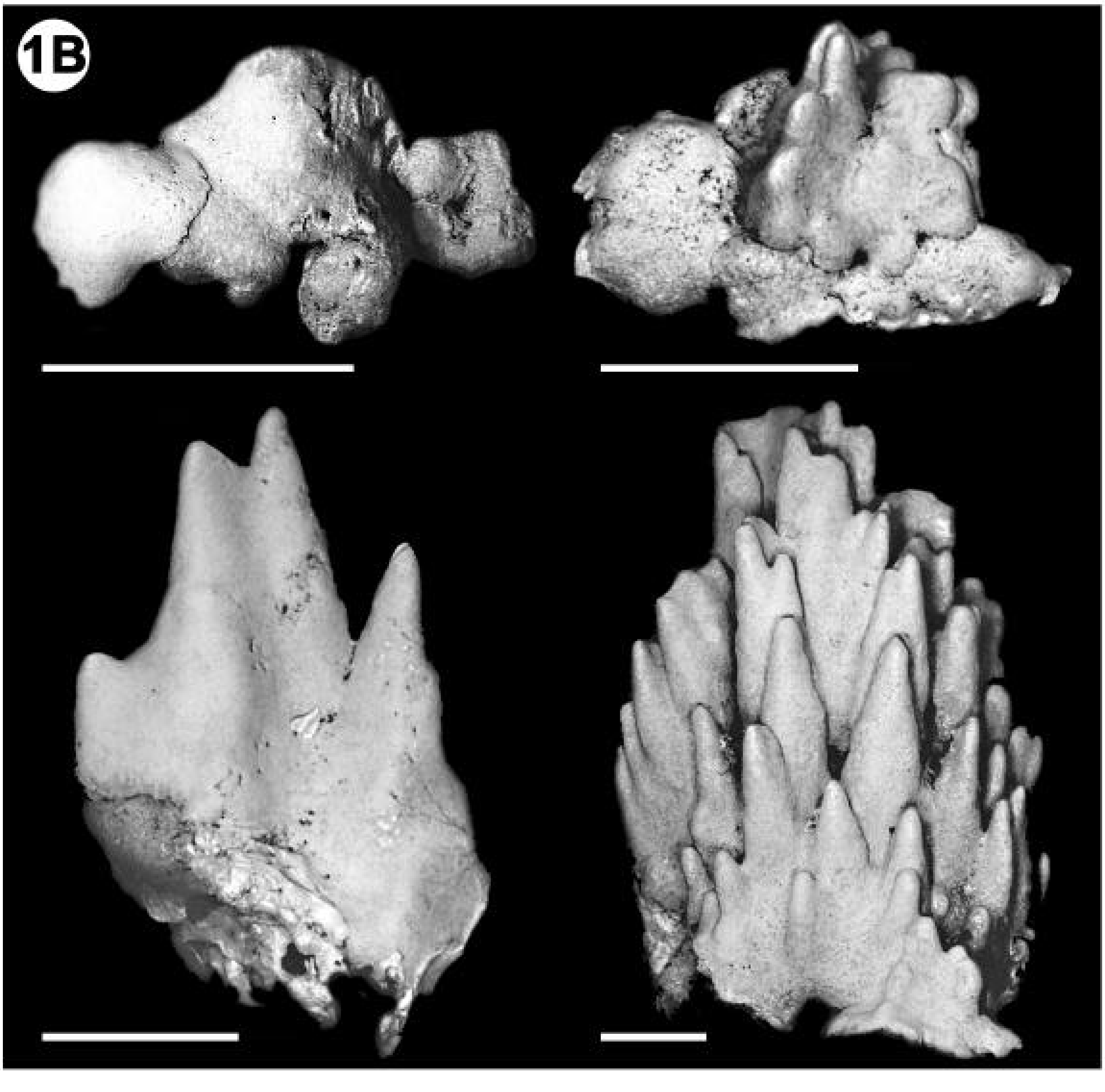
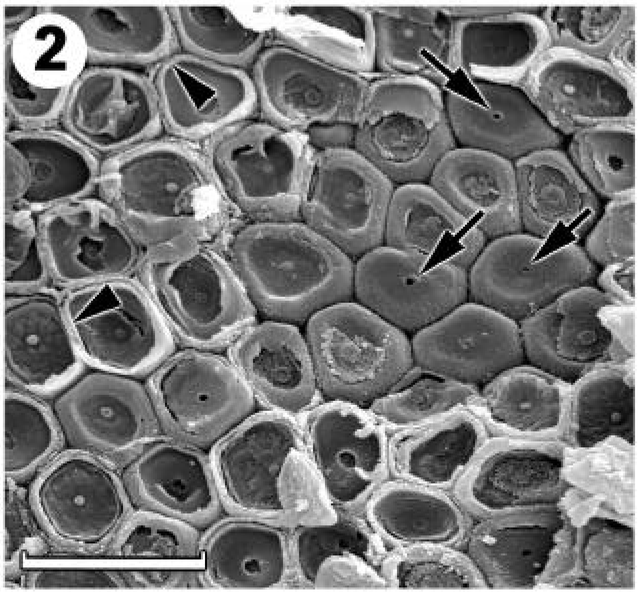
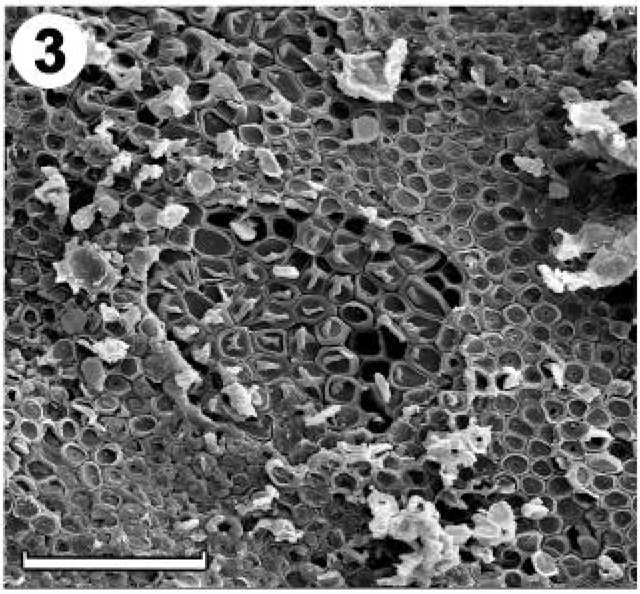
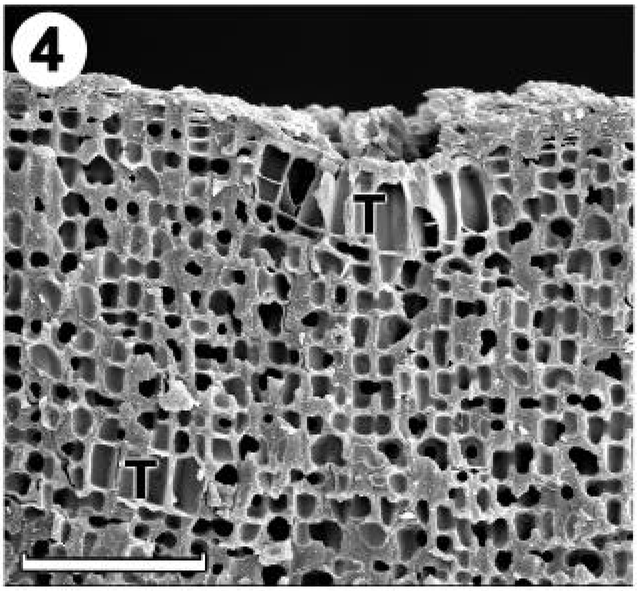
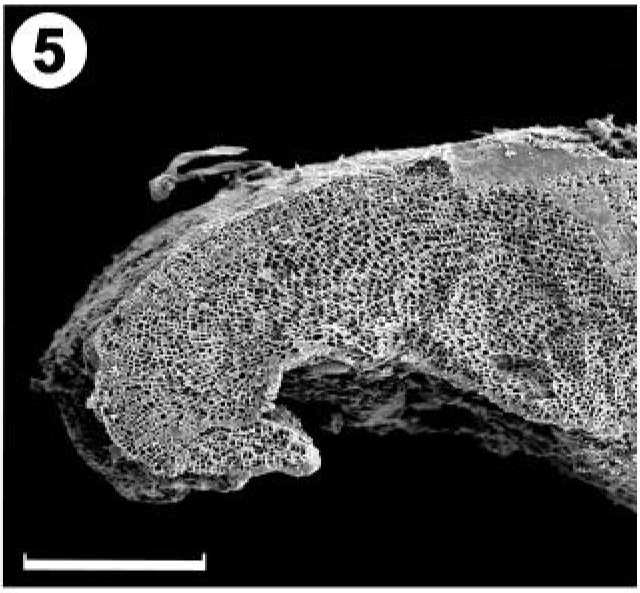


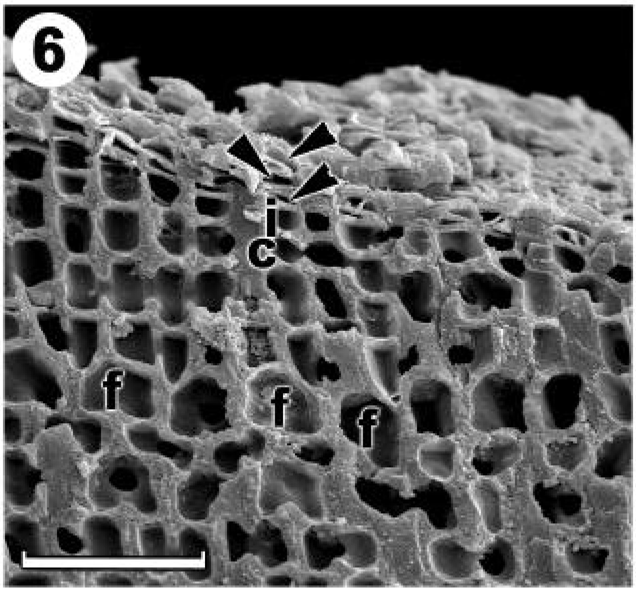
Plate 38











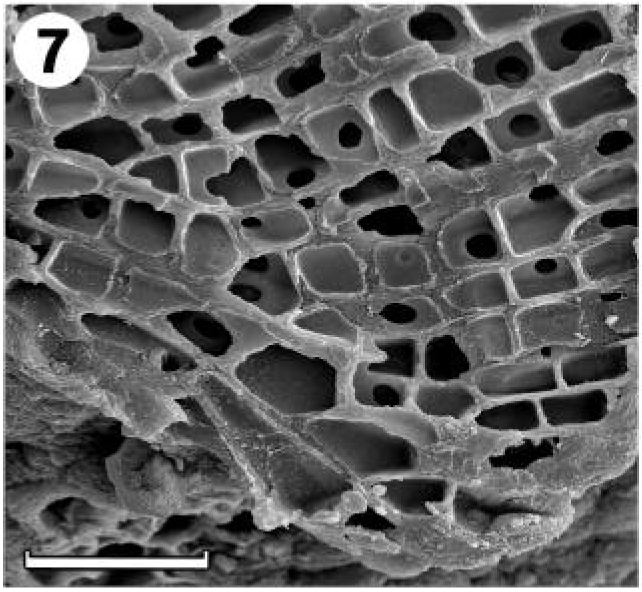


Plate 39

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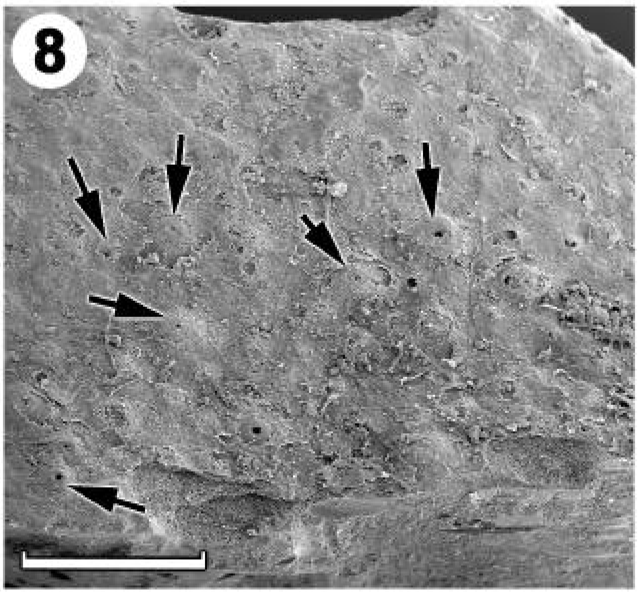

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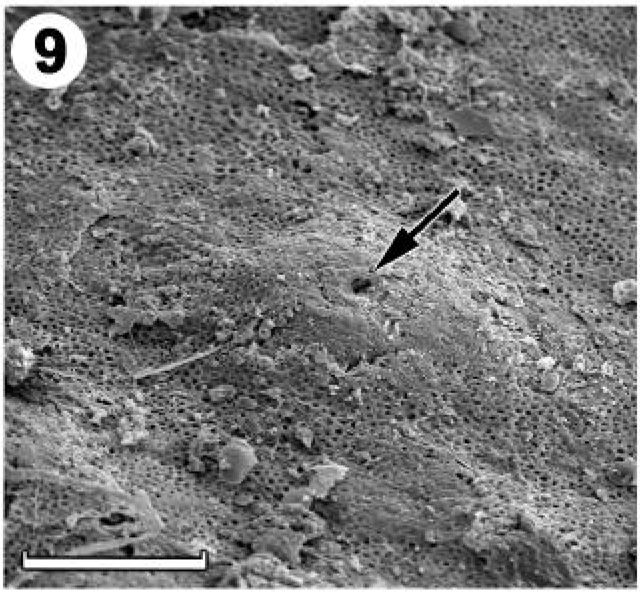

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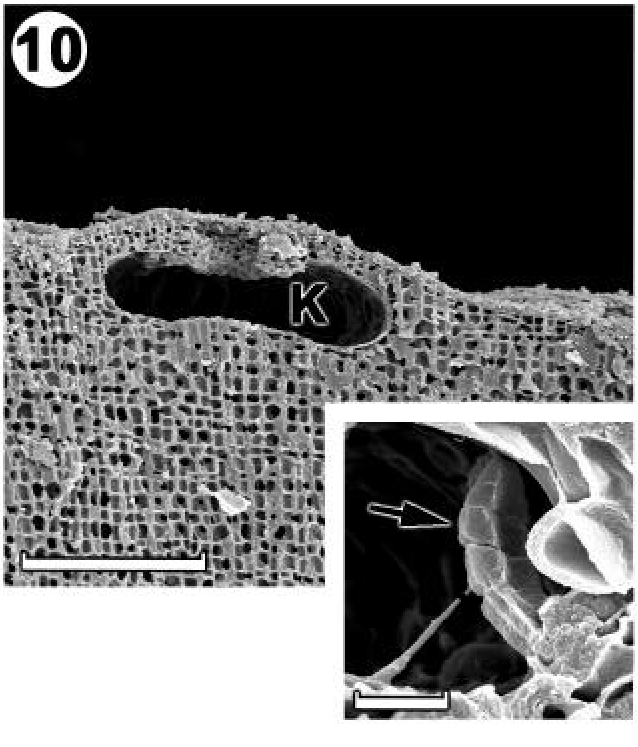

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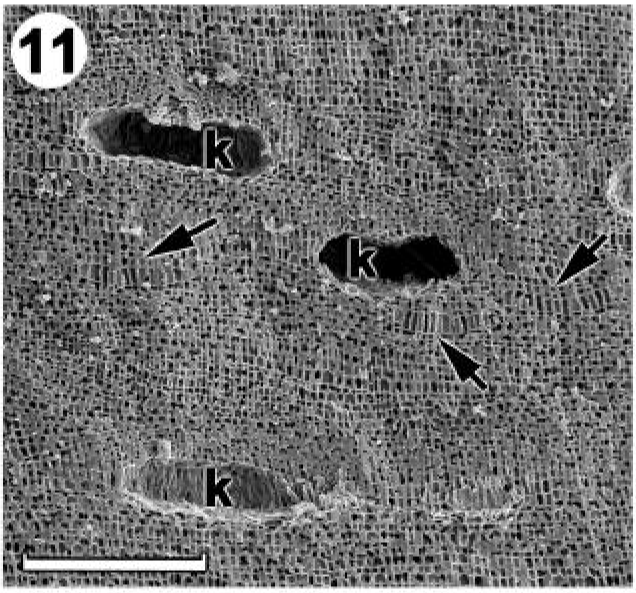

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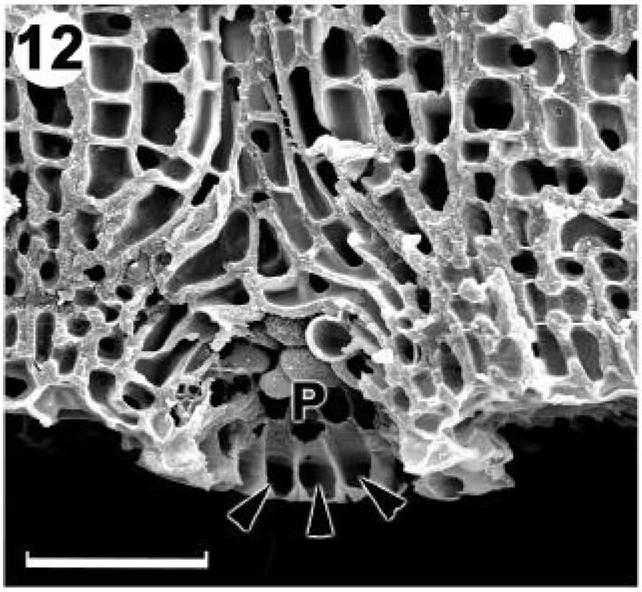

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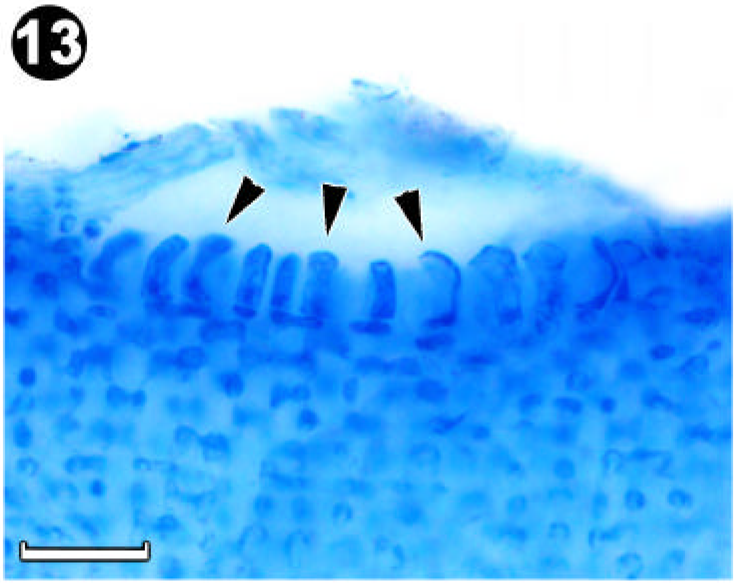


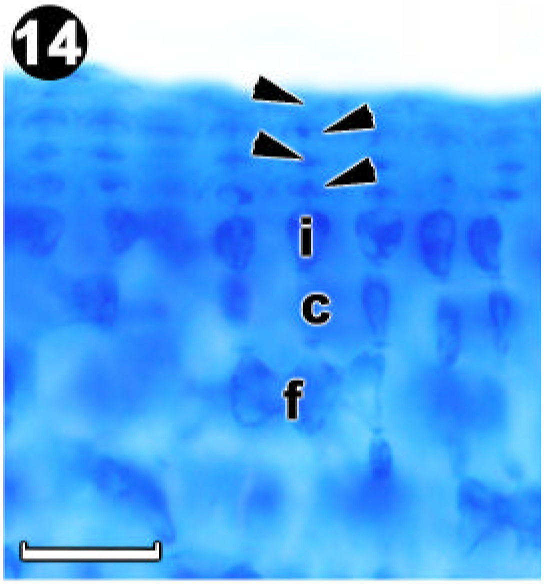
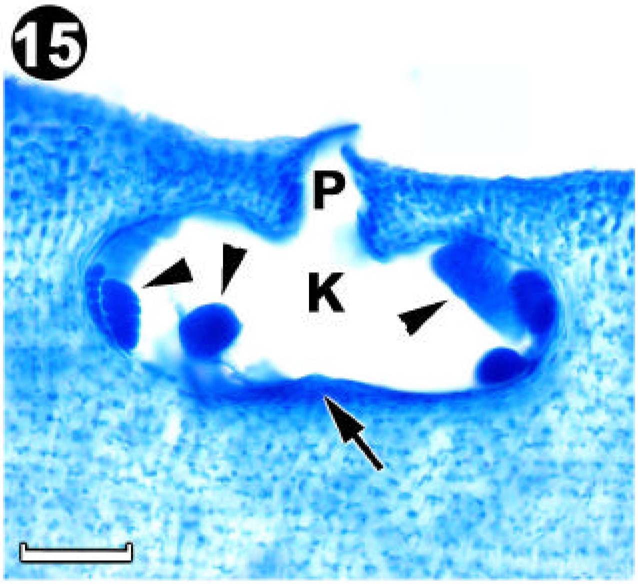
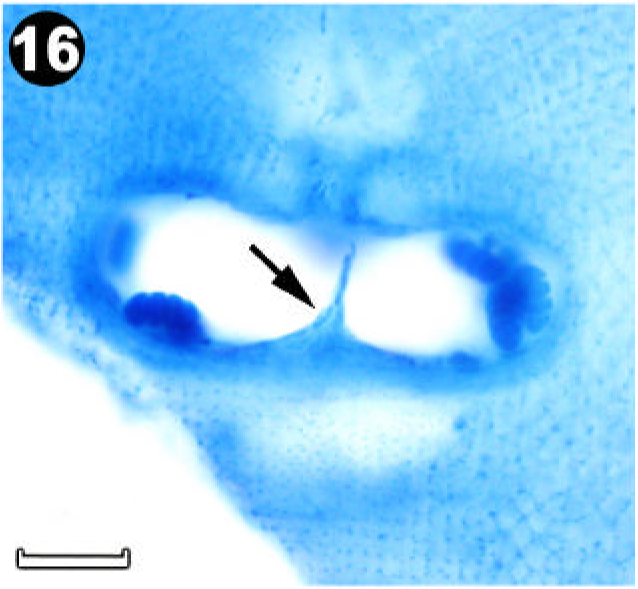
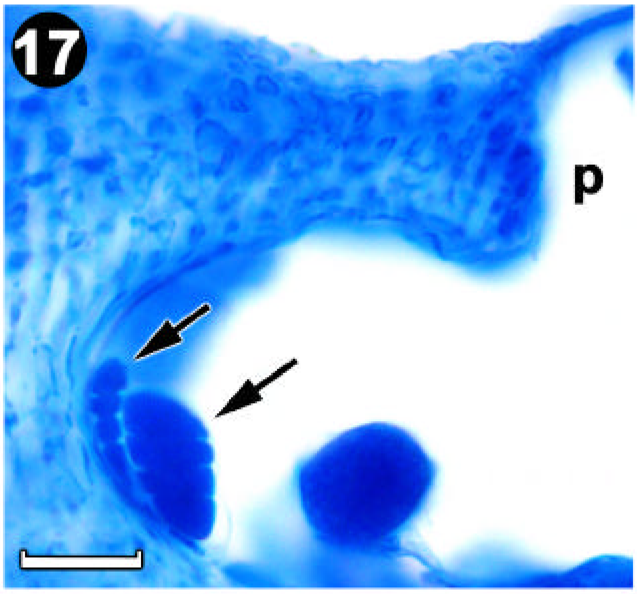
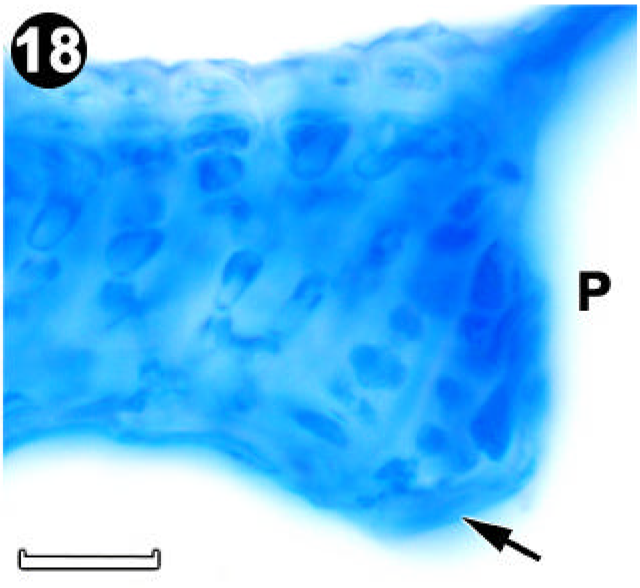


Plate 41









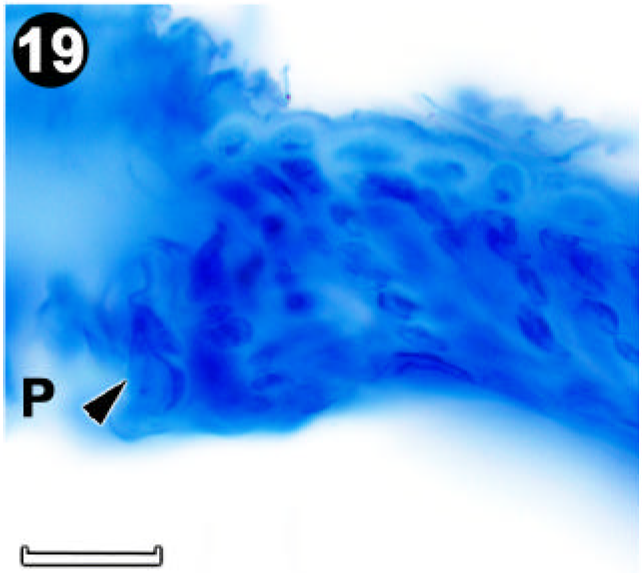


Plate 42

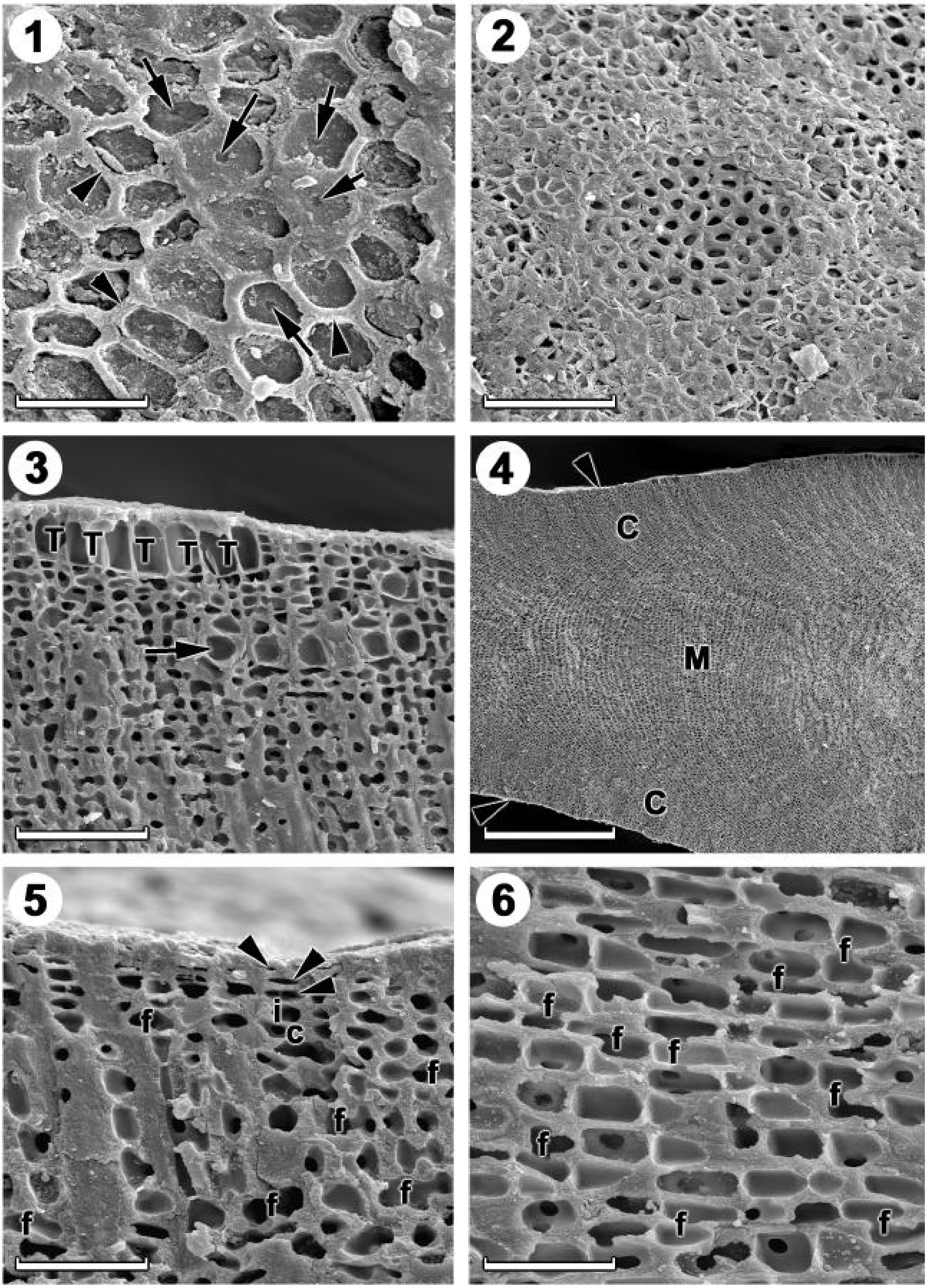
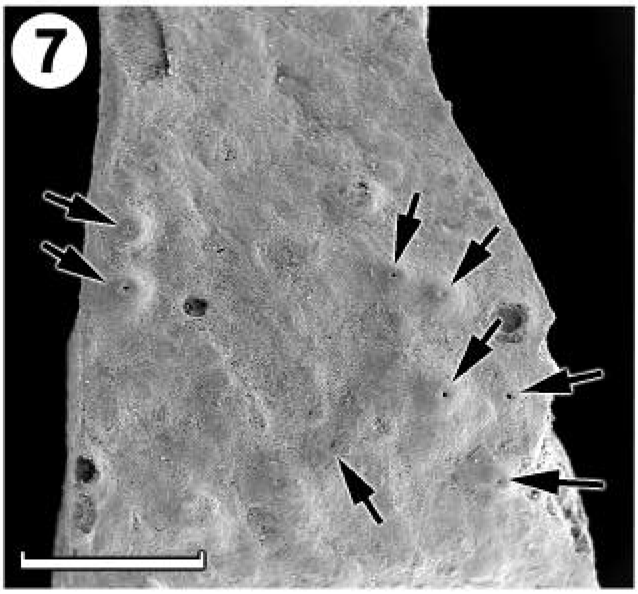
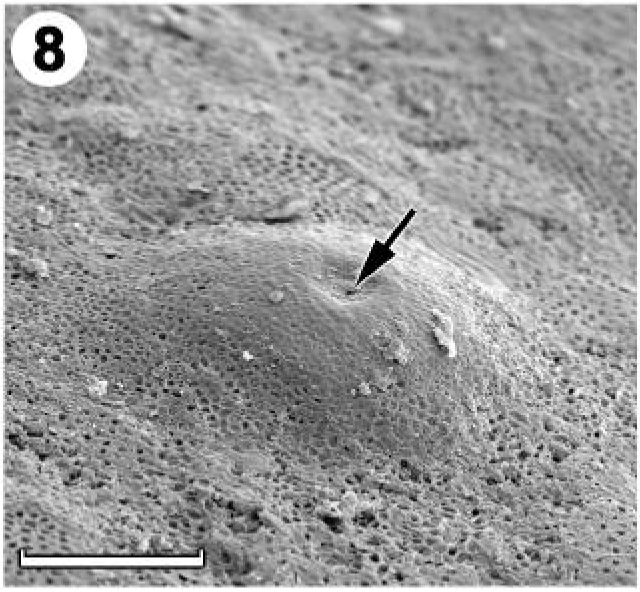
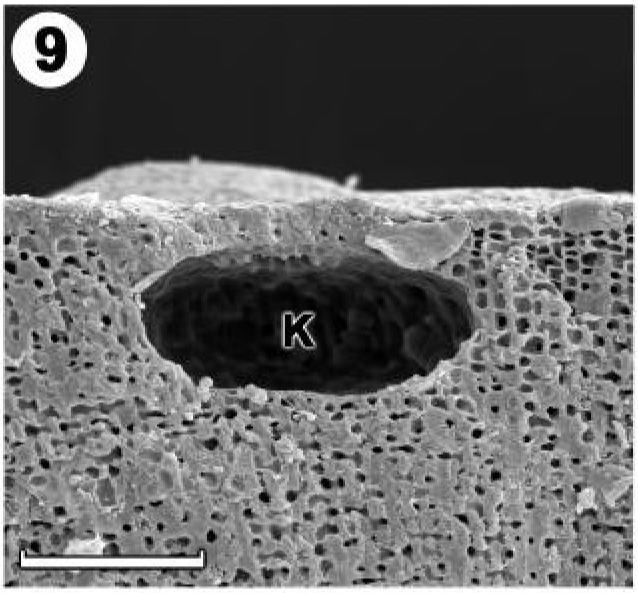
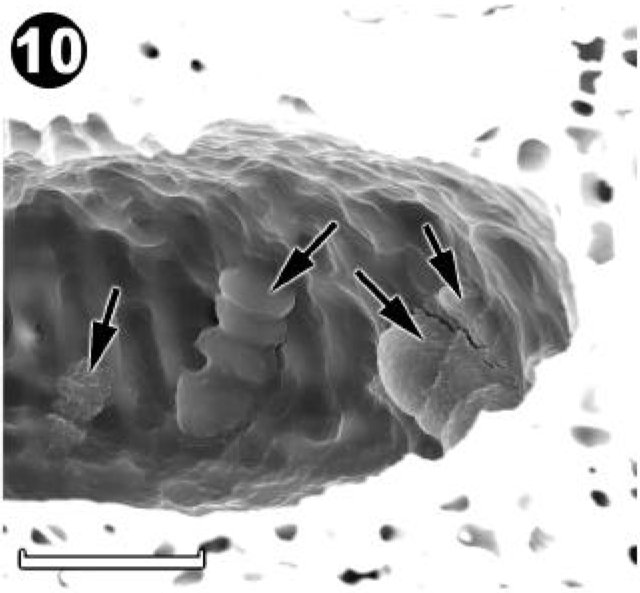


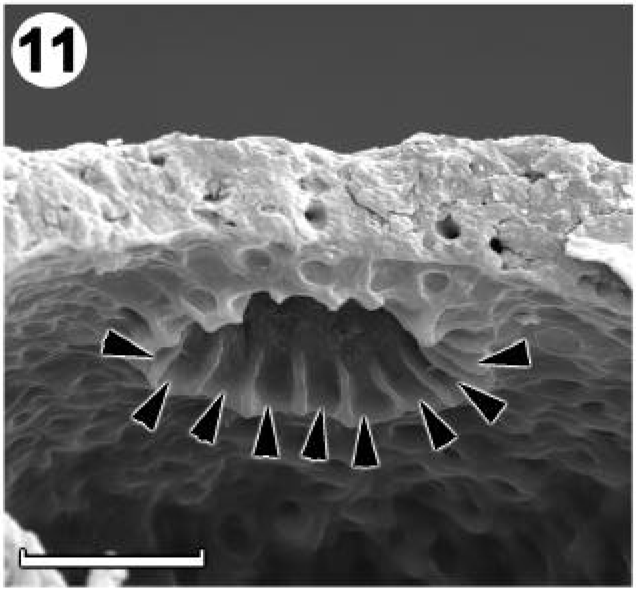
Plate 43











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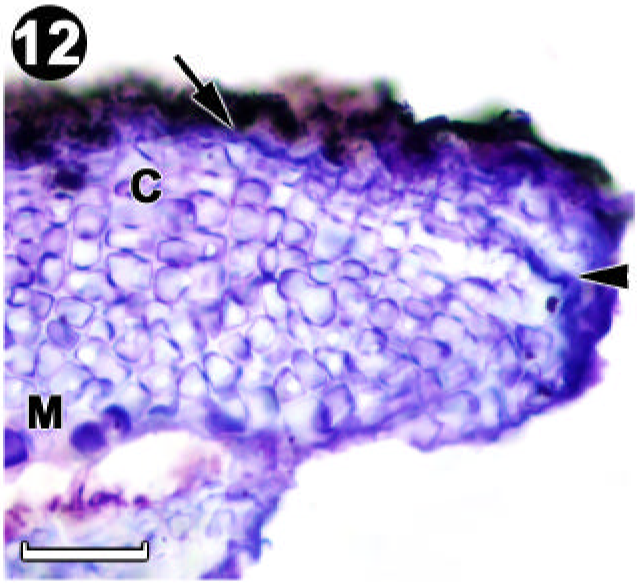
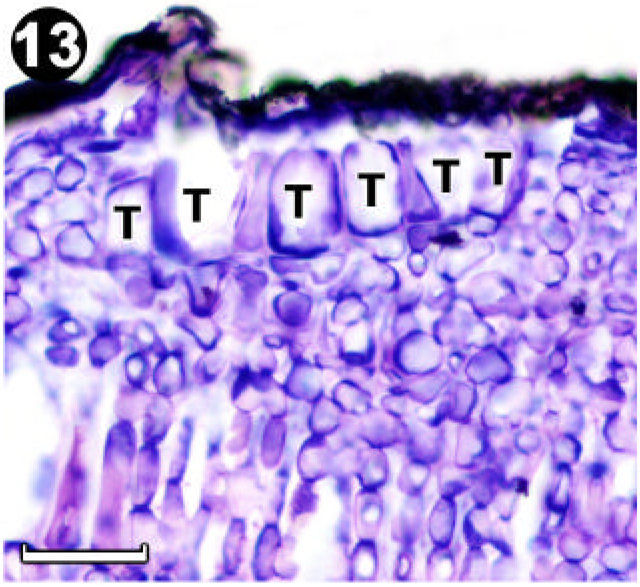
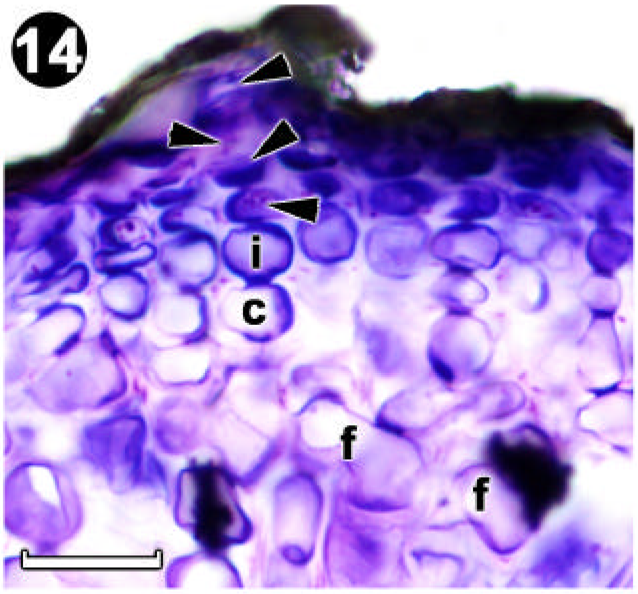
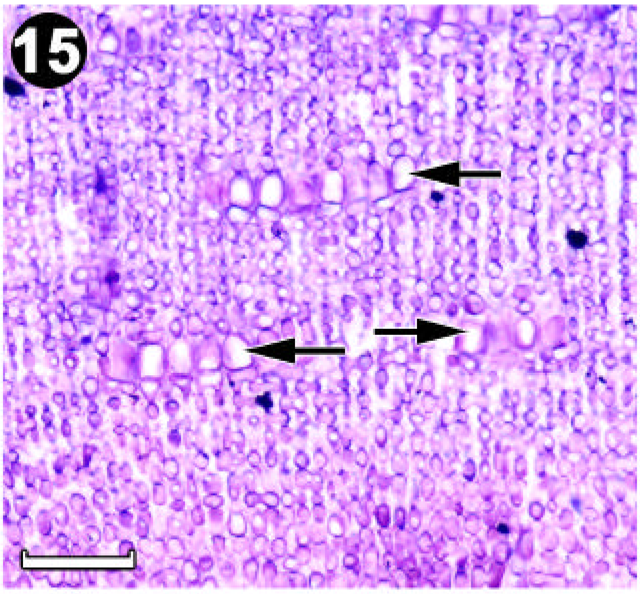
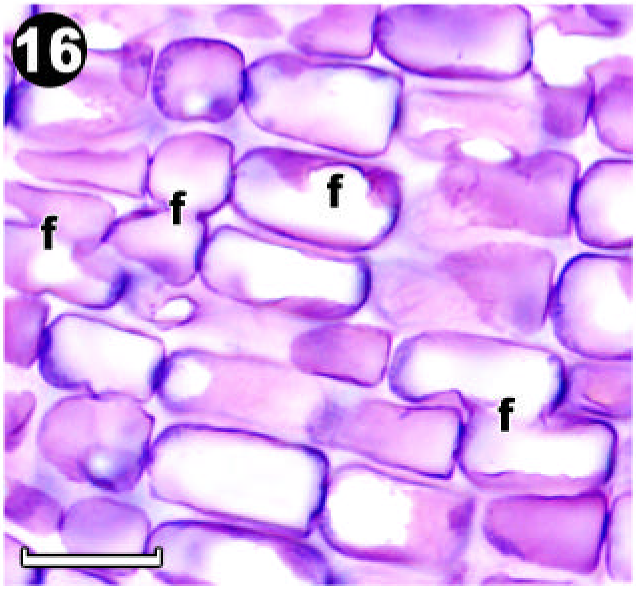










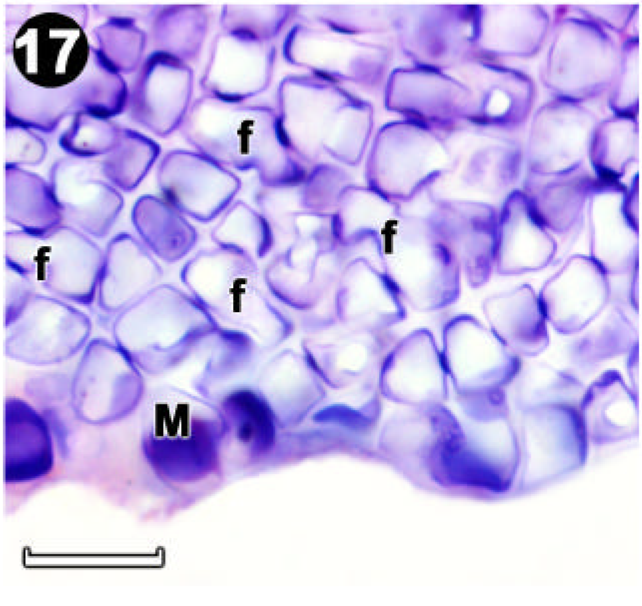
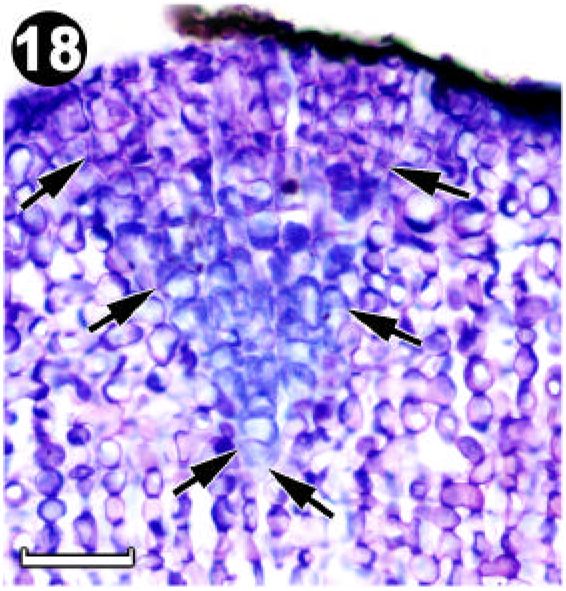
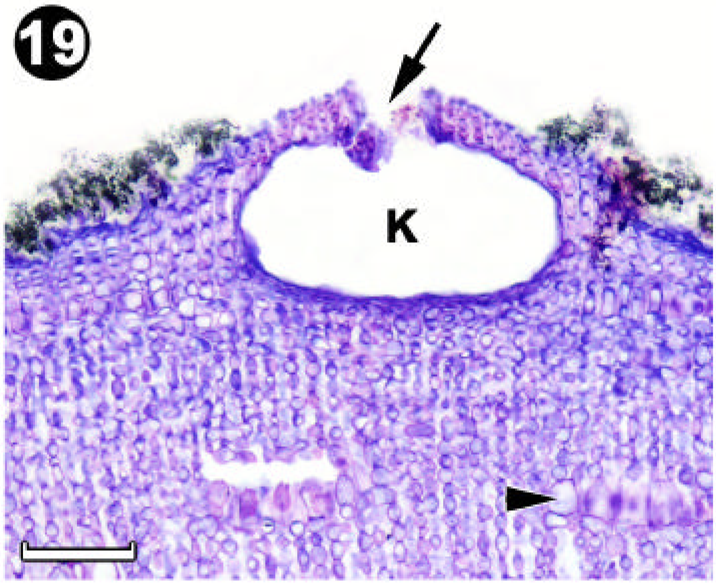
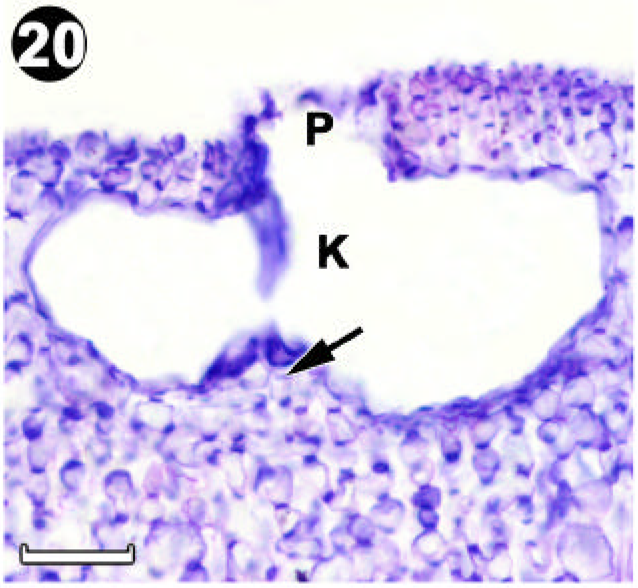
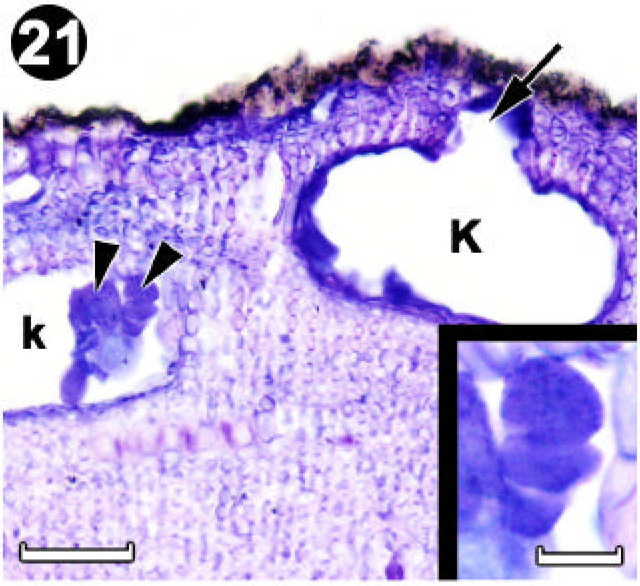


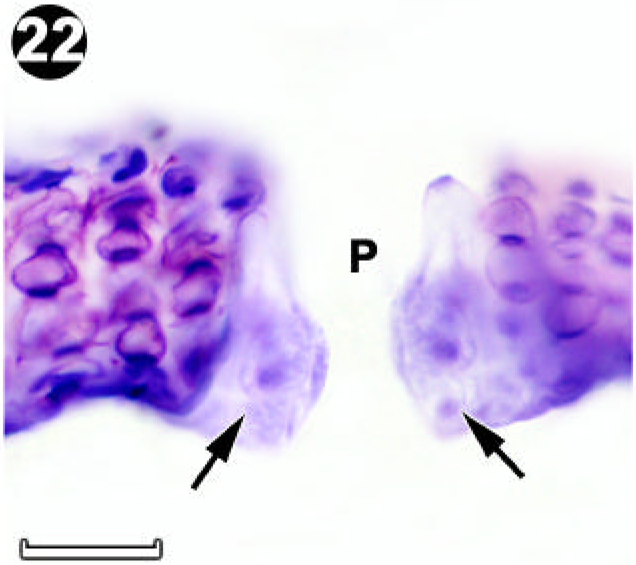
Plate 45

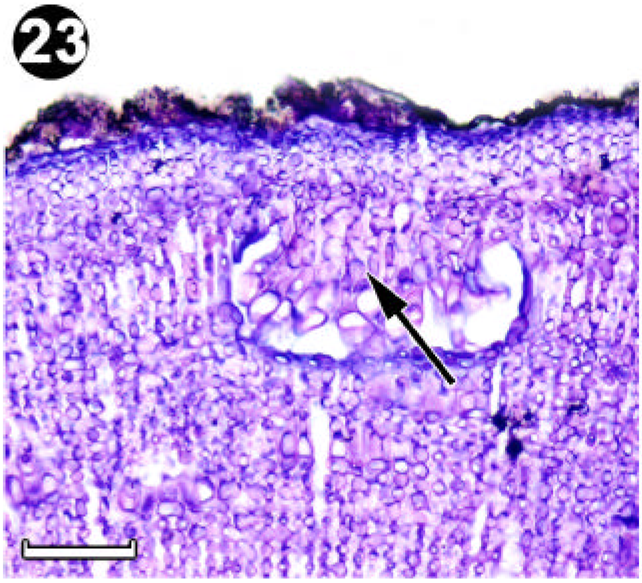












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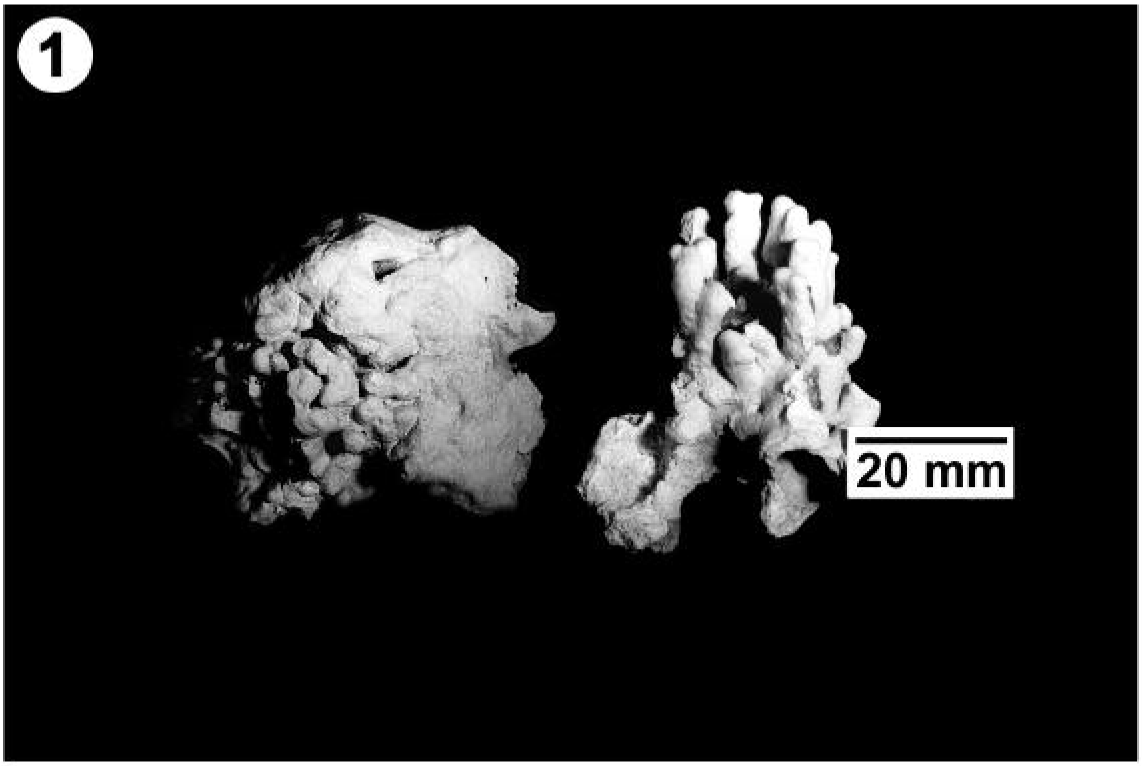

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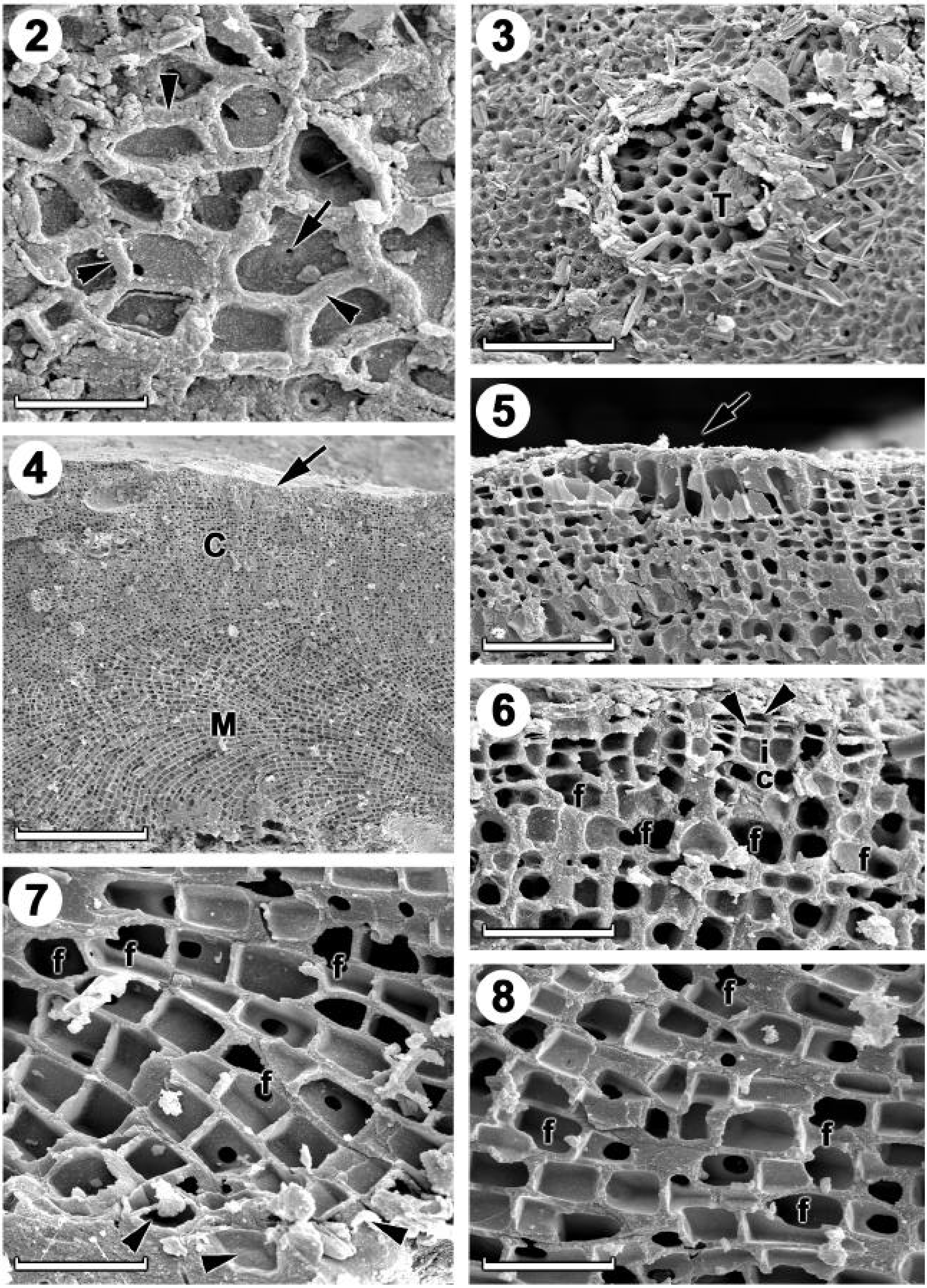

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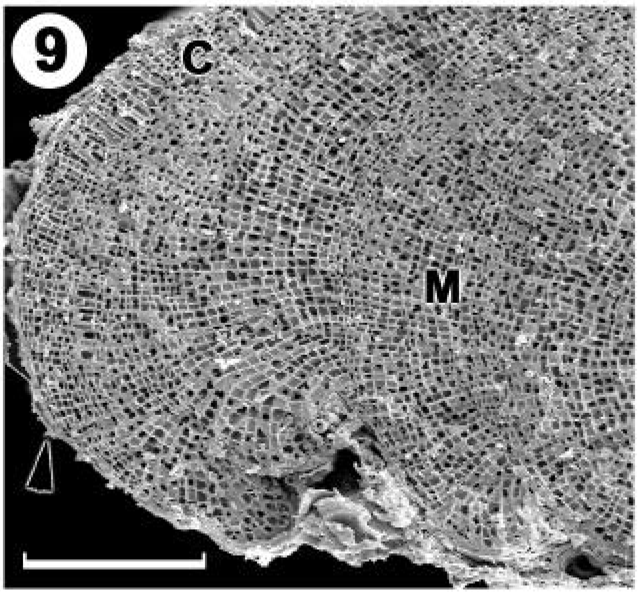

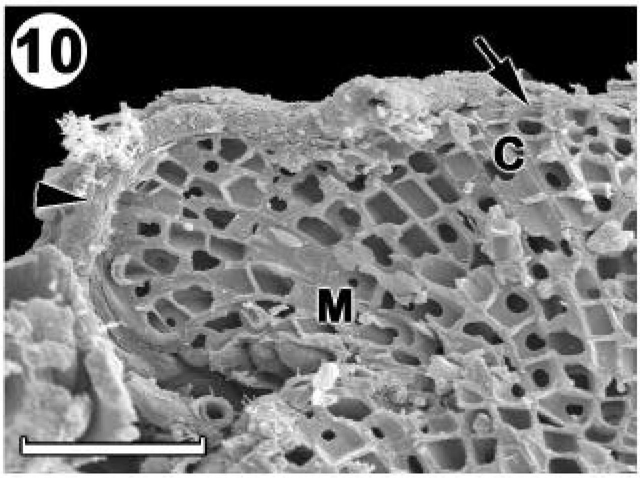

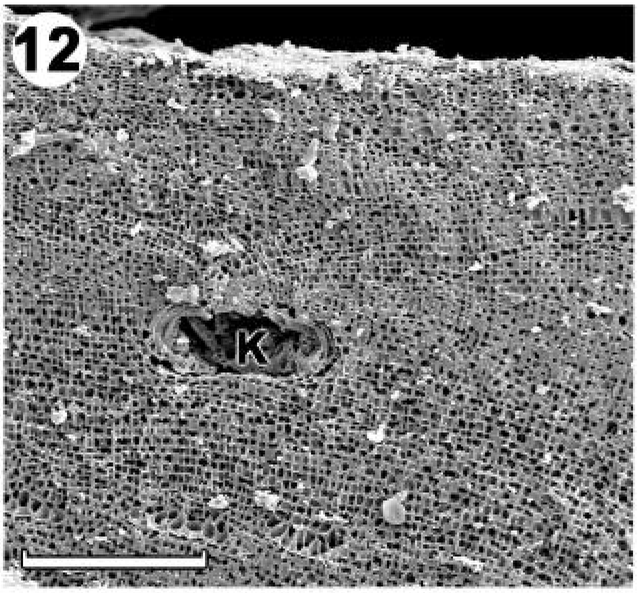

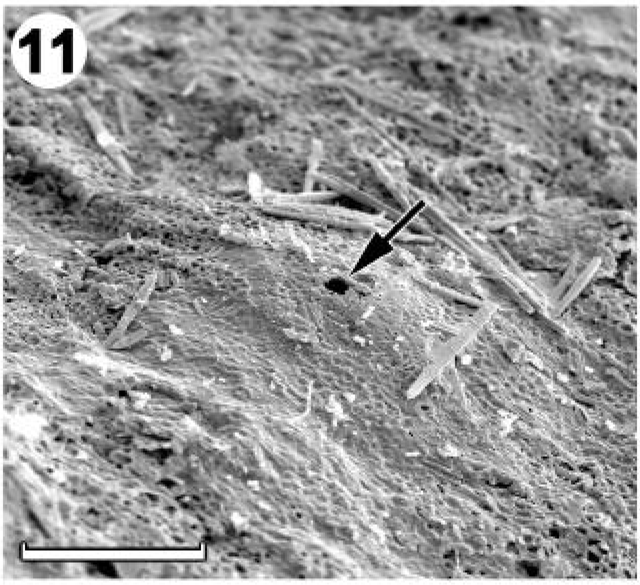

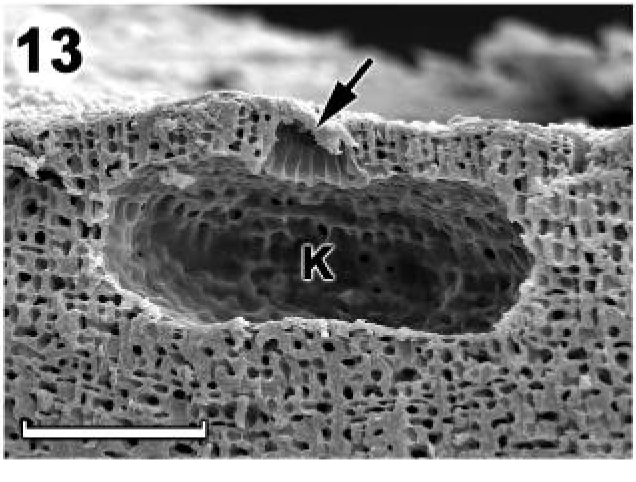

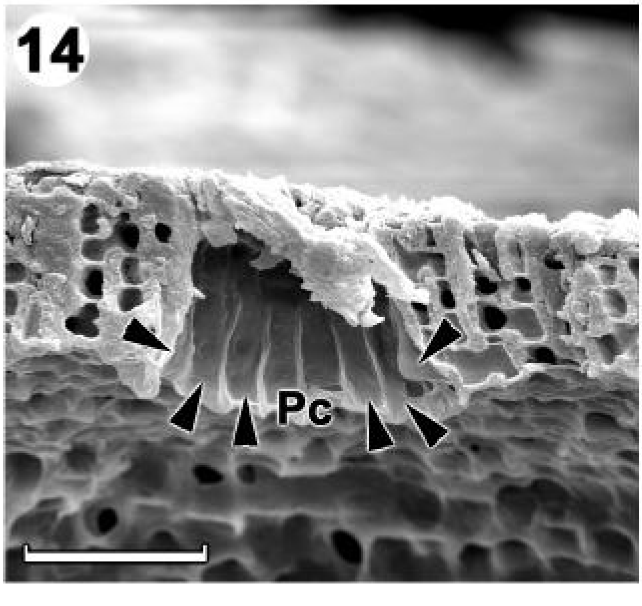

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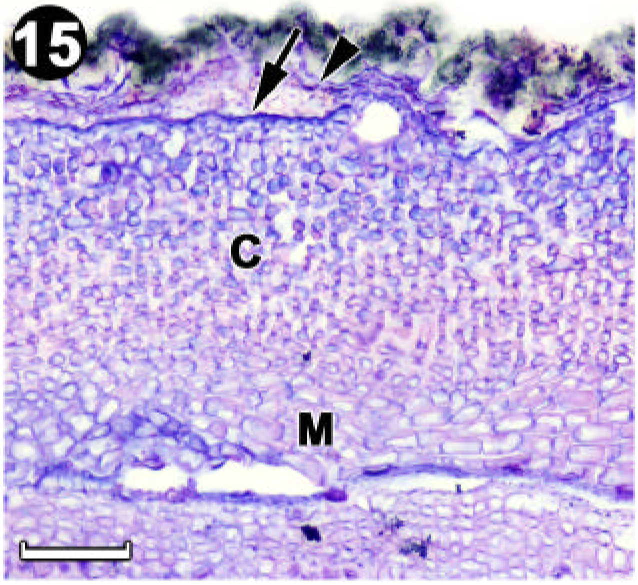
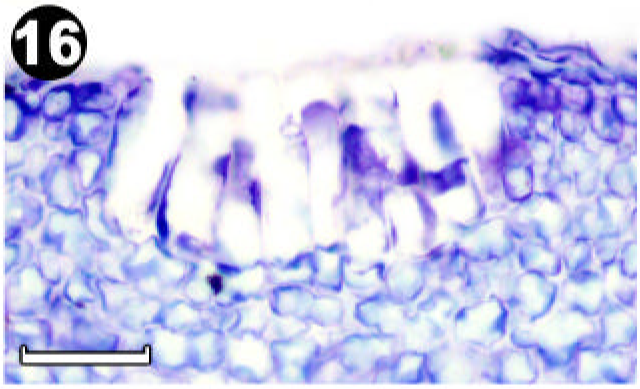
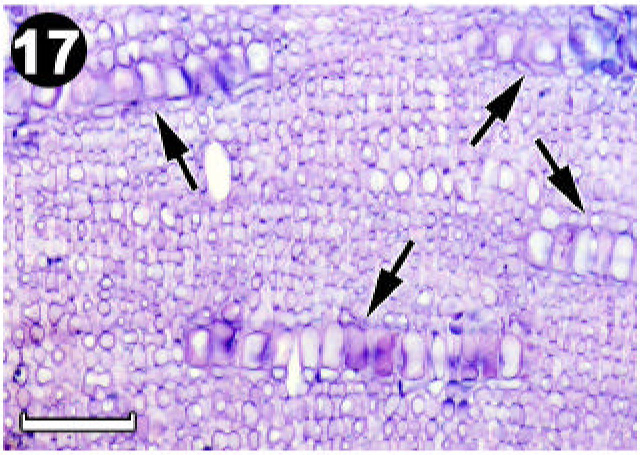
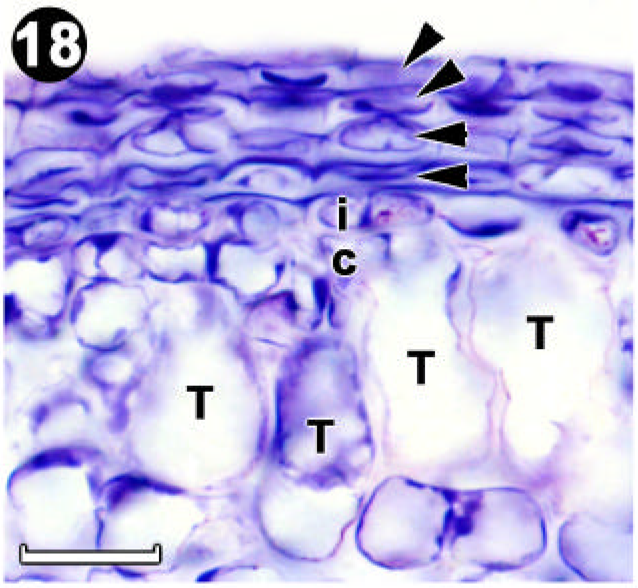
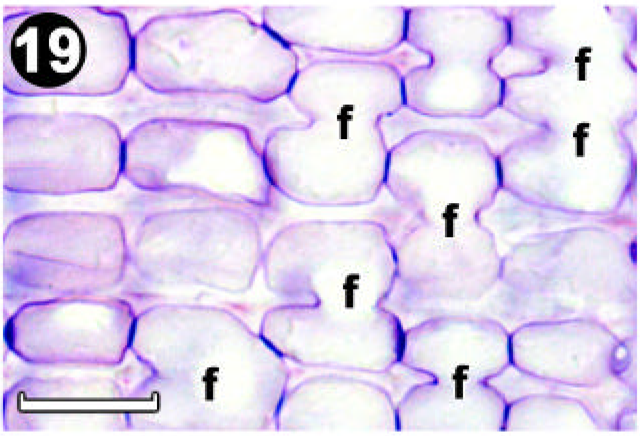
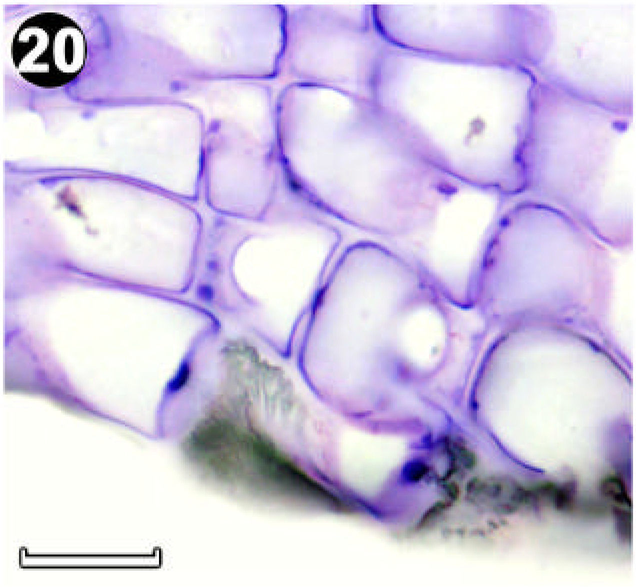












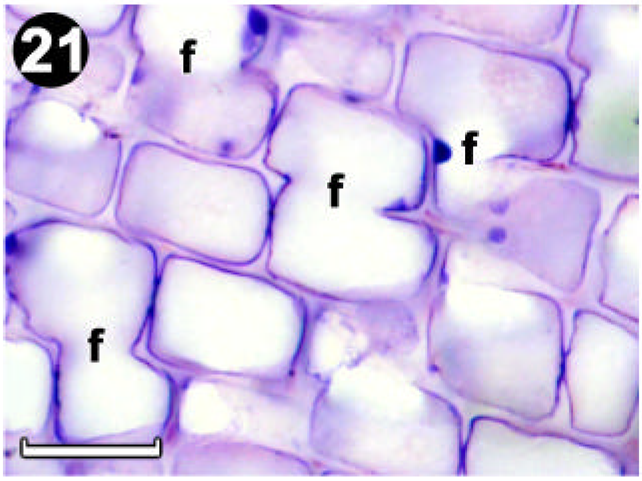
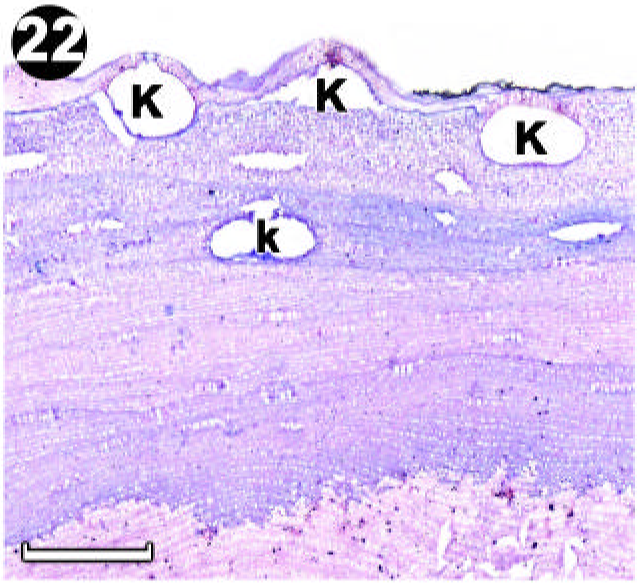
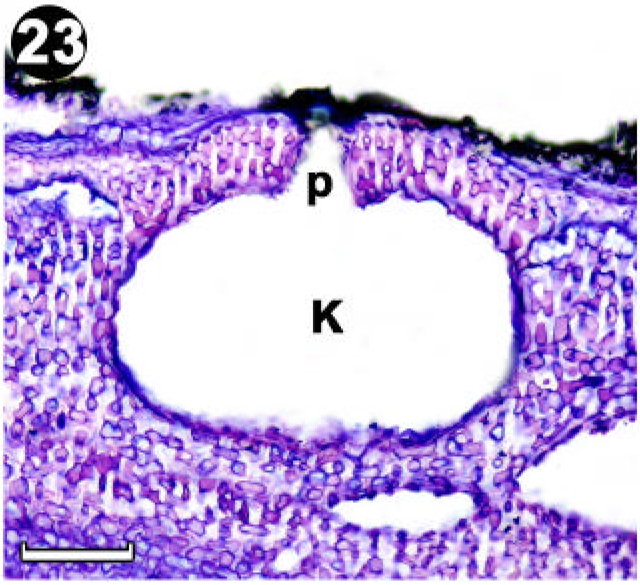


Plate 50





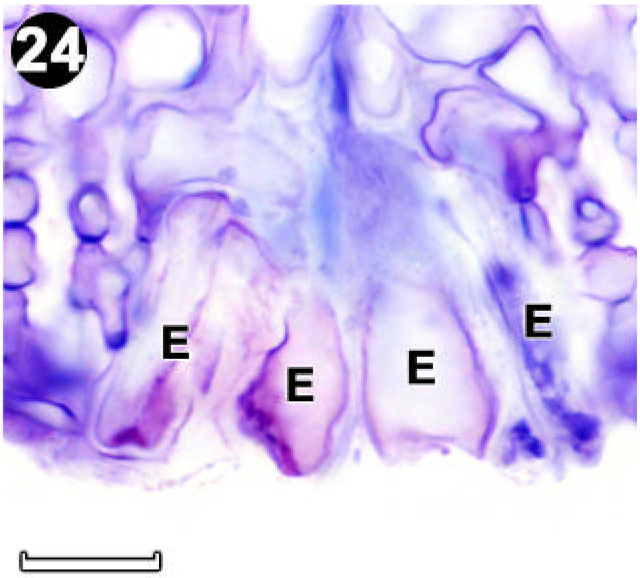
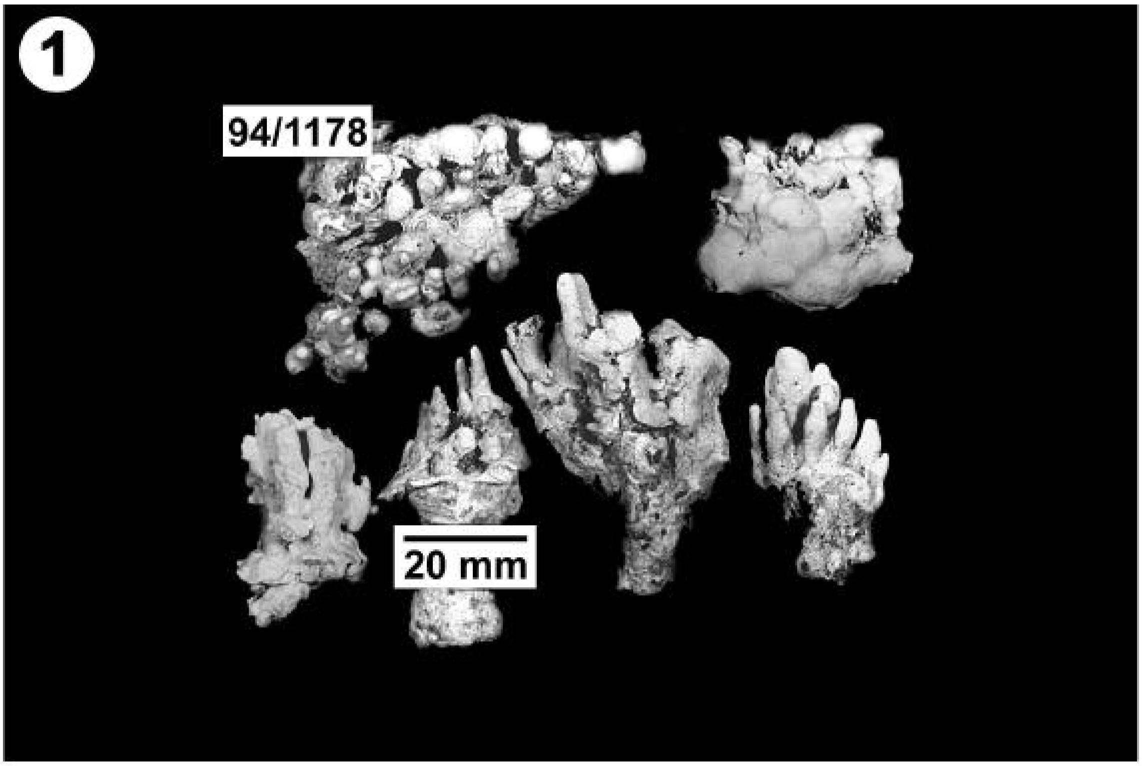


Plate 51



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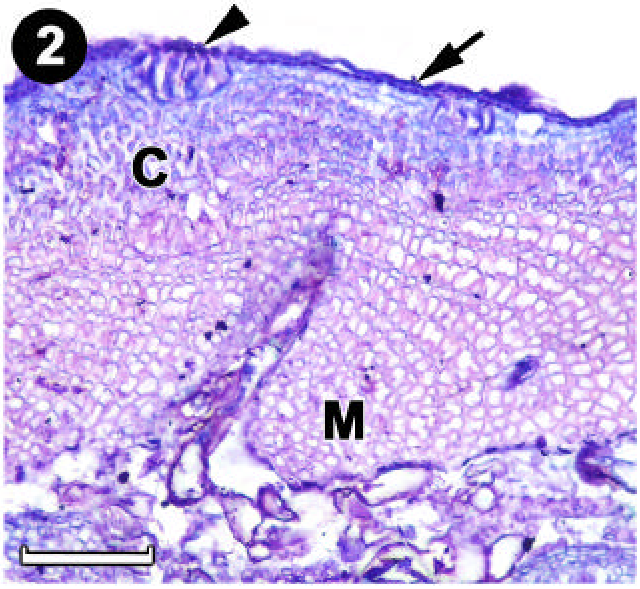

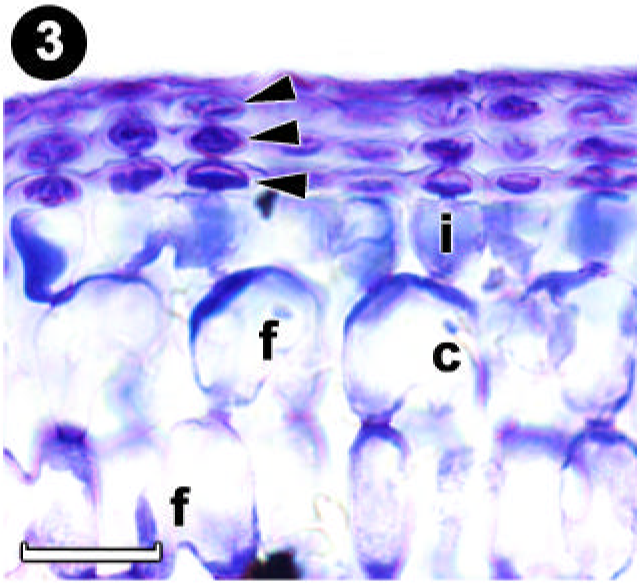

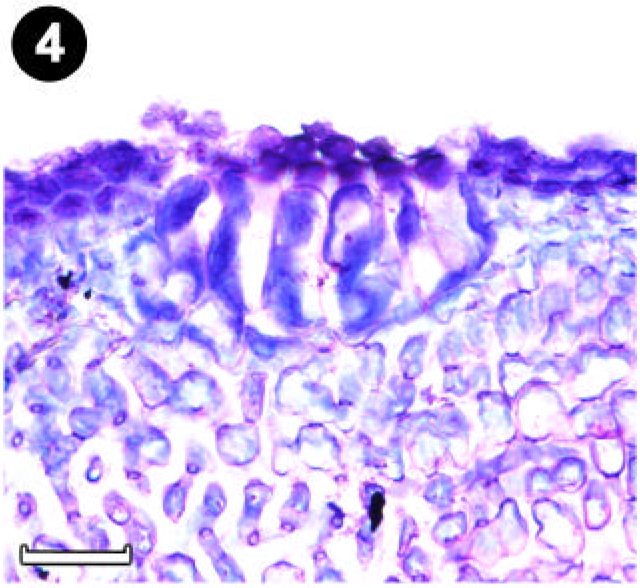

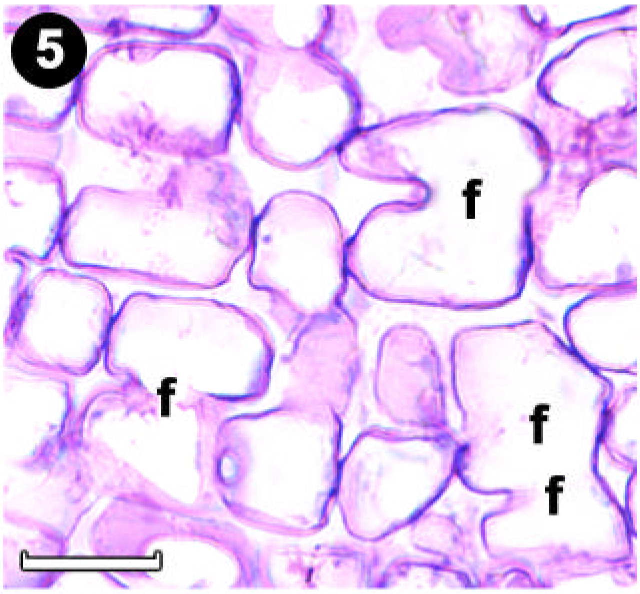

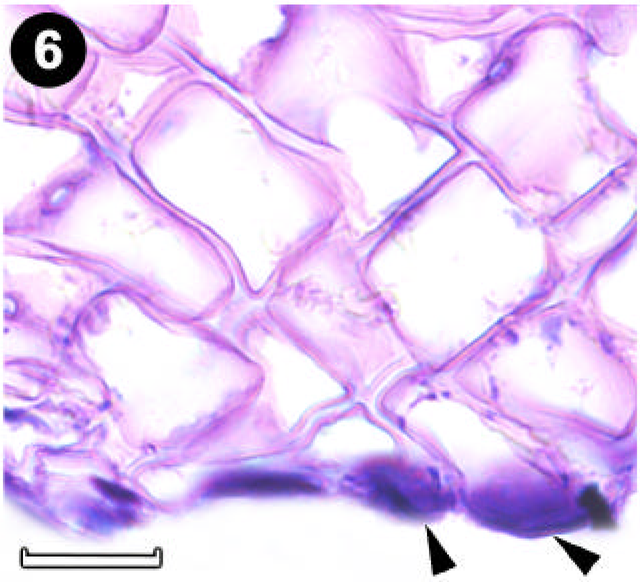

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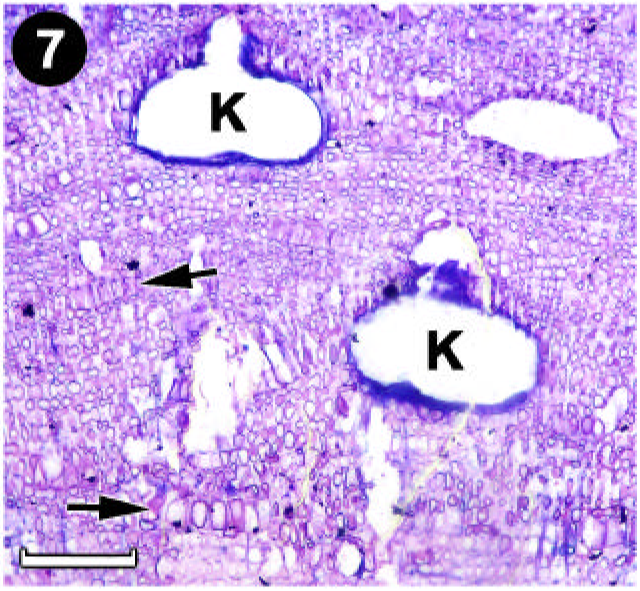

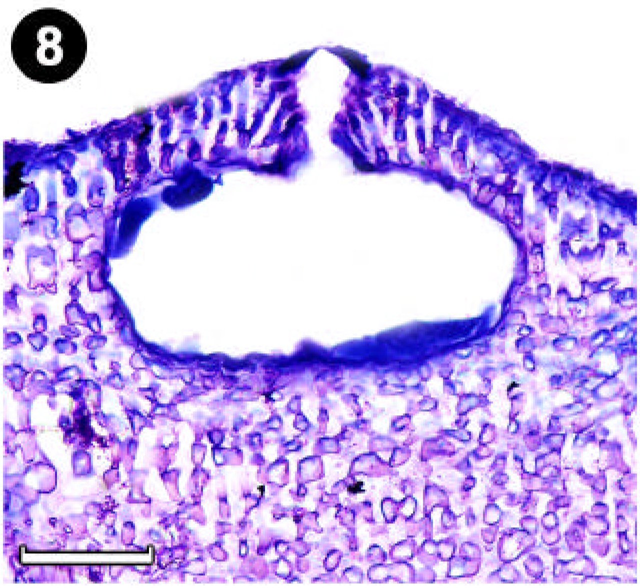

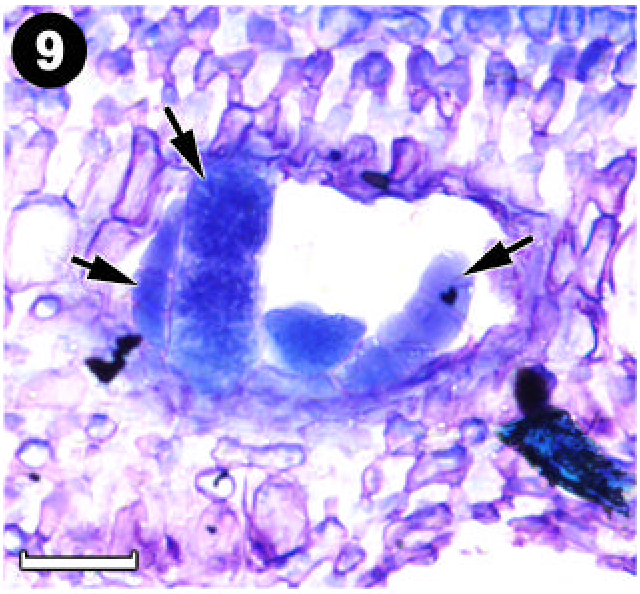

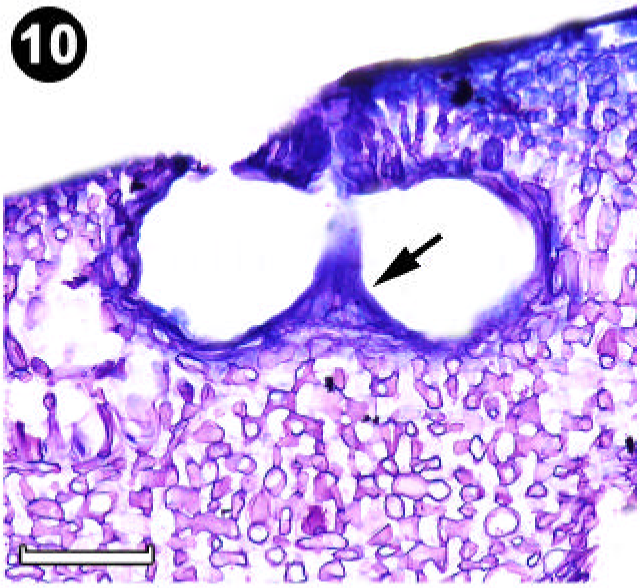

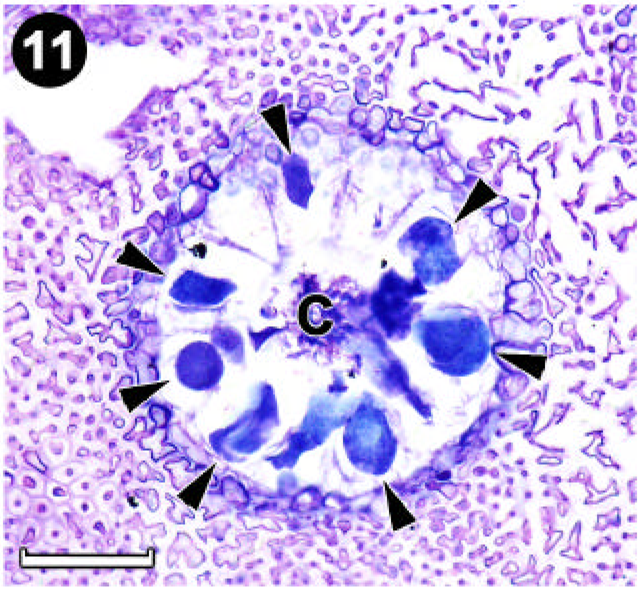

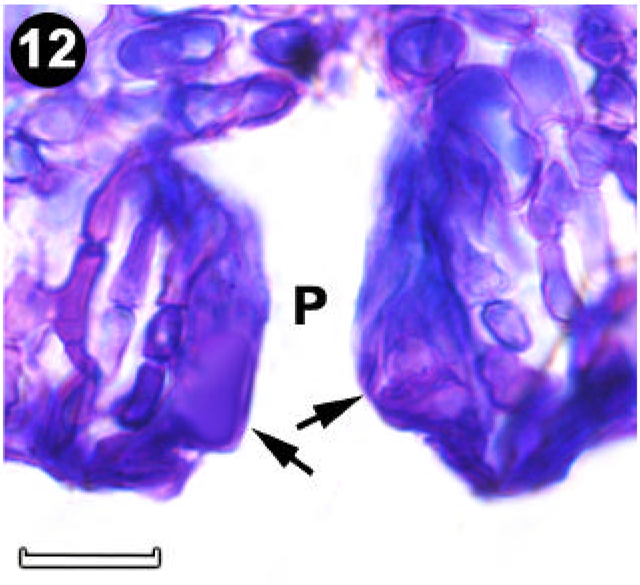

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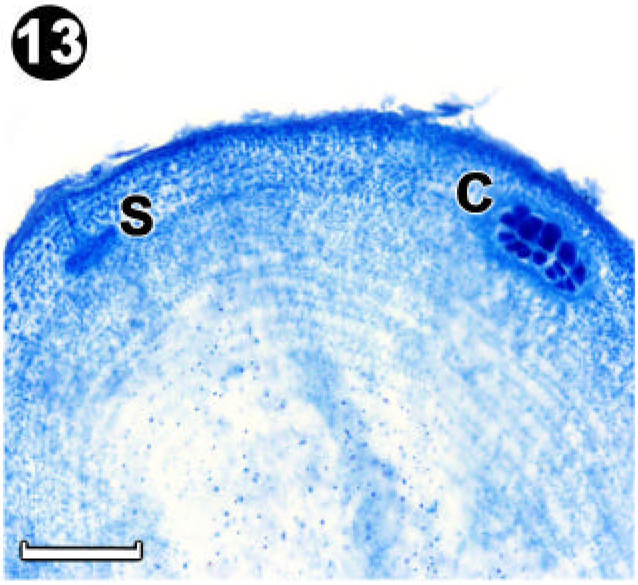
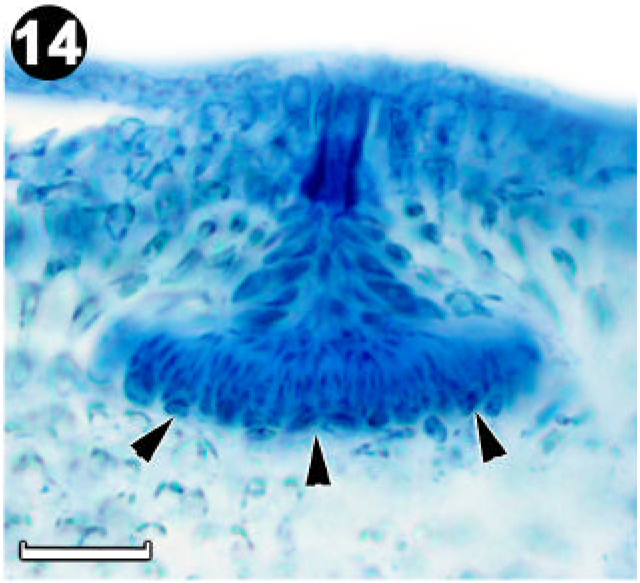




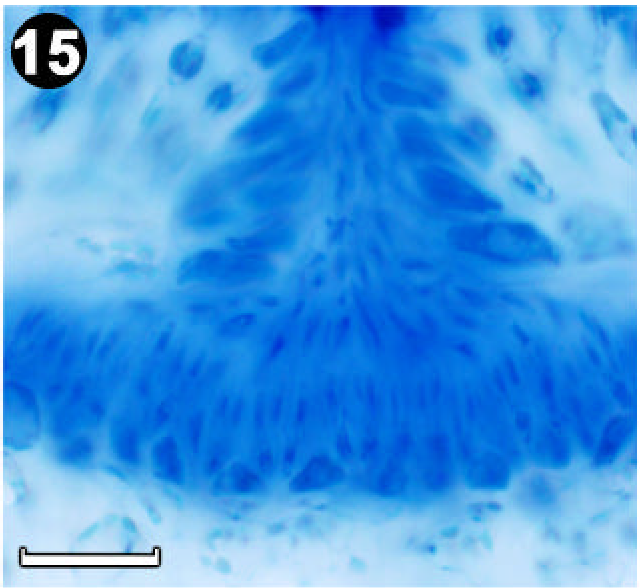
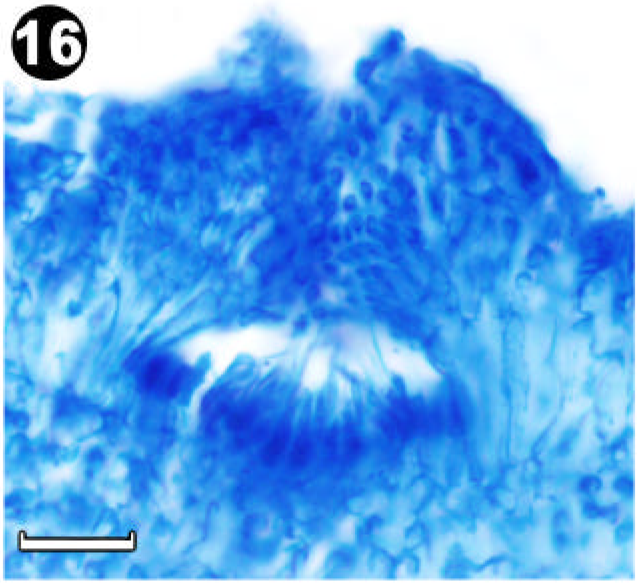
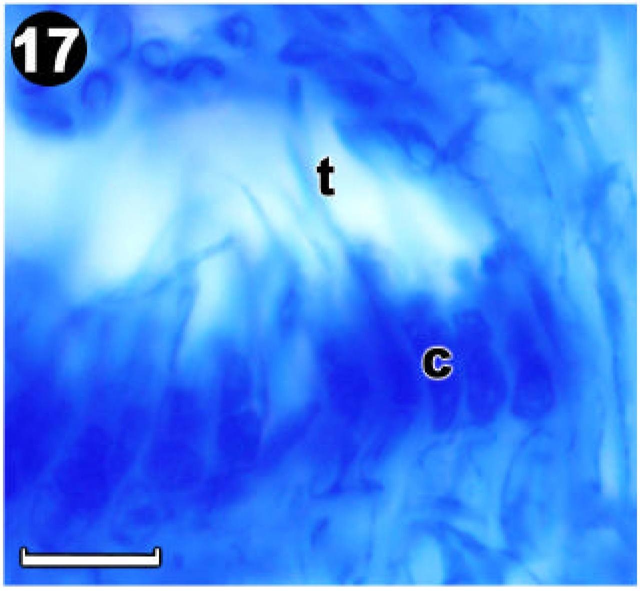
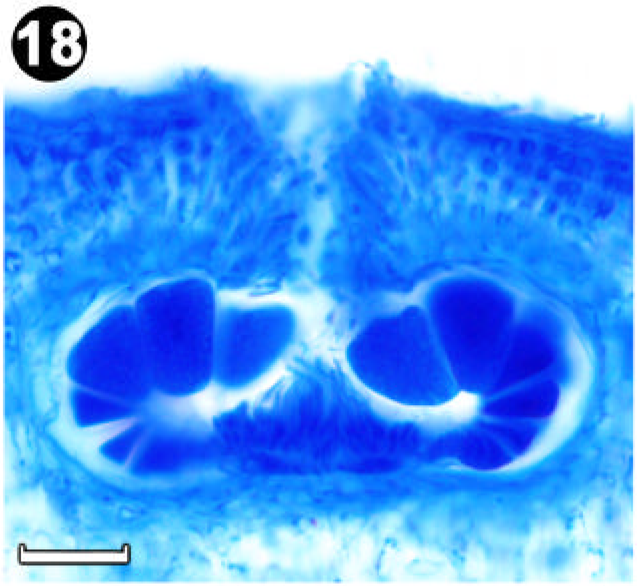


Plate 55







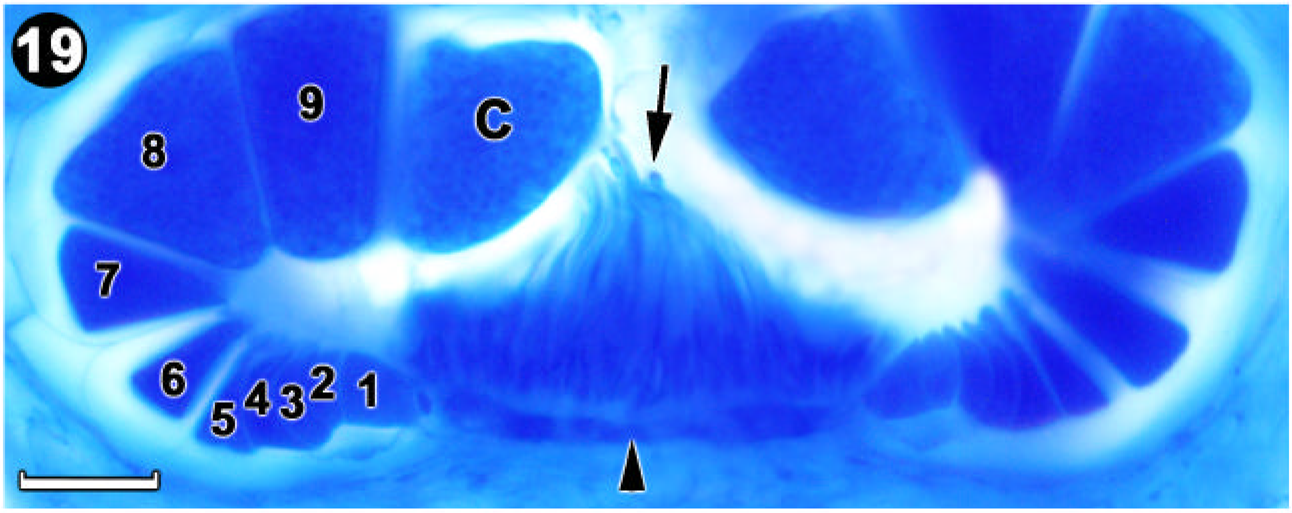
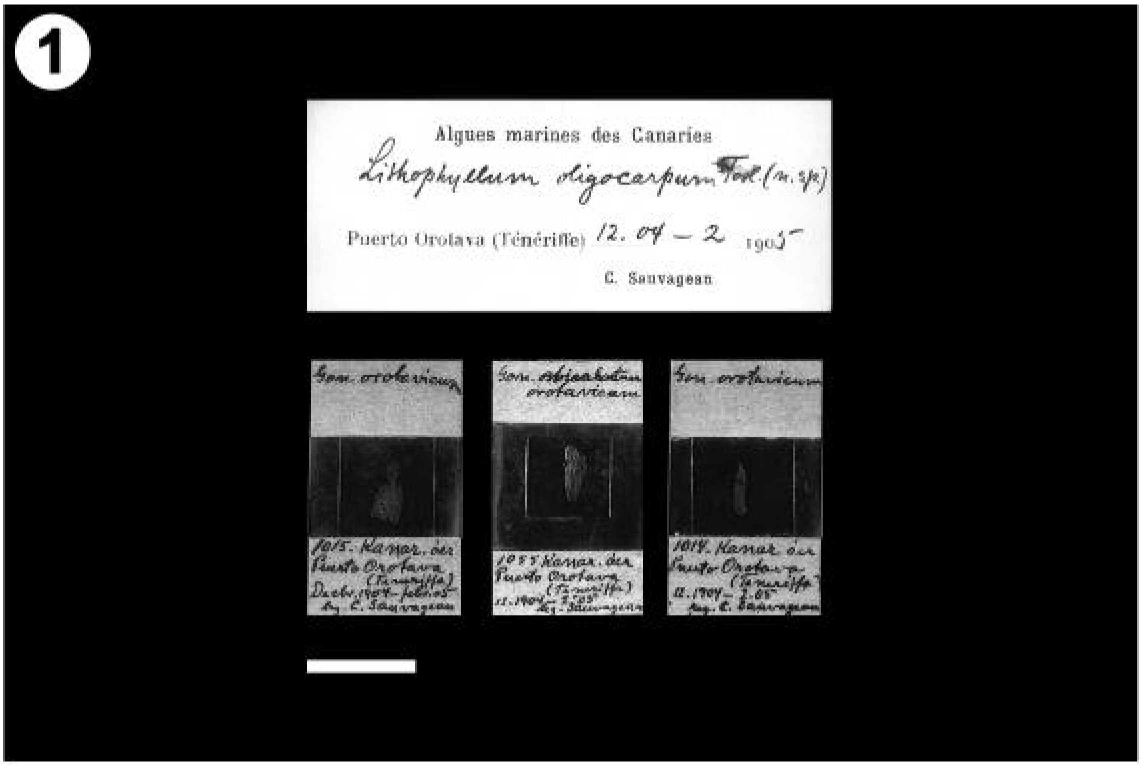


Plate 56



Algues marines des Canaries

Lithophyllum oligocarpum Fosl. (n. sp.)

Puerto Orotava (Ténériffe) 12. 04 – 2 1905

C. Sauvagean

Gon. orotavicum

1015. Kanar. der Puerto Orotava (Teneriffa)

Gon. orotavicum

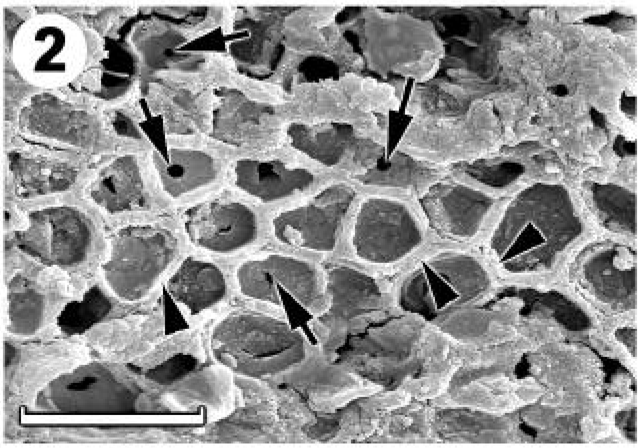
1055 Kanar. der Puerto Orotava (Teneriffa)

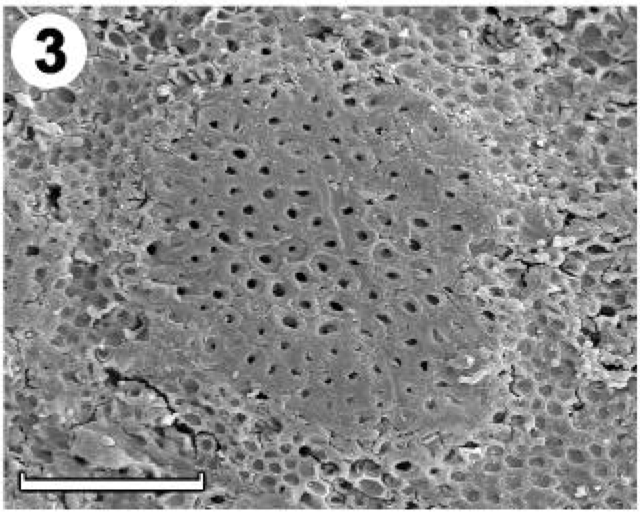
Gon. orotavicum

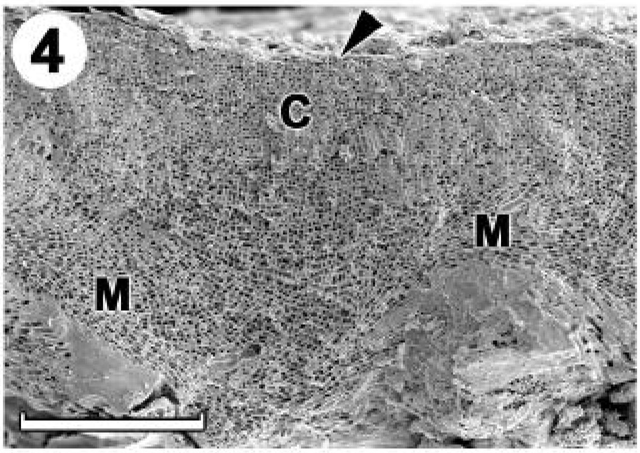
1014. Kanar. der Puerto Orotava (Teneriffa) 12.1904 – 2.05

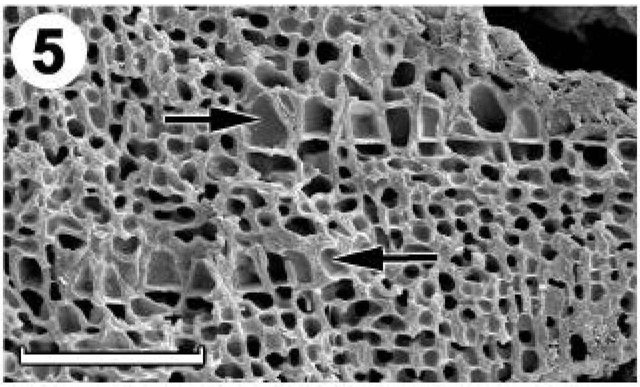
leg. C. Sauvageau

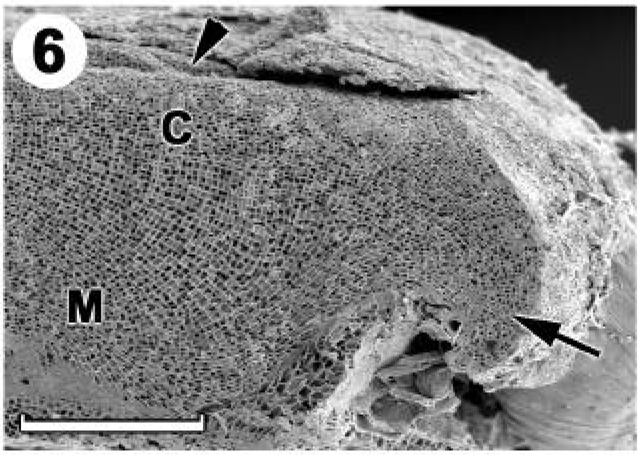
Plate 57

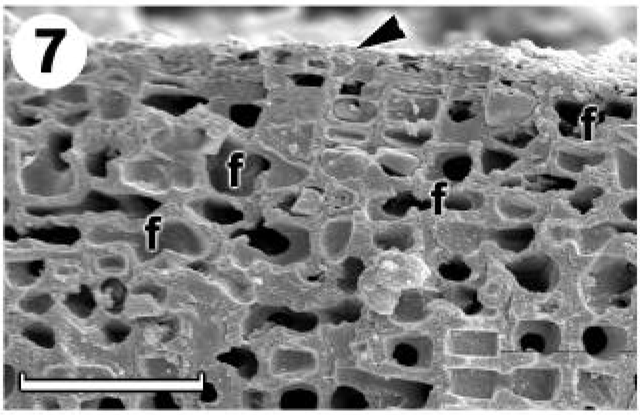


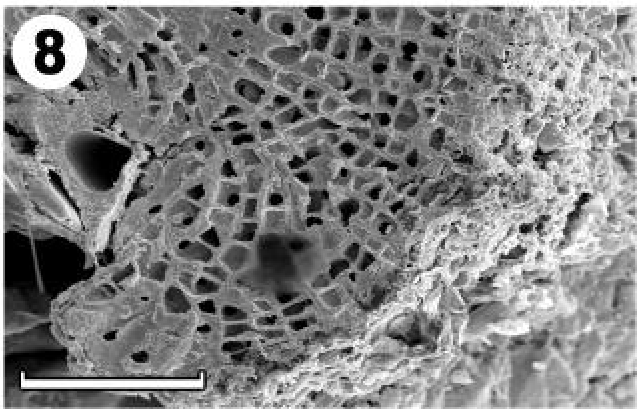












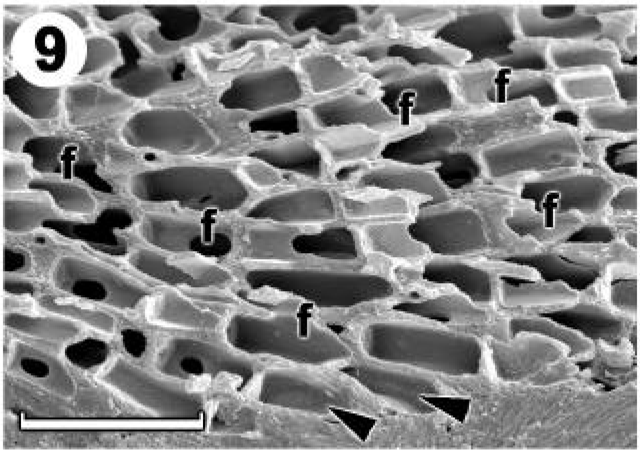
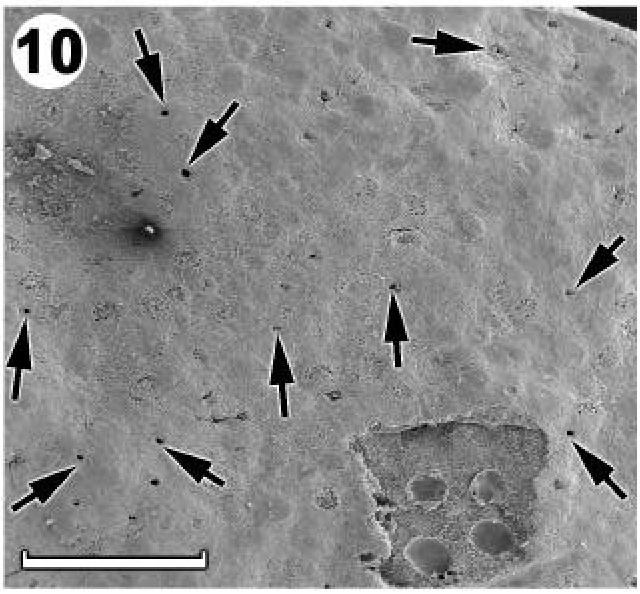


Plate 58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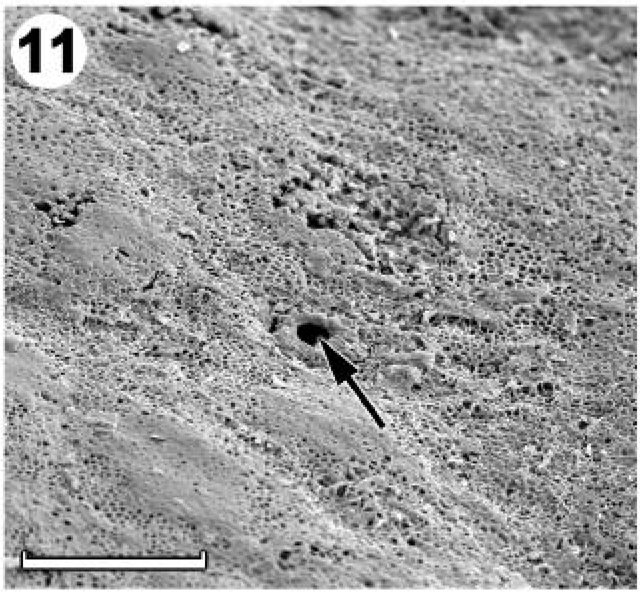
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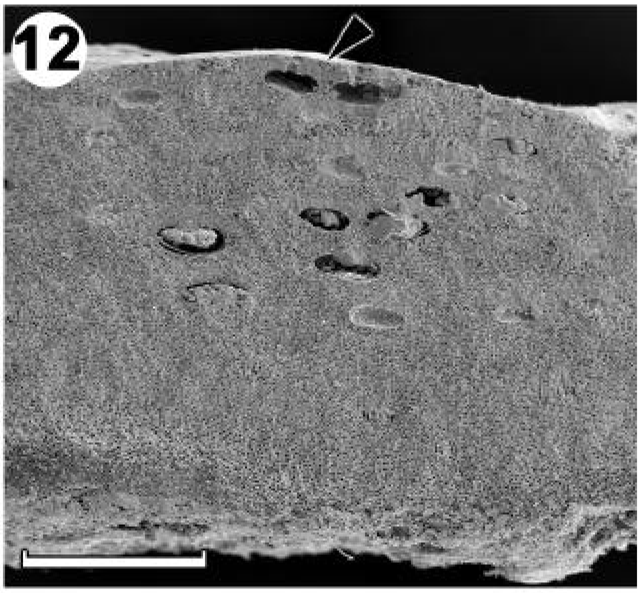
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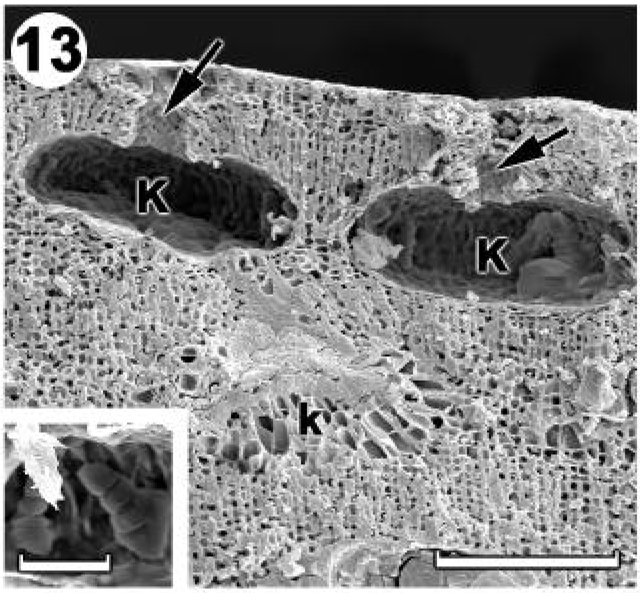
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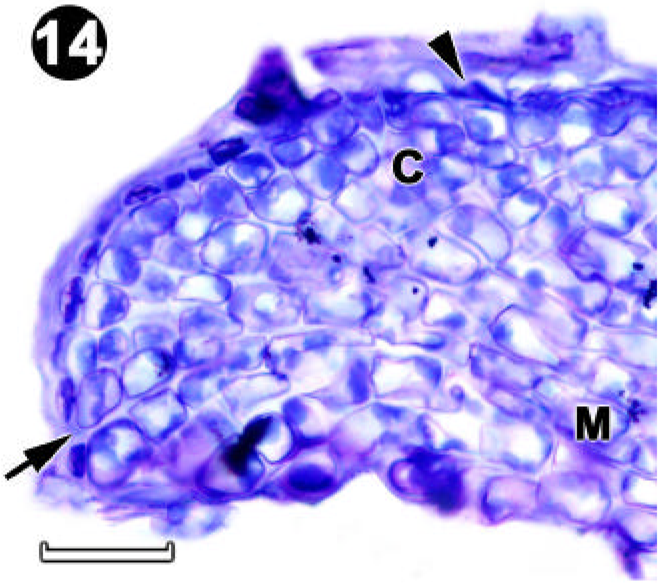
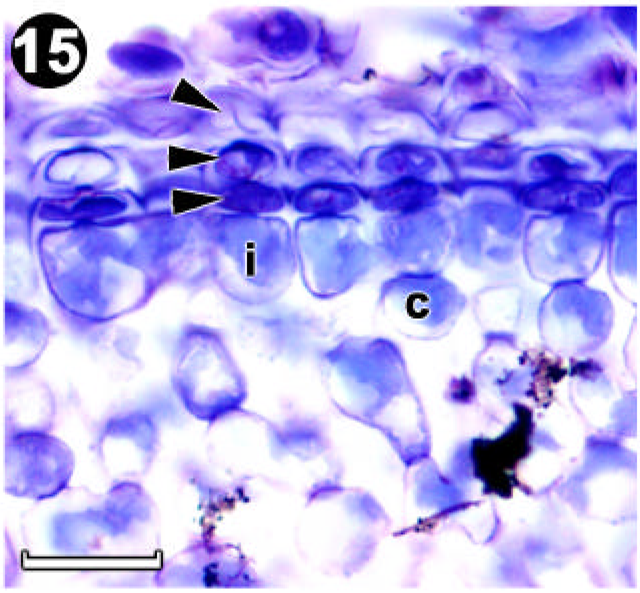
Plate 59





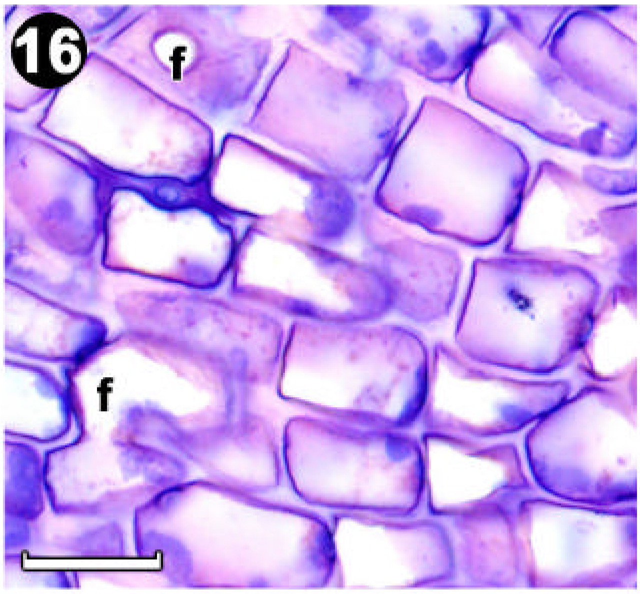
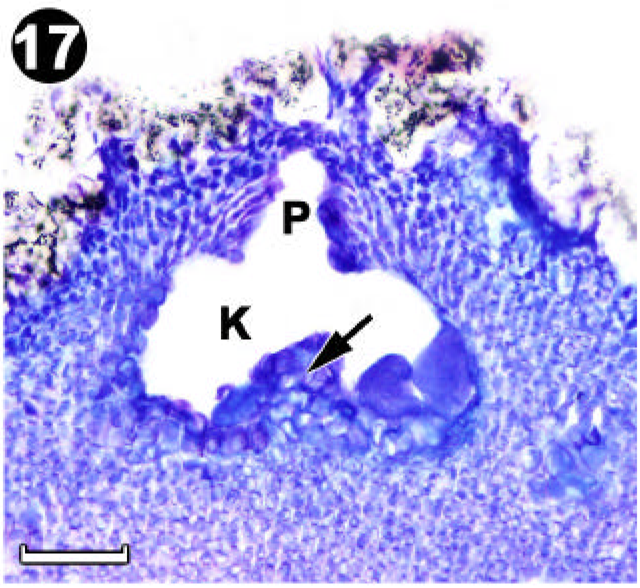
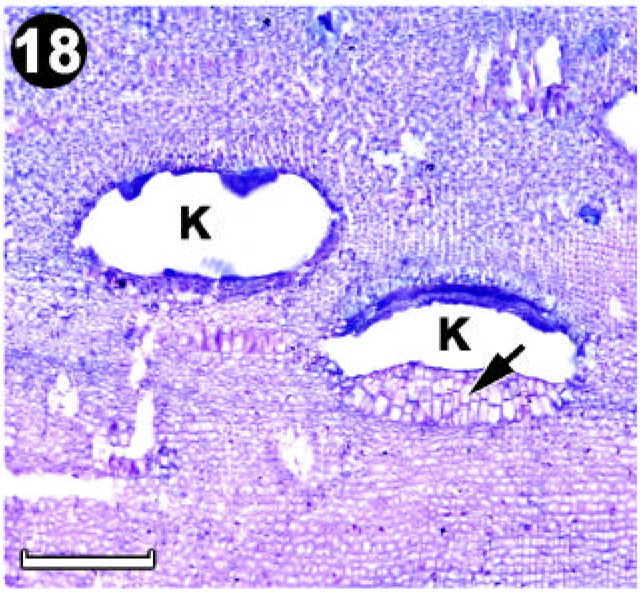
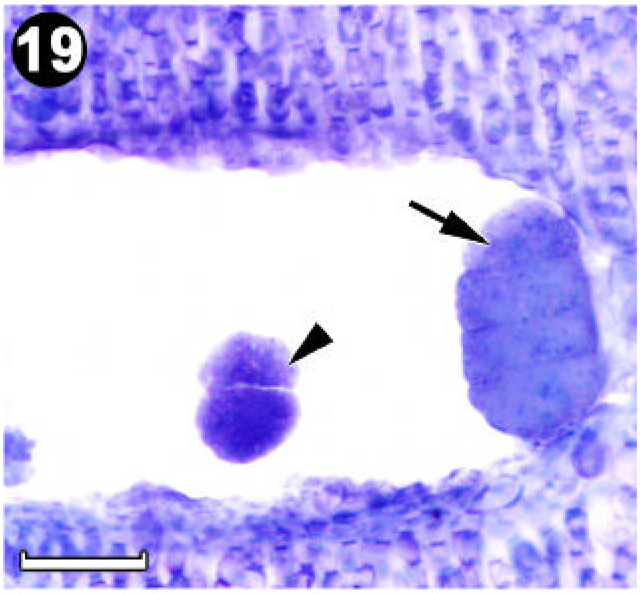
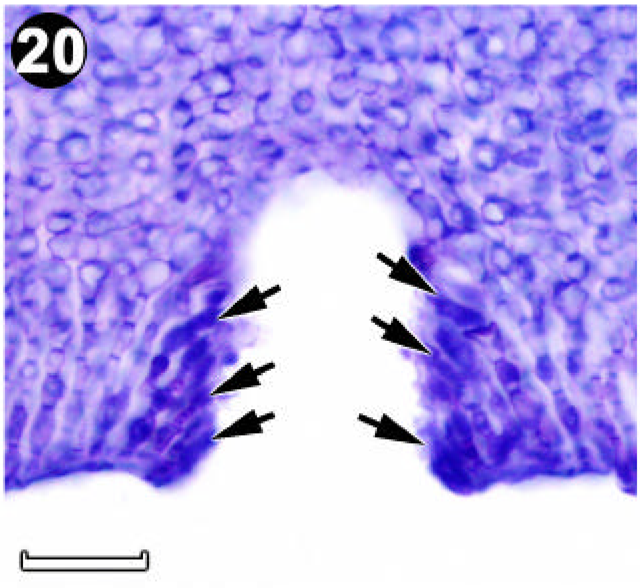


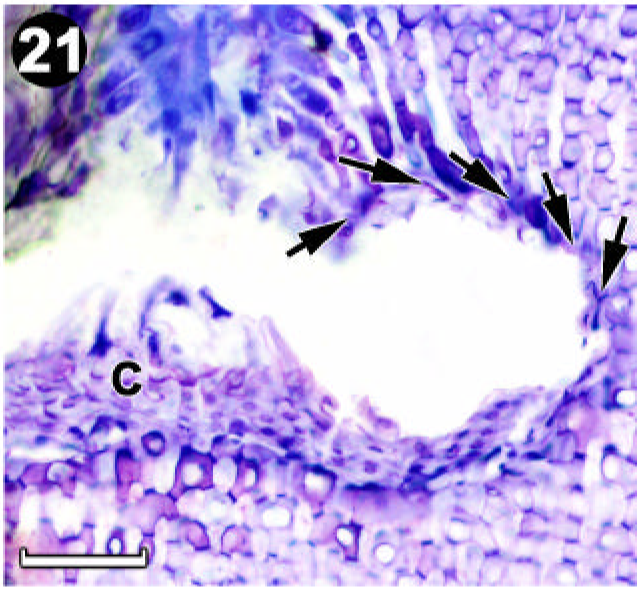
Plate 60











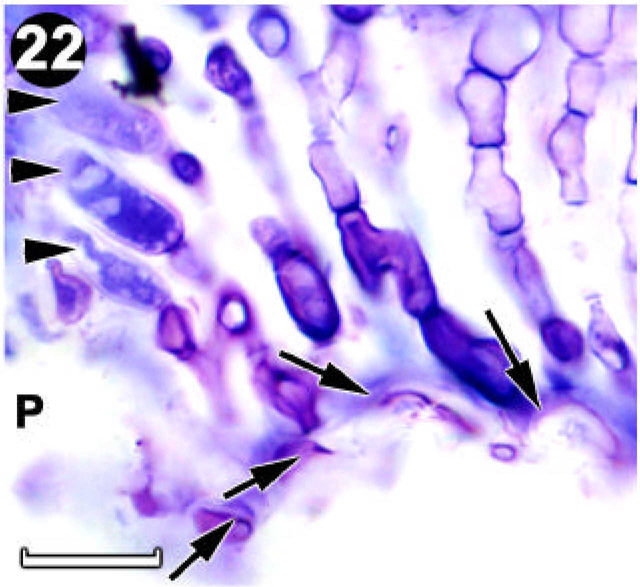


Plate 61

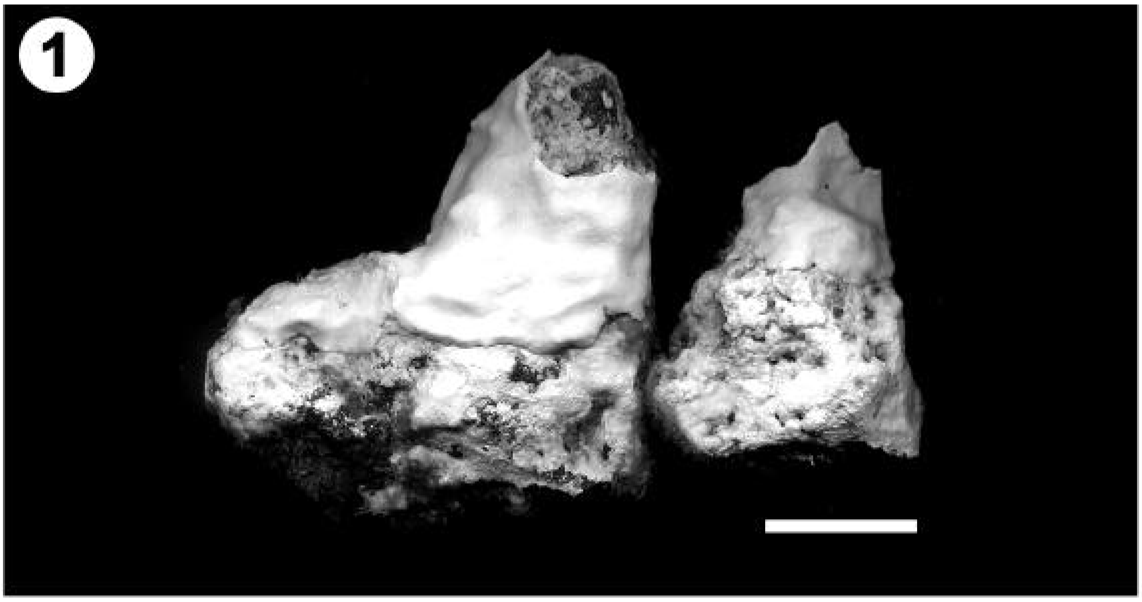
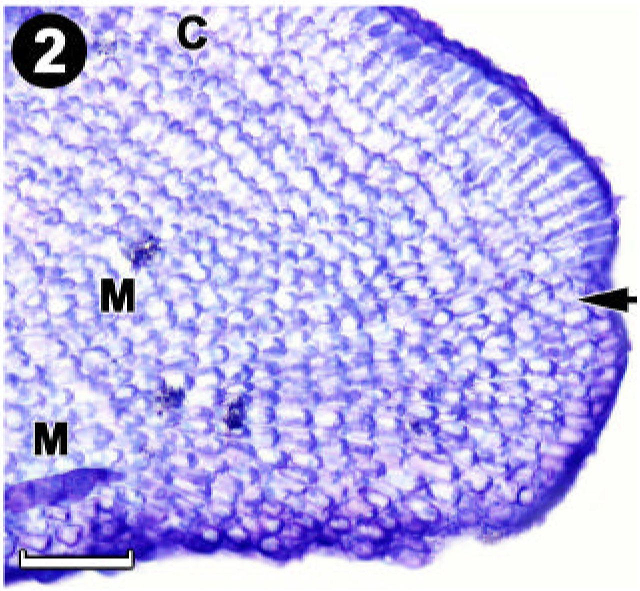
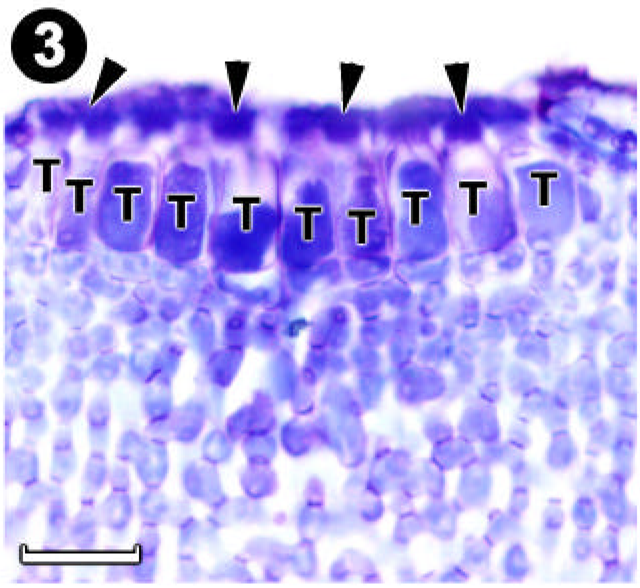
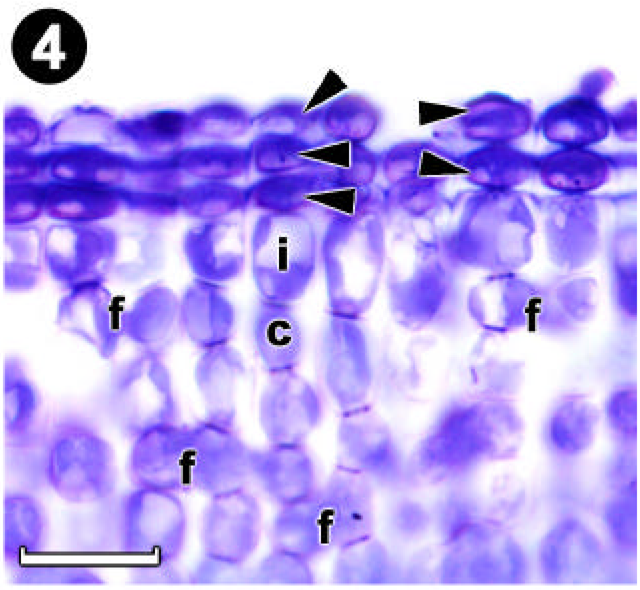
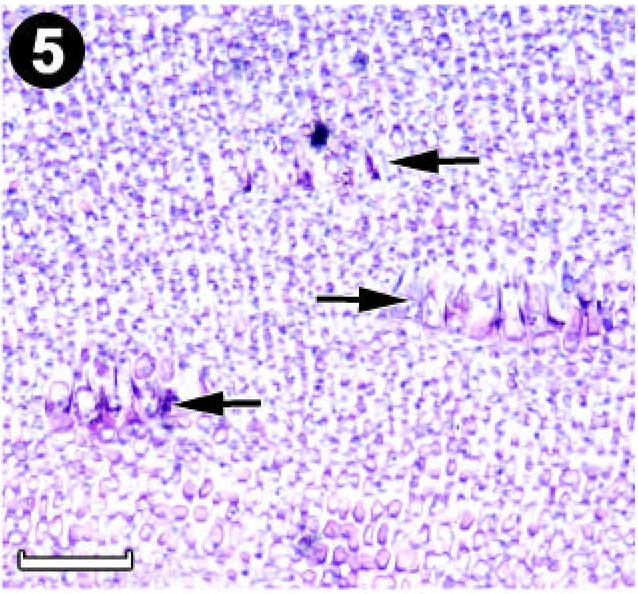


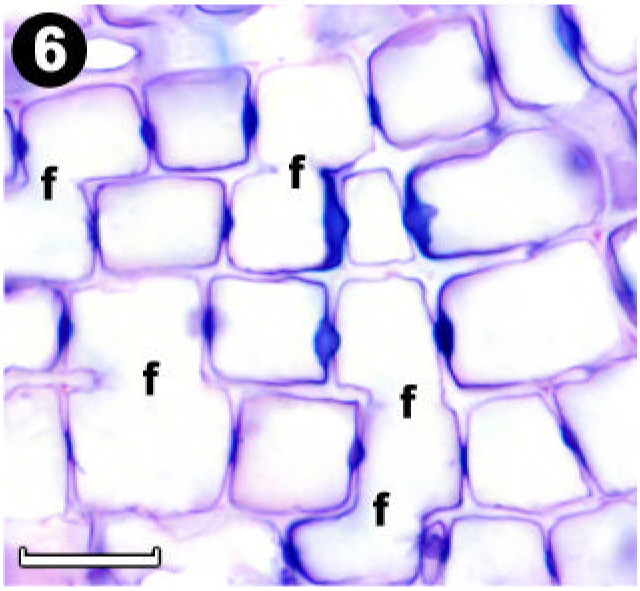
Plate 62











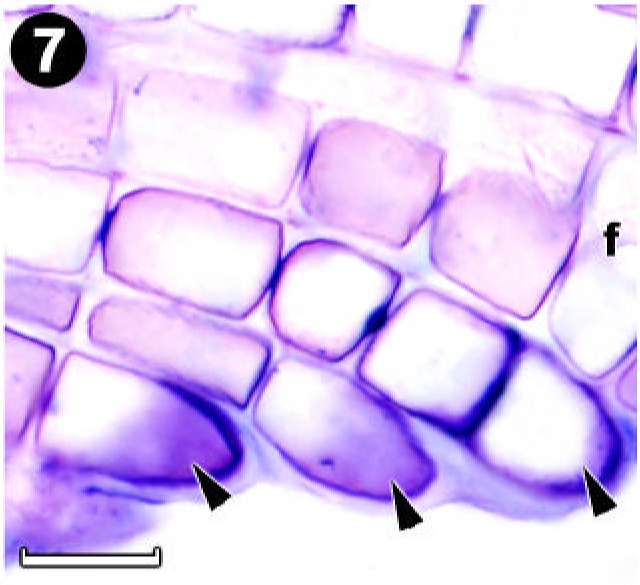
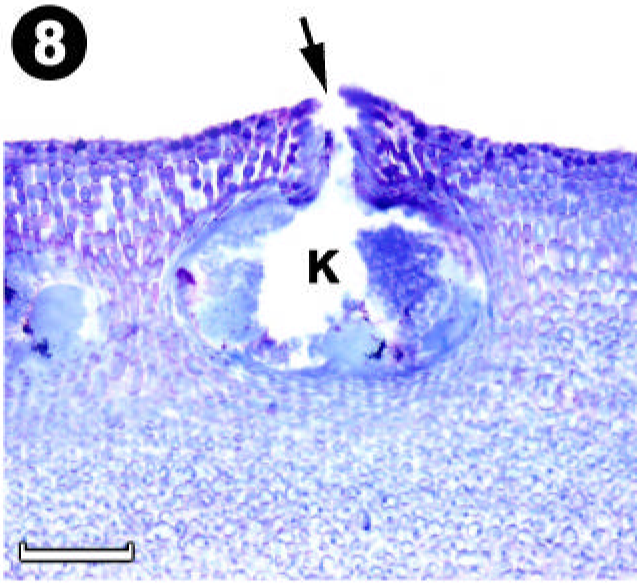
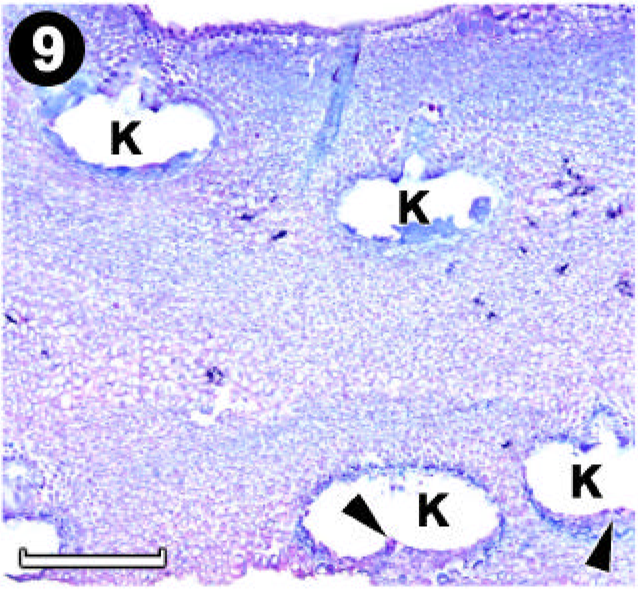
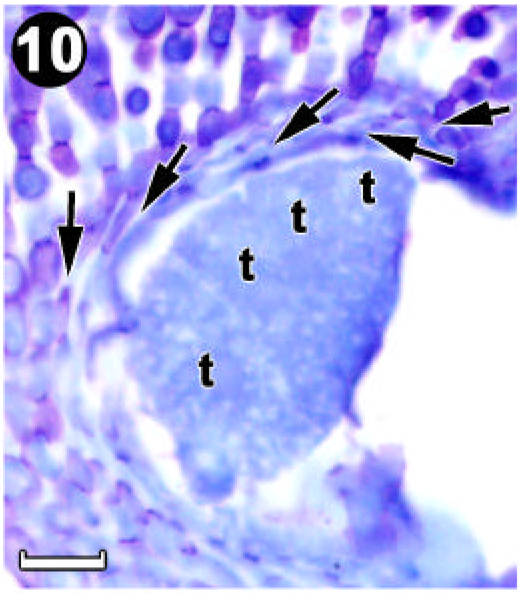
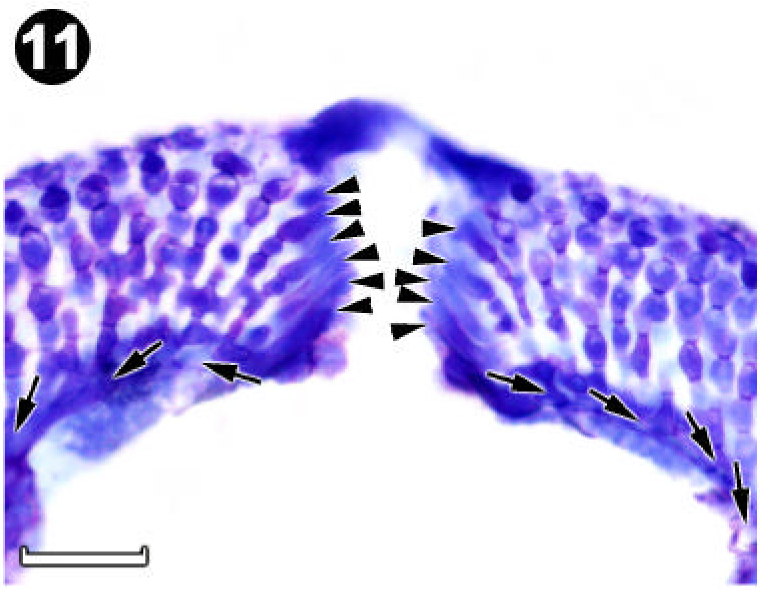


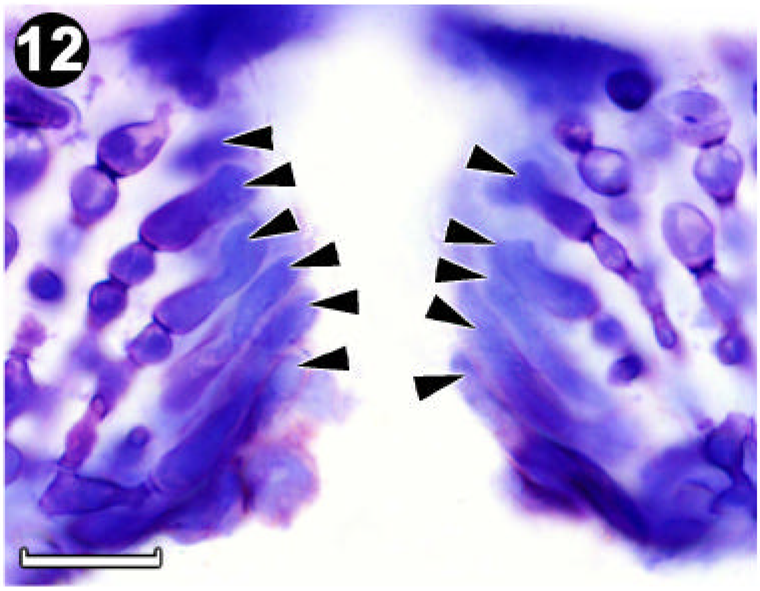
Plate 63











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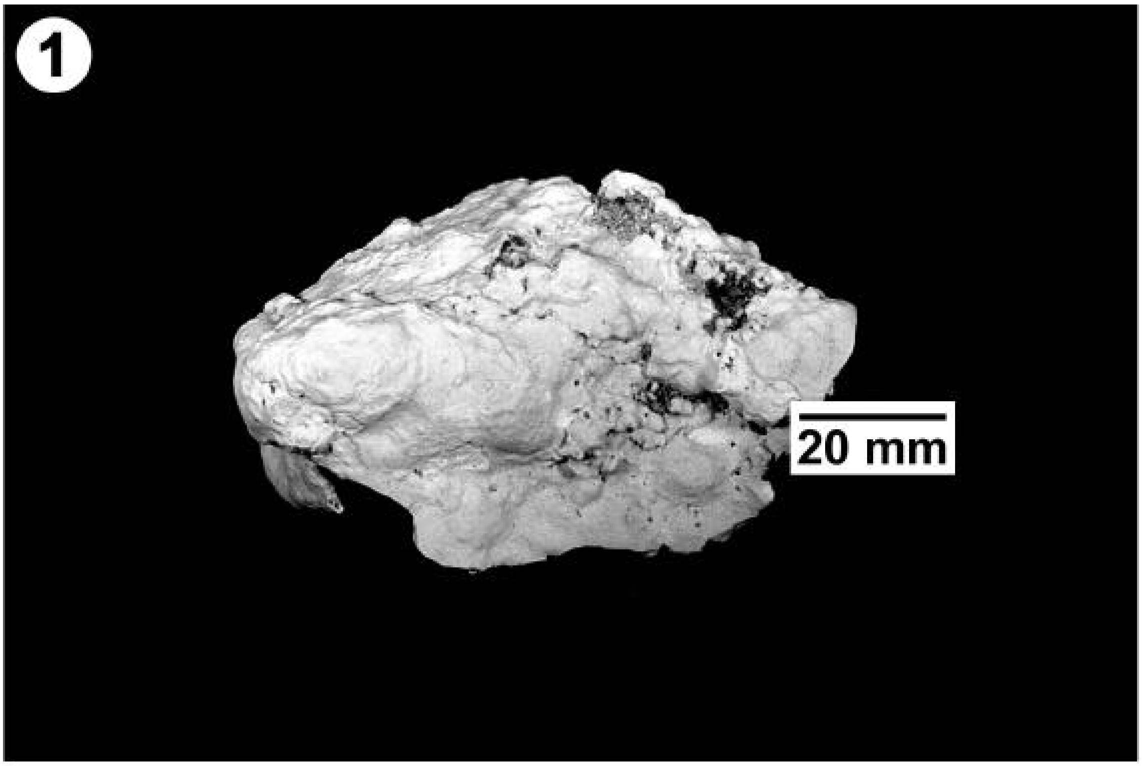
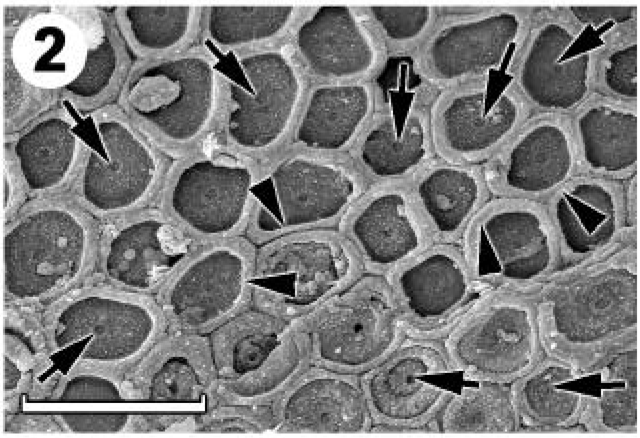
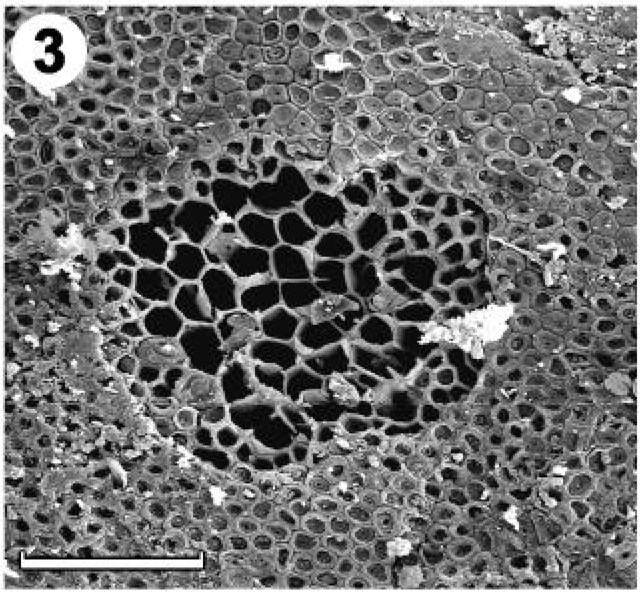
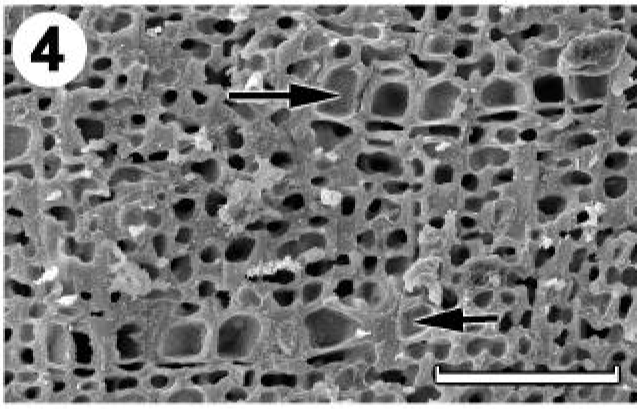
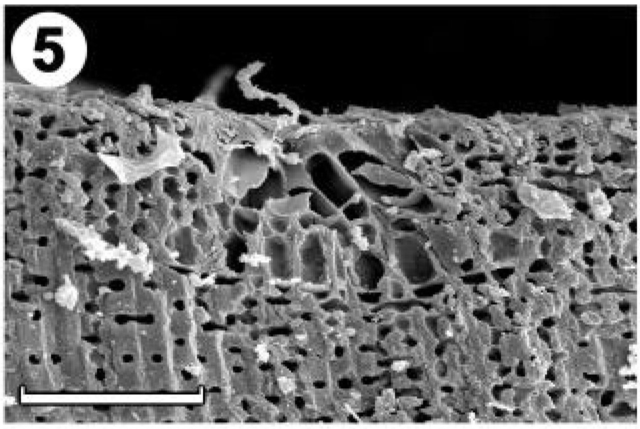


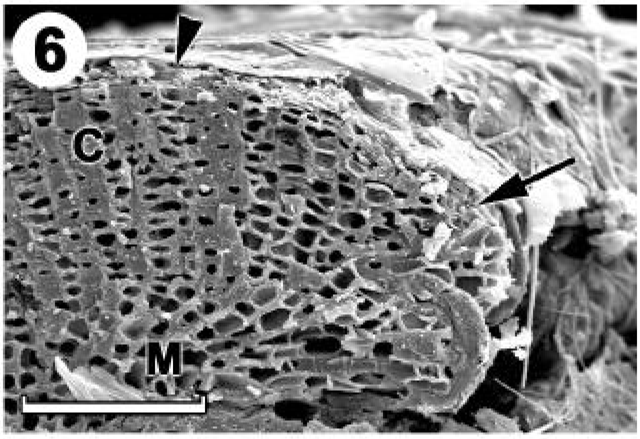
Plate 65

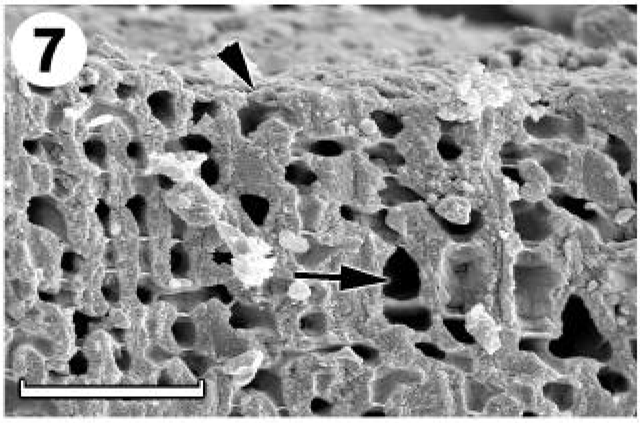


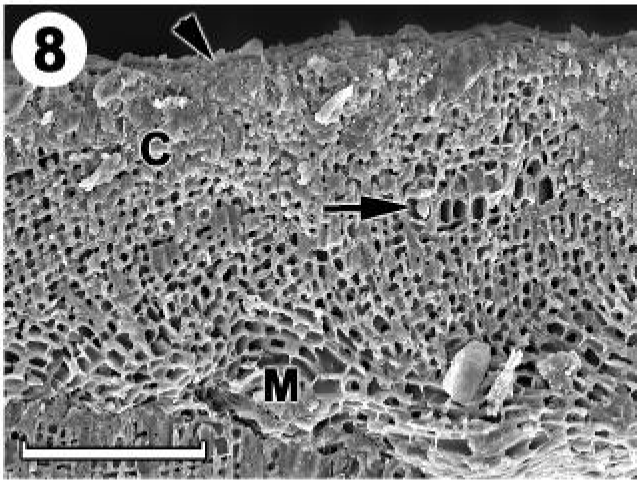












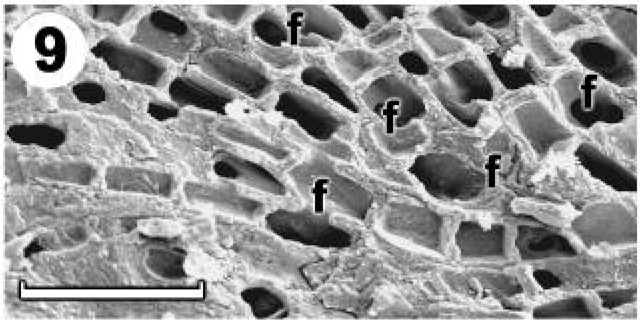
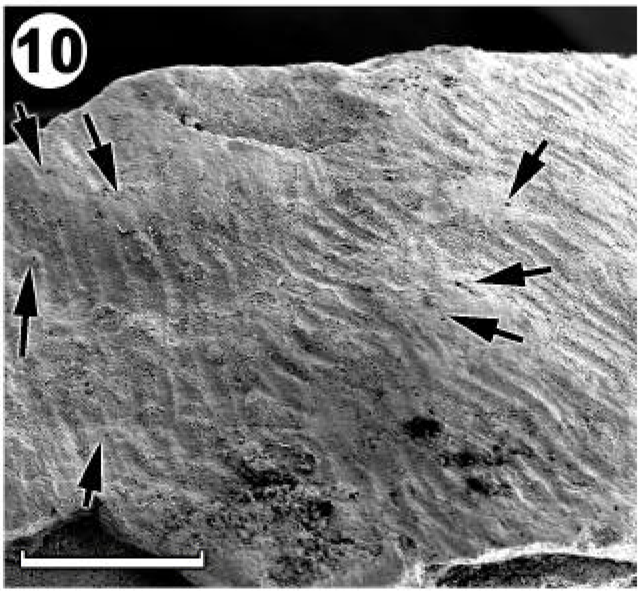
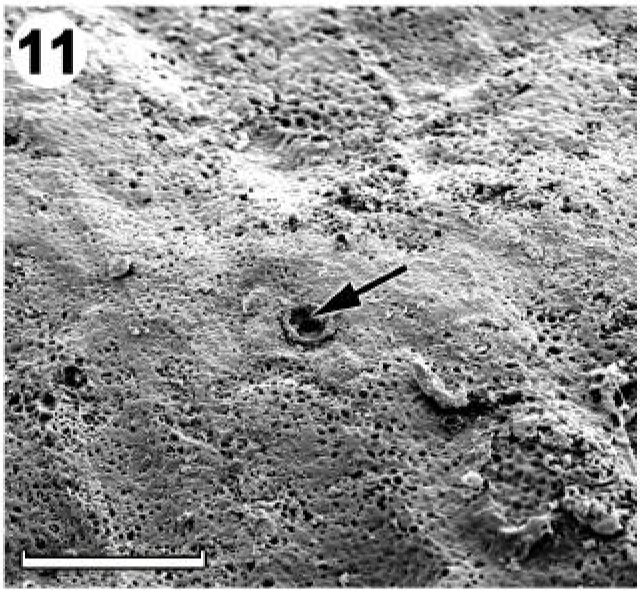
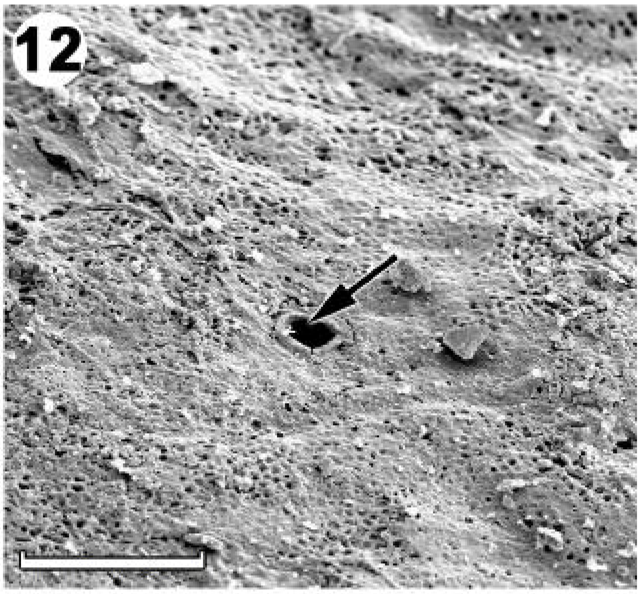
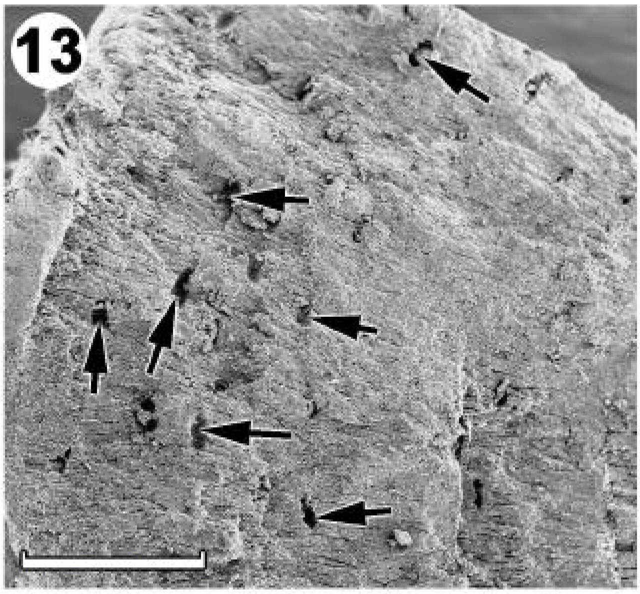


Plate 66









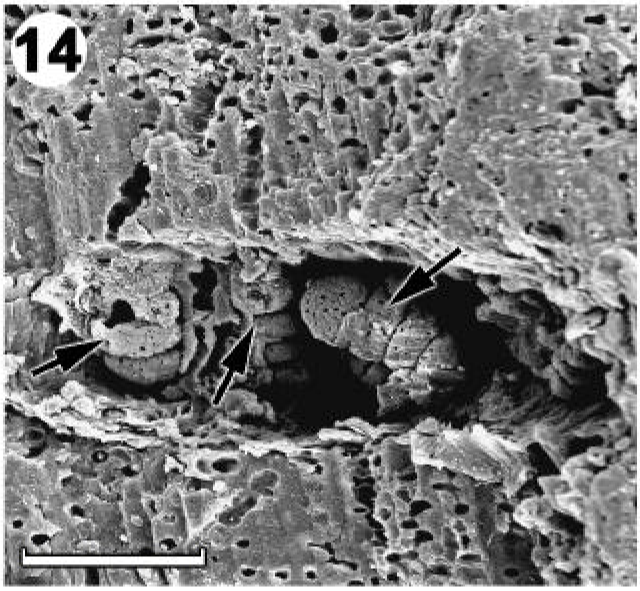
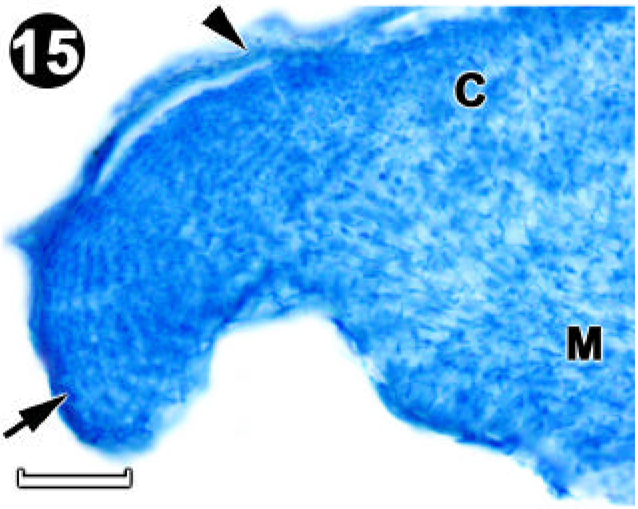
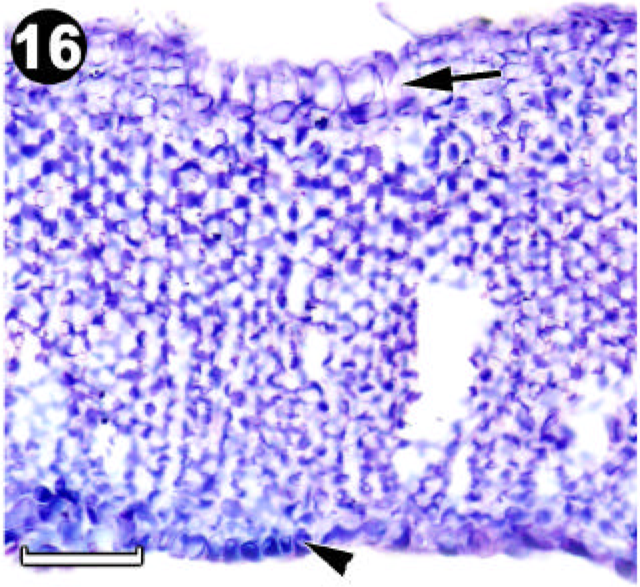
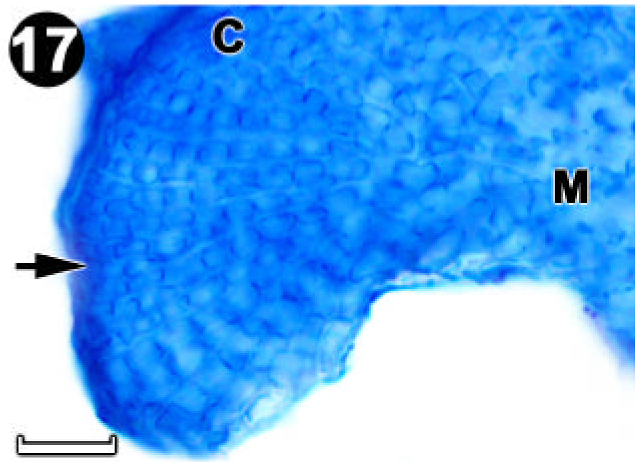
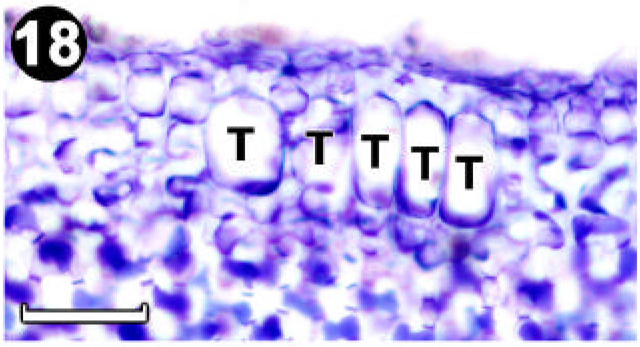


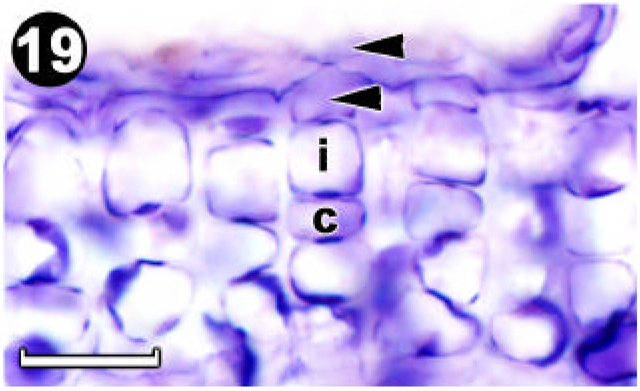
Plate 67

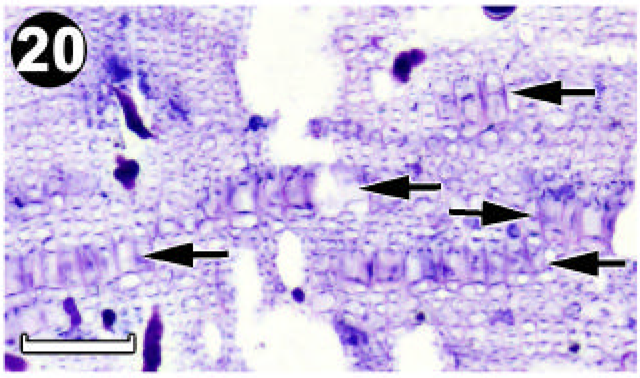


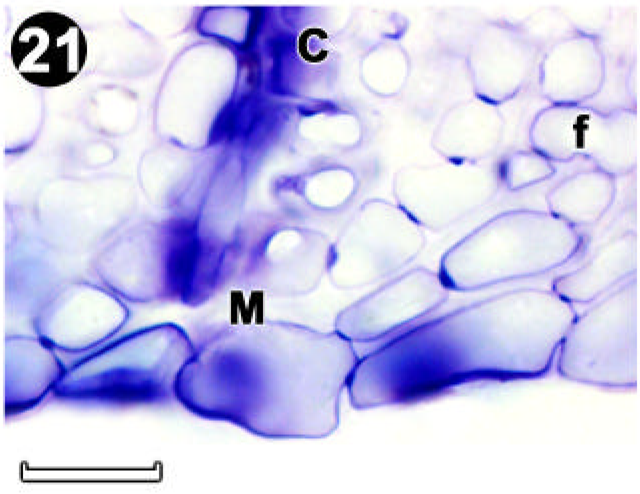












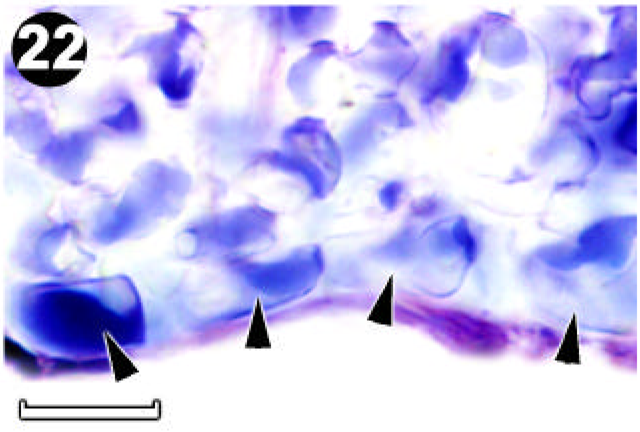
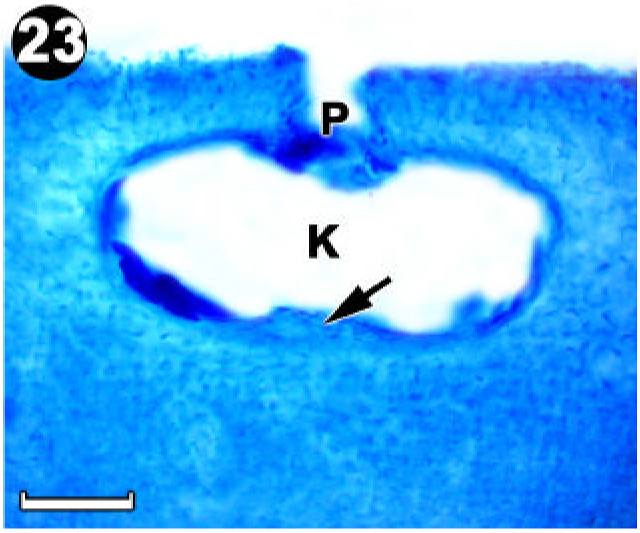


Plate 68

23



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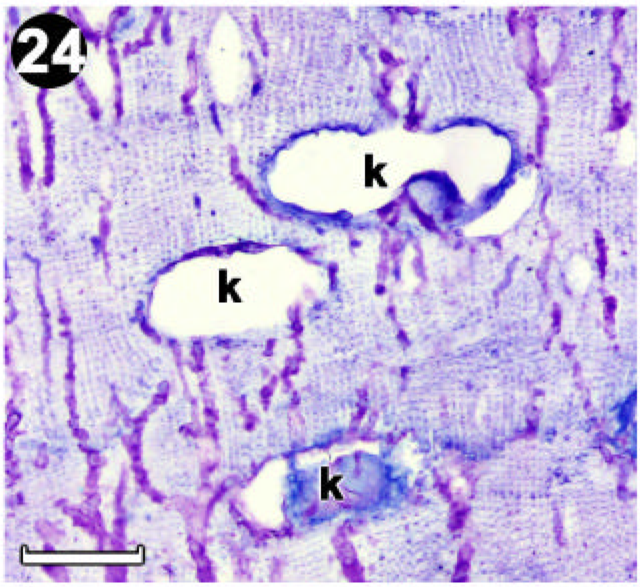

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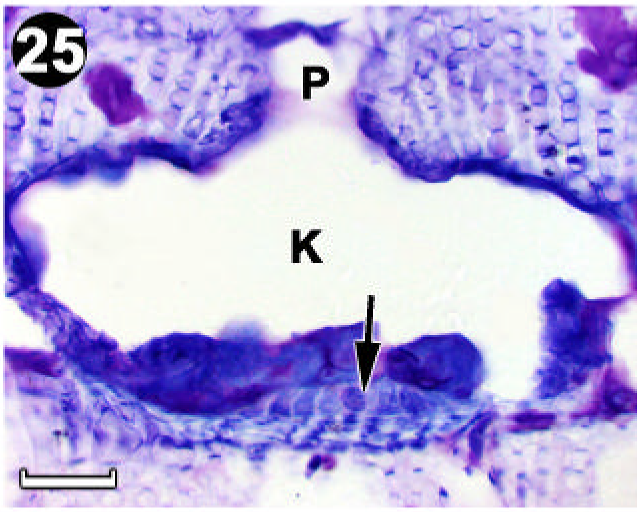

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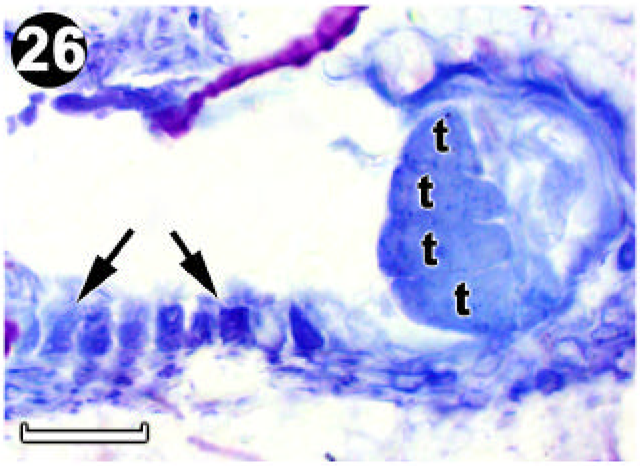

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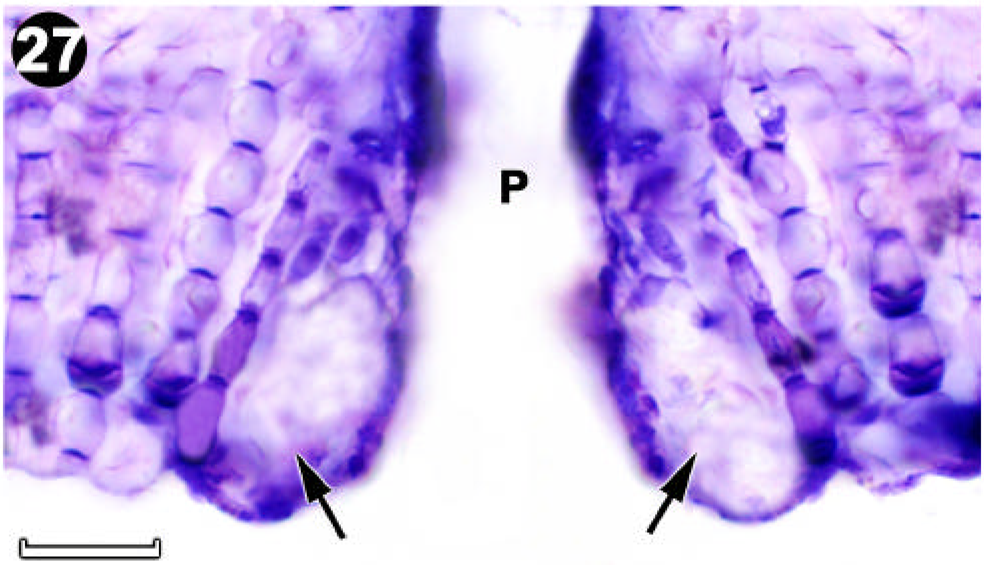


Plate 69

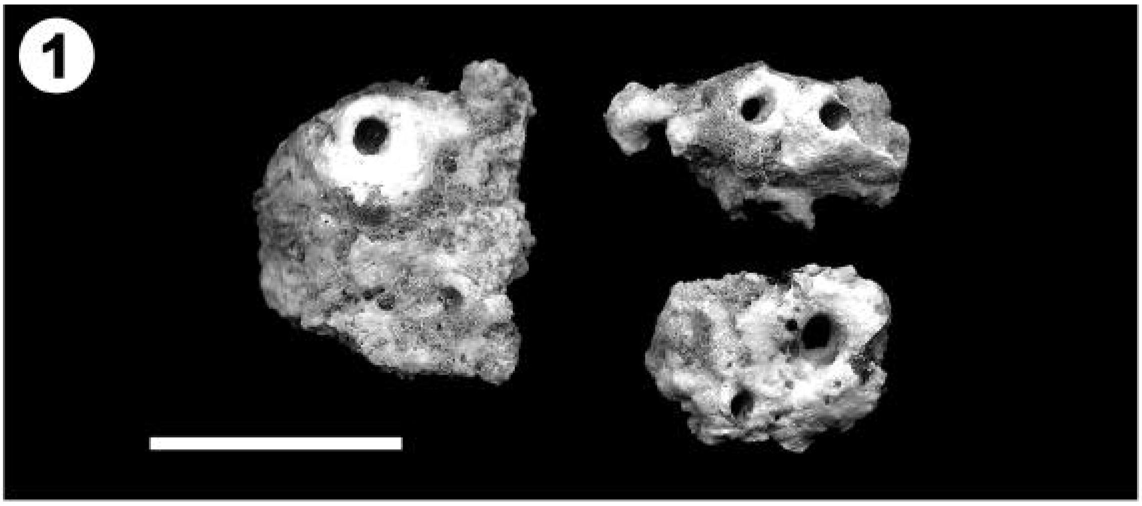


Plate 70

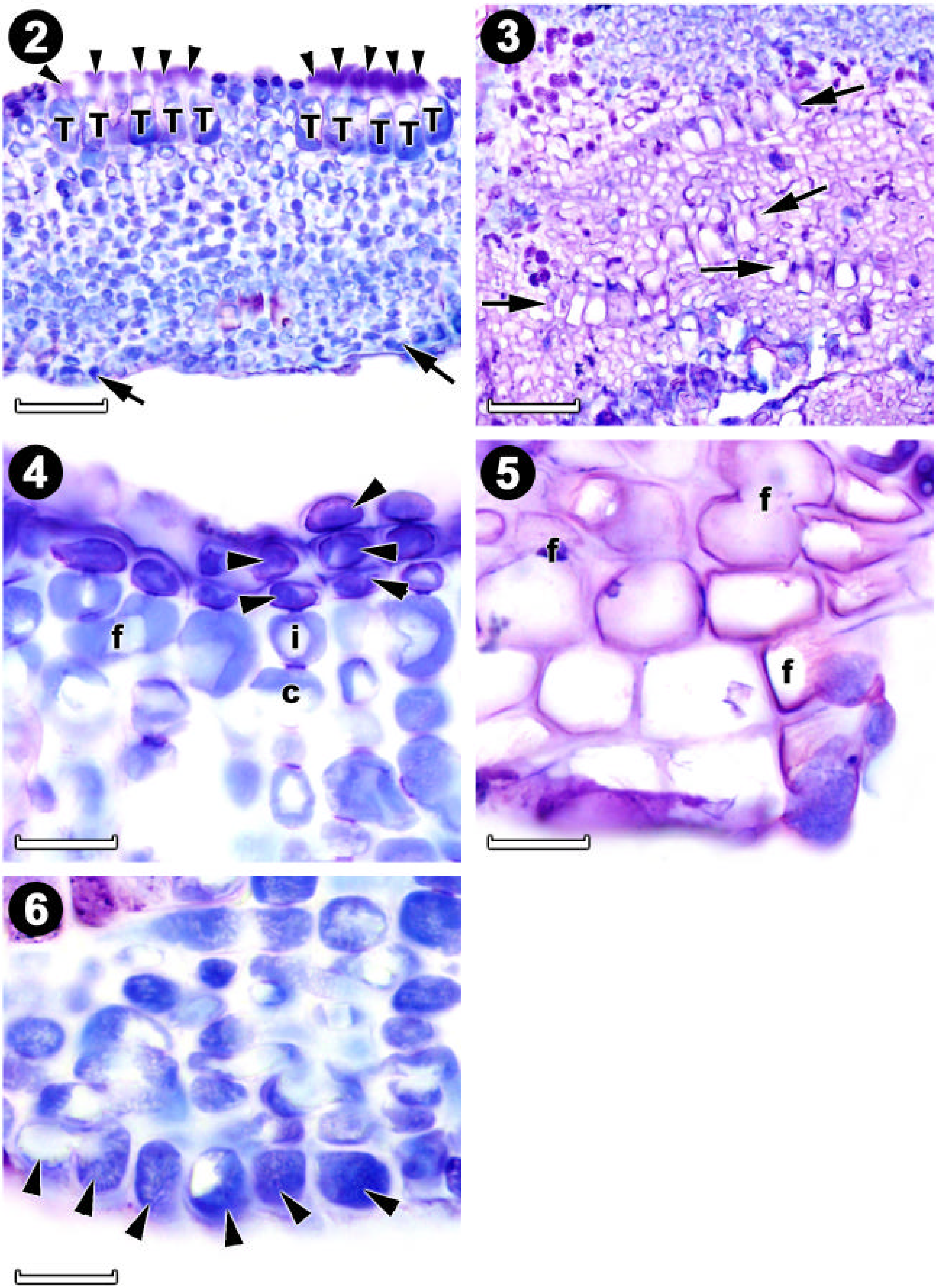
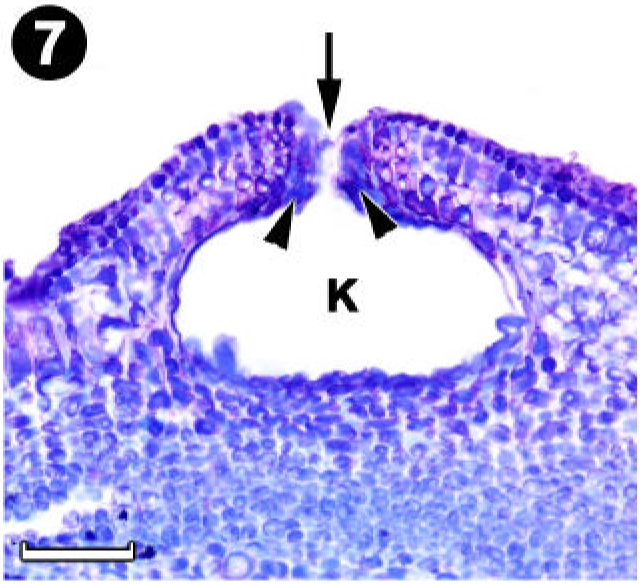
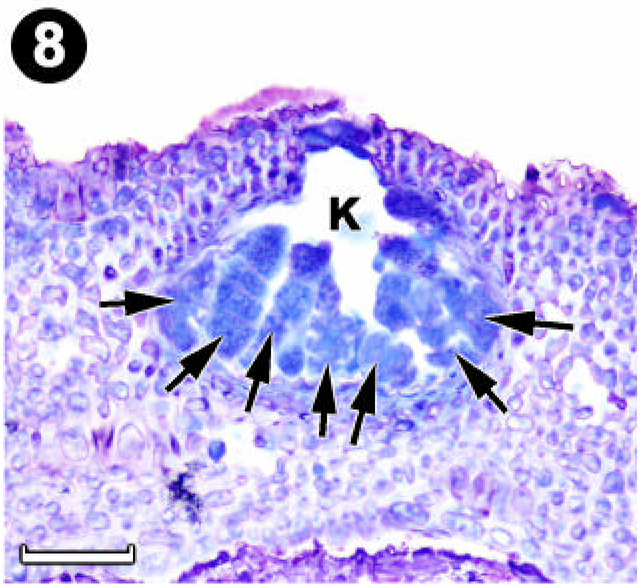
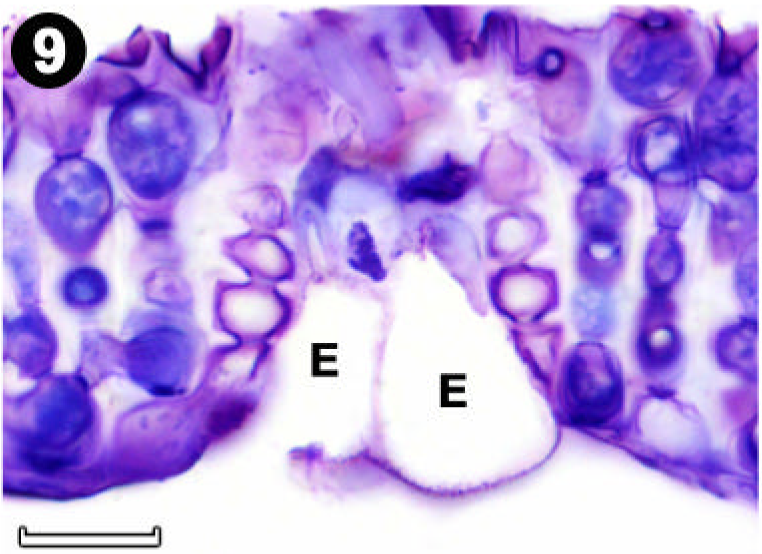


Plate 71







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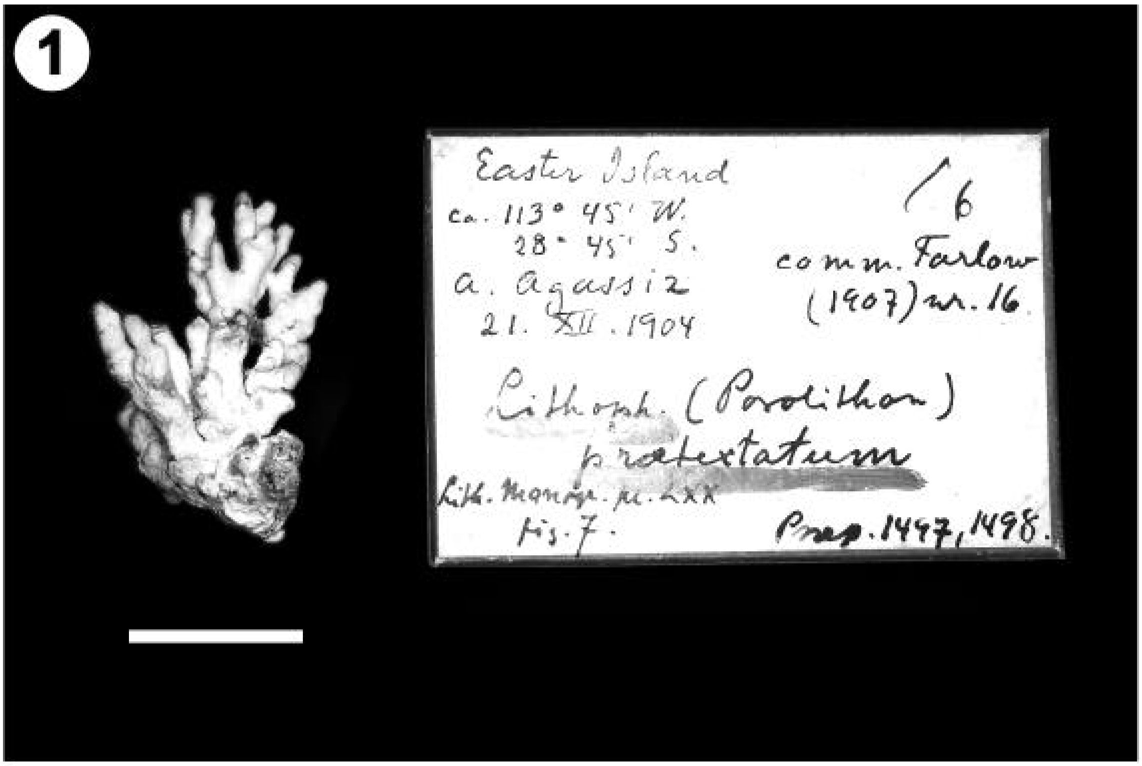


Easter Island
ca. 113° 45' W.
28° 45' S.
a. Agassiz
21. XII. 1904

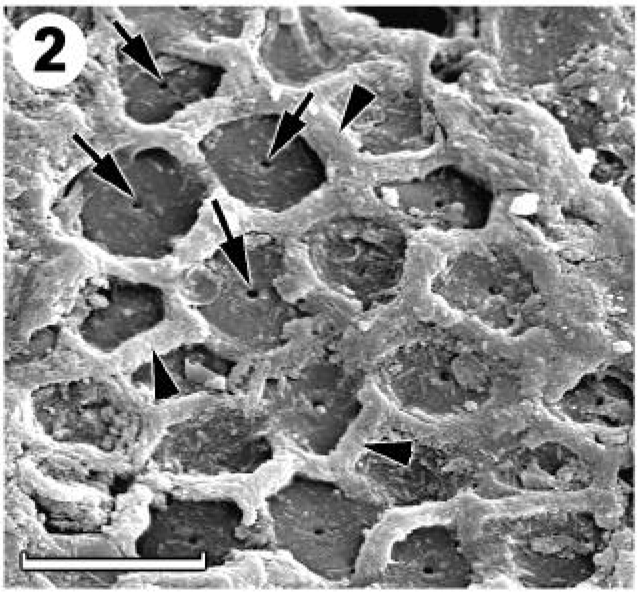
16
comm. Farlow
(1907) nr. 16.

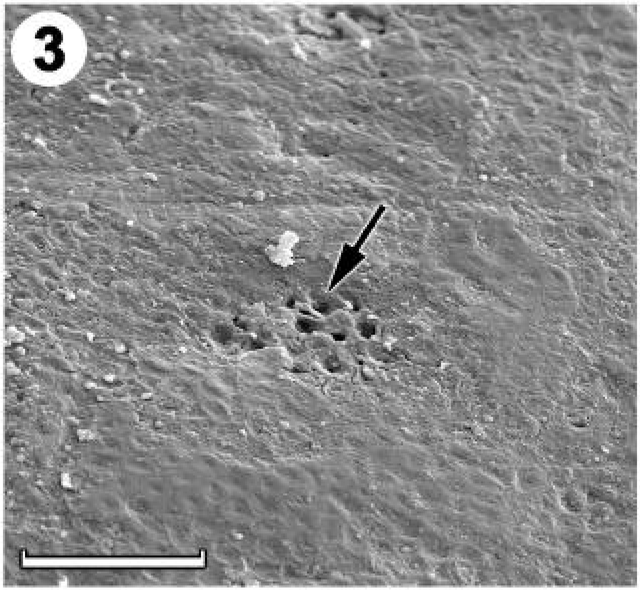
Lithoph. (Porolithon)
praetextatum

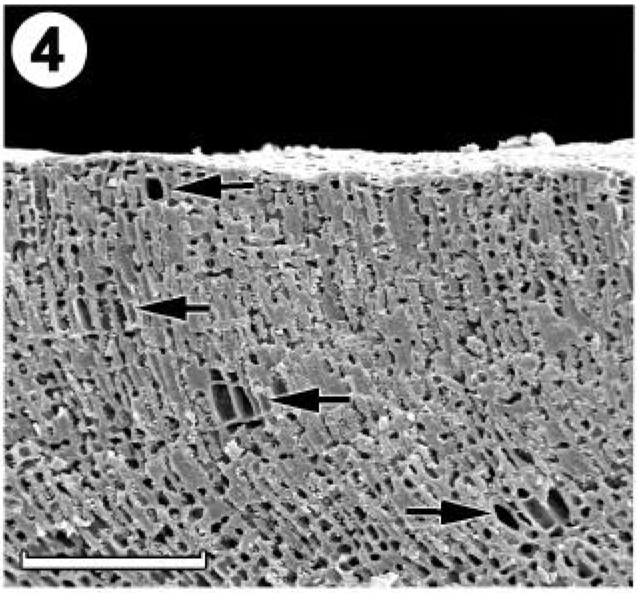
Lith. Monogr. pl. LXX
Fig. 7.

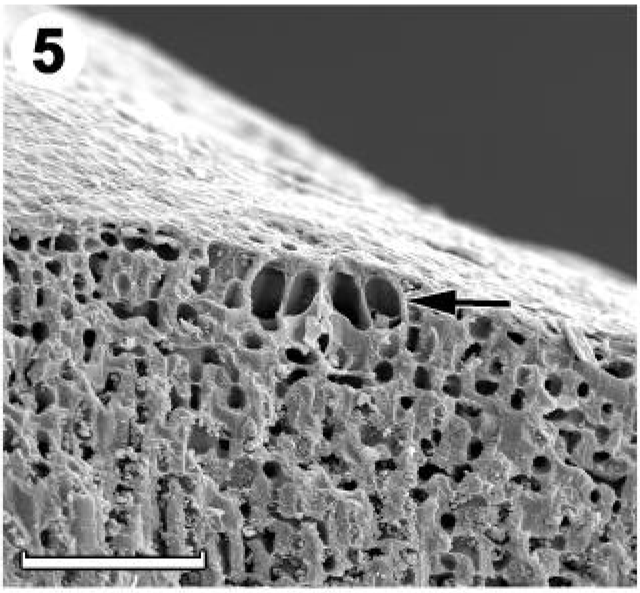
Prep. 1447, 1498.

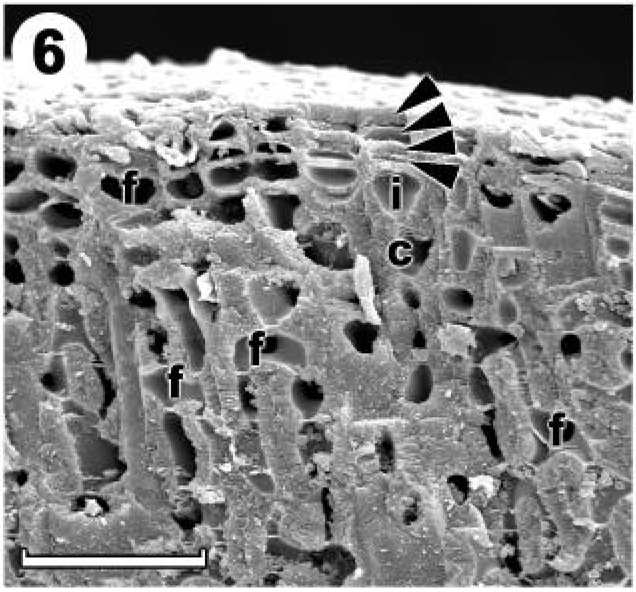
Plate 73











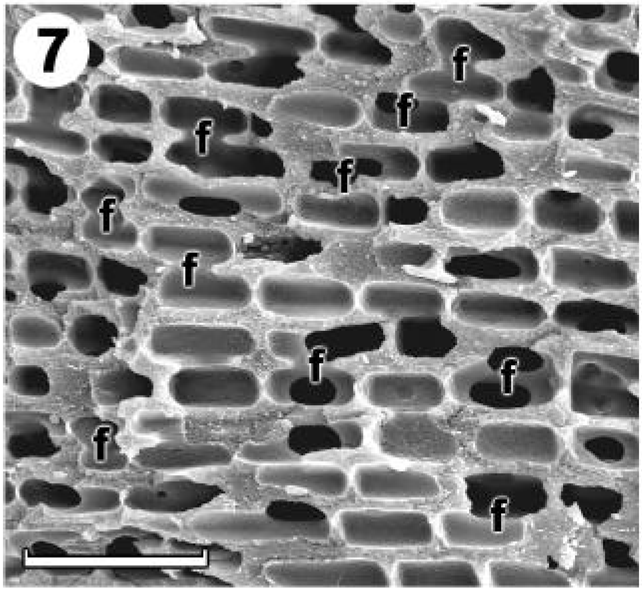
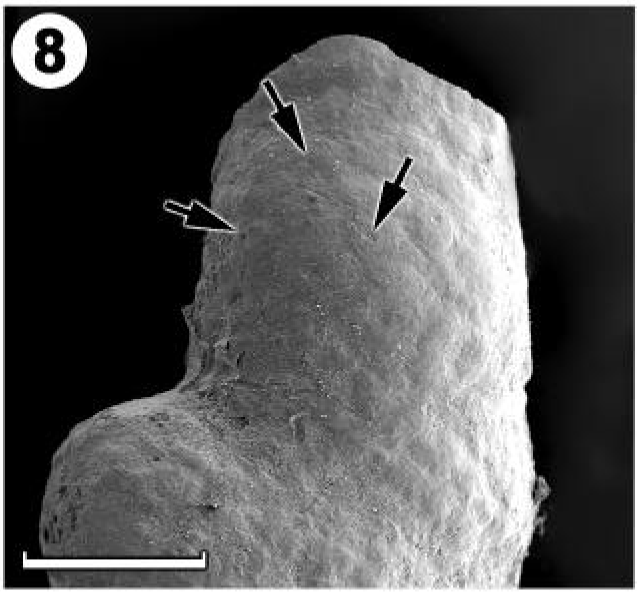


Plate 74



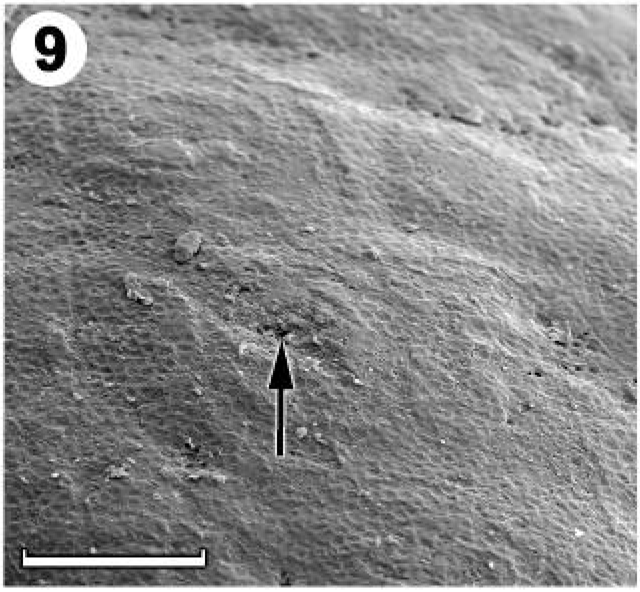


Plate 75

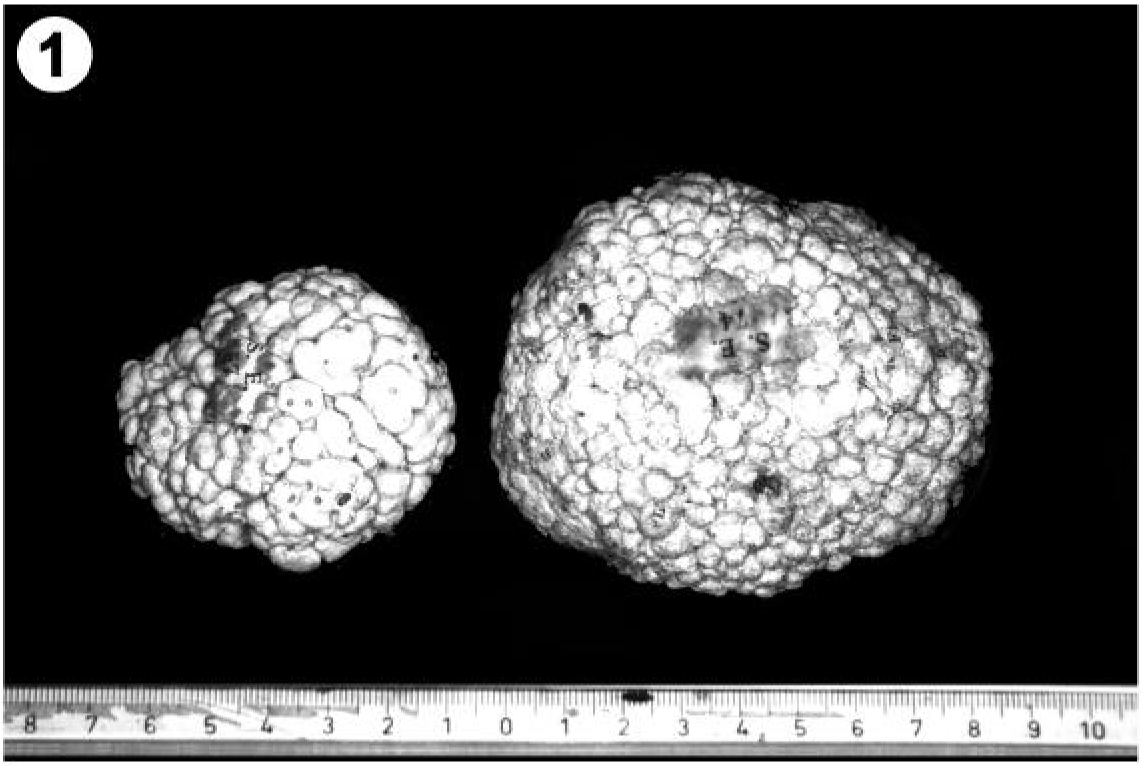

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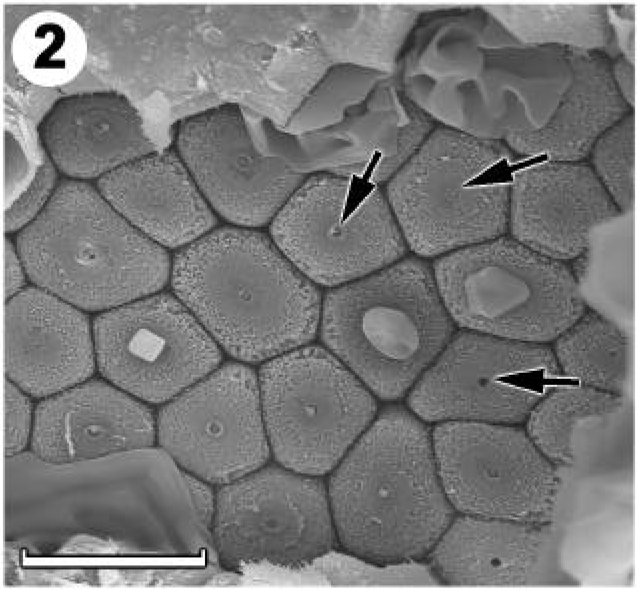
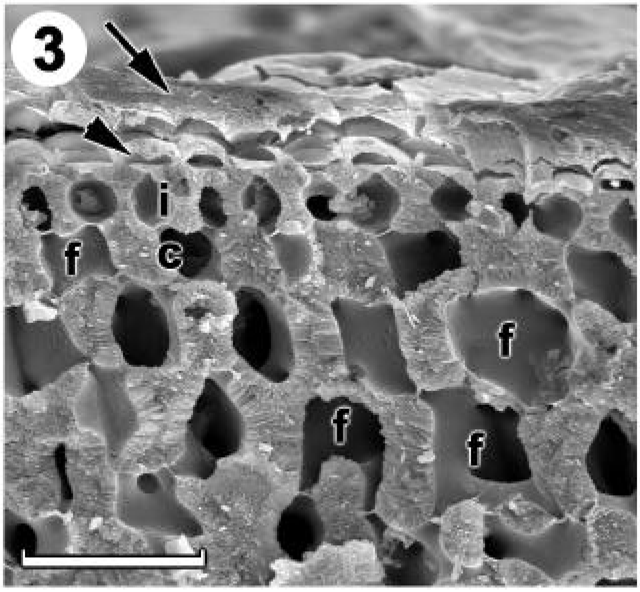
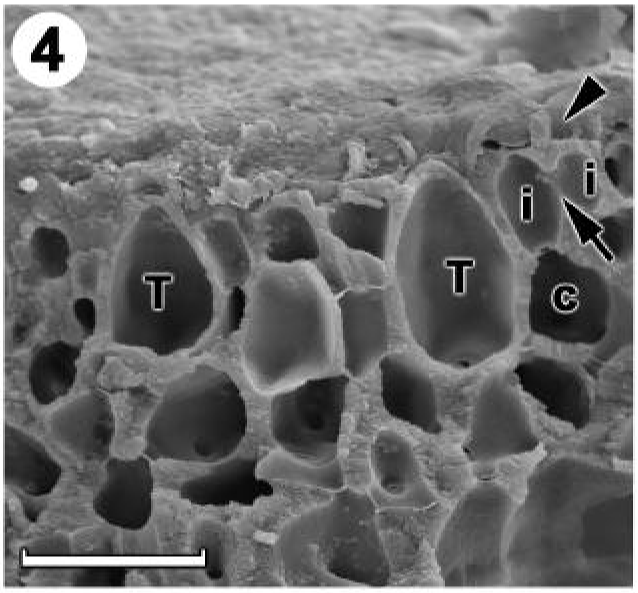
Plate 76







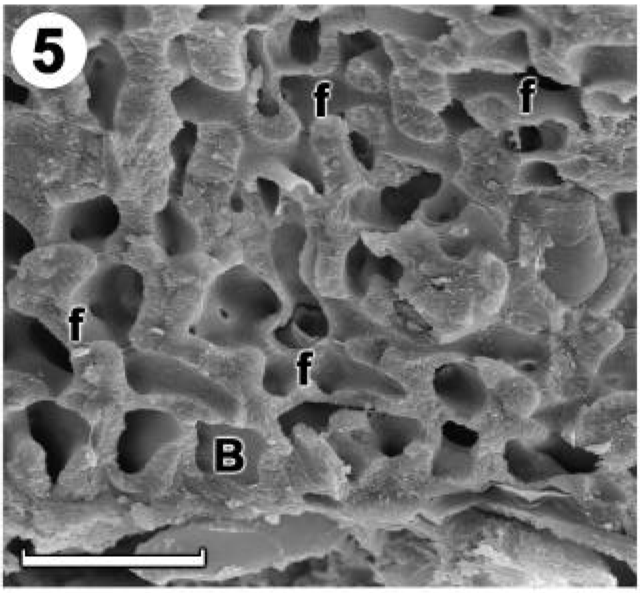
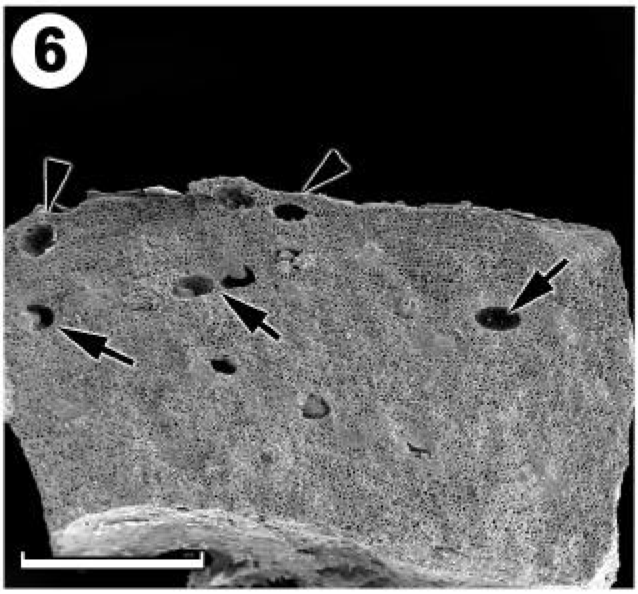
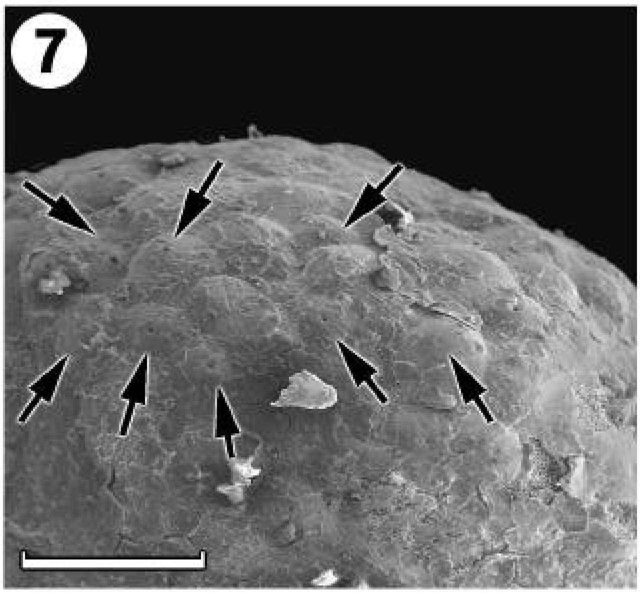
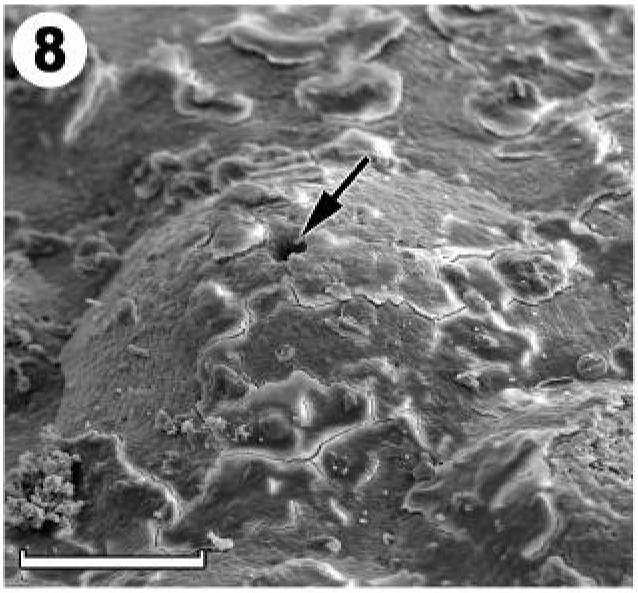
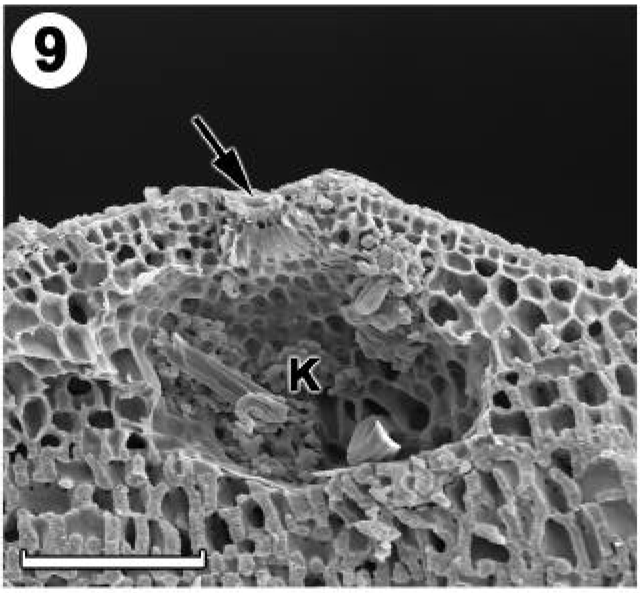


Plate 77









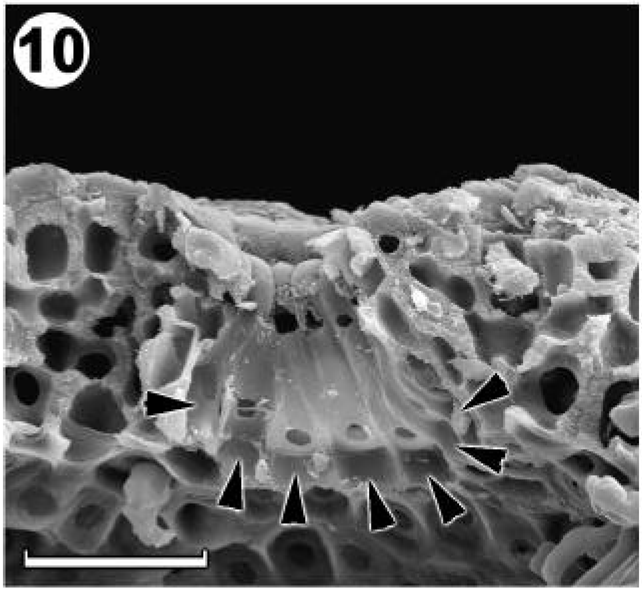
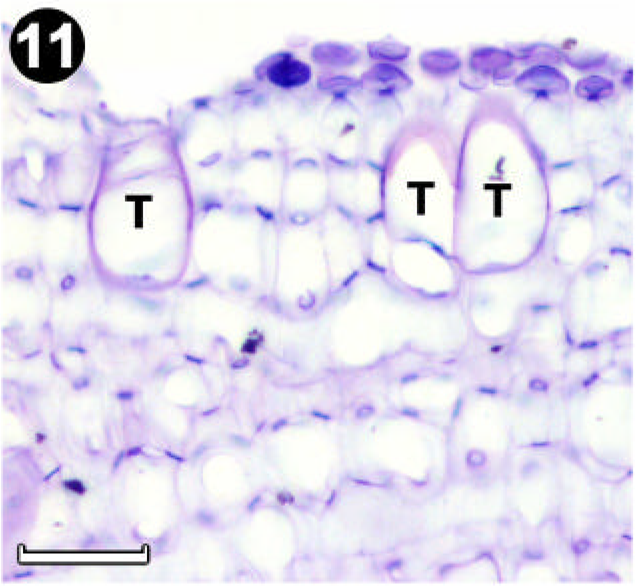
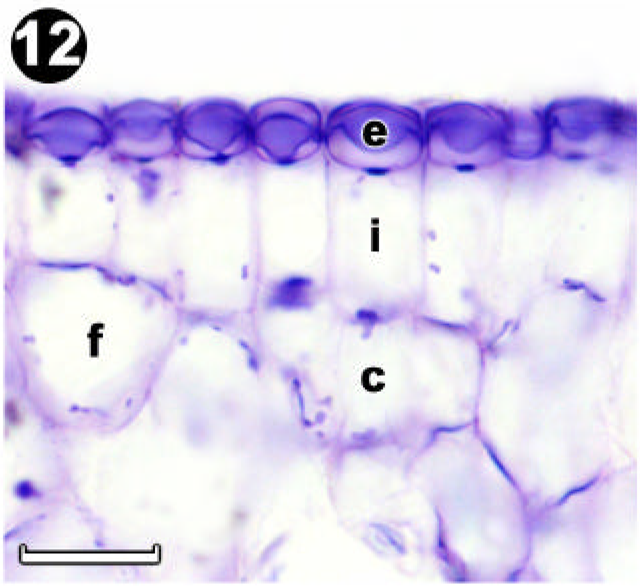
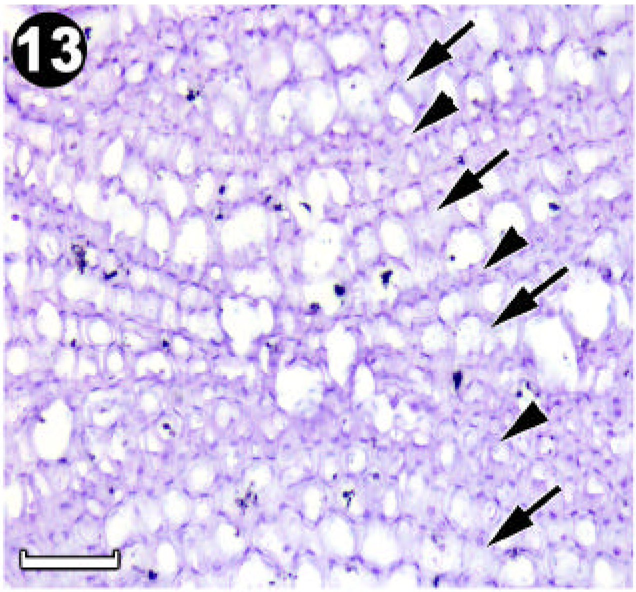
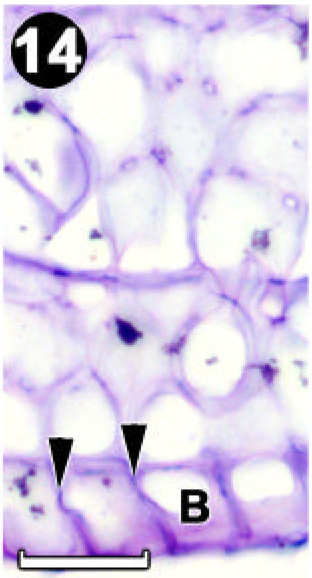


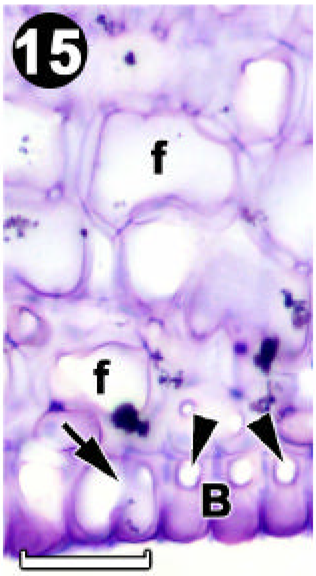
Plate 78

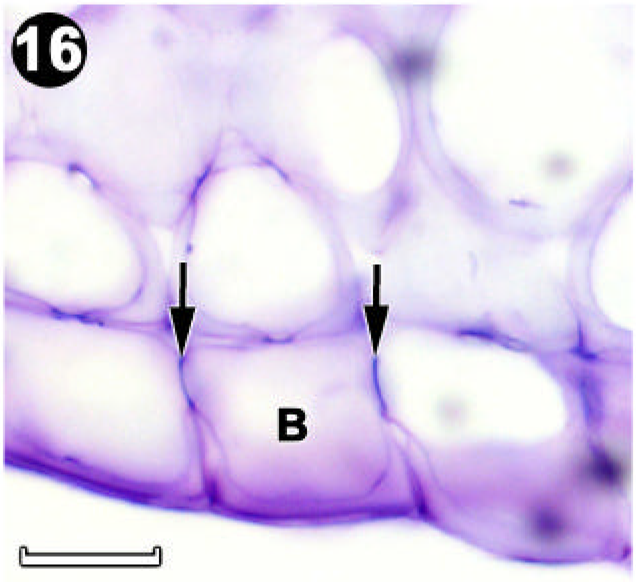












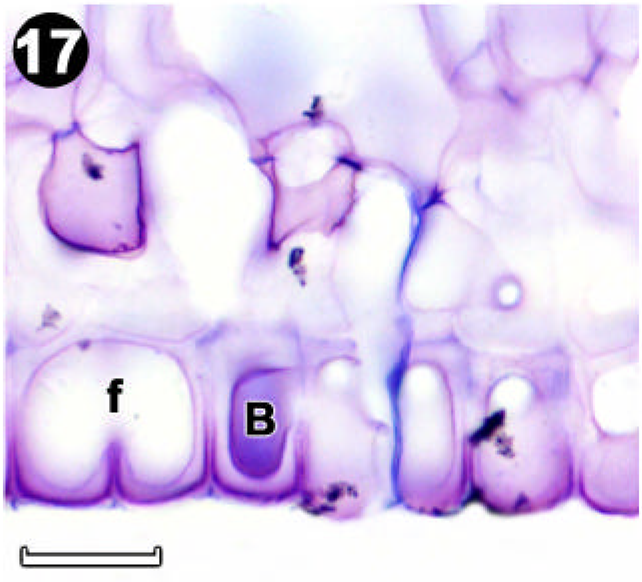


Plate 79

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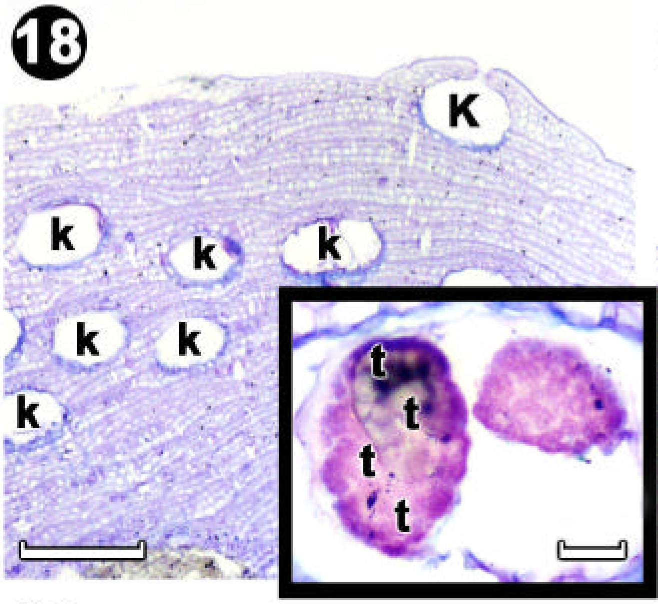

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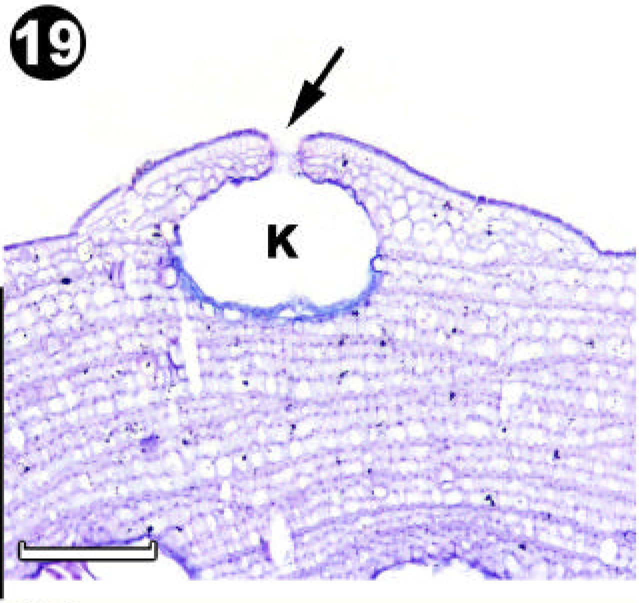

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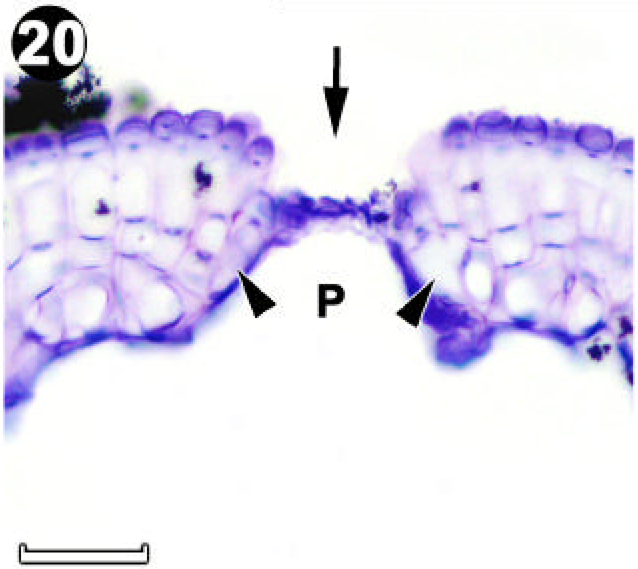

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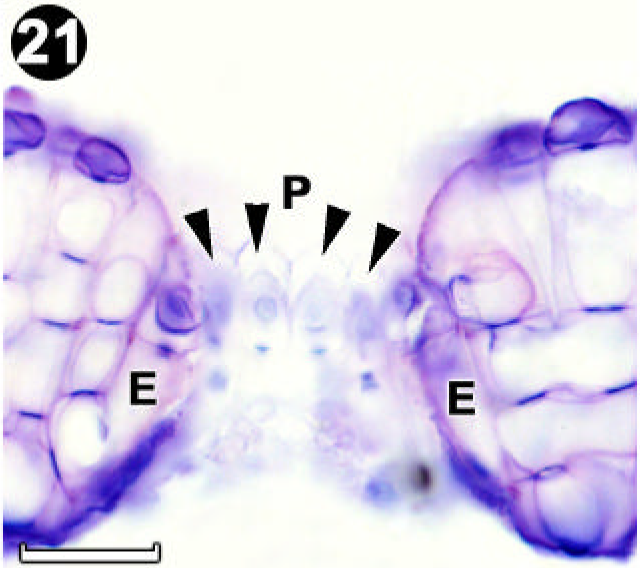


Plate 80

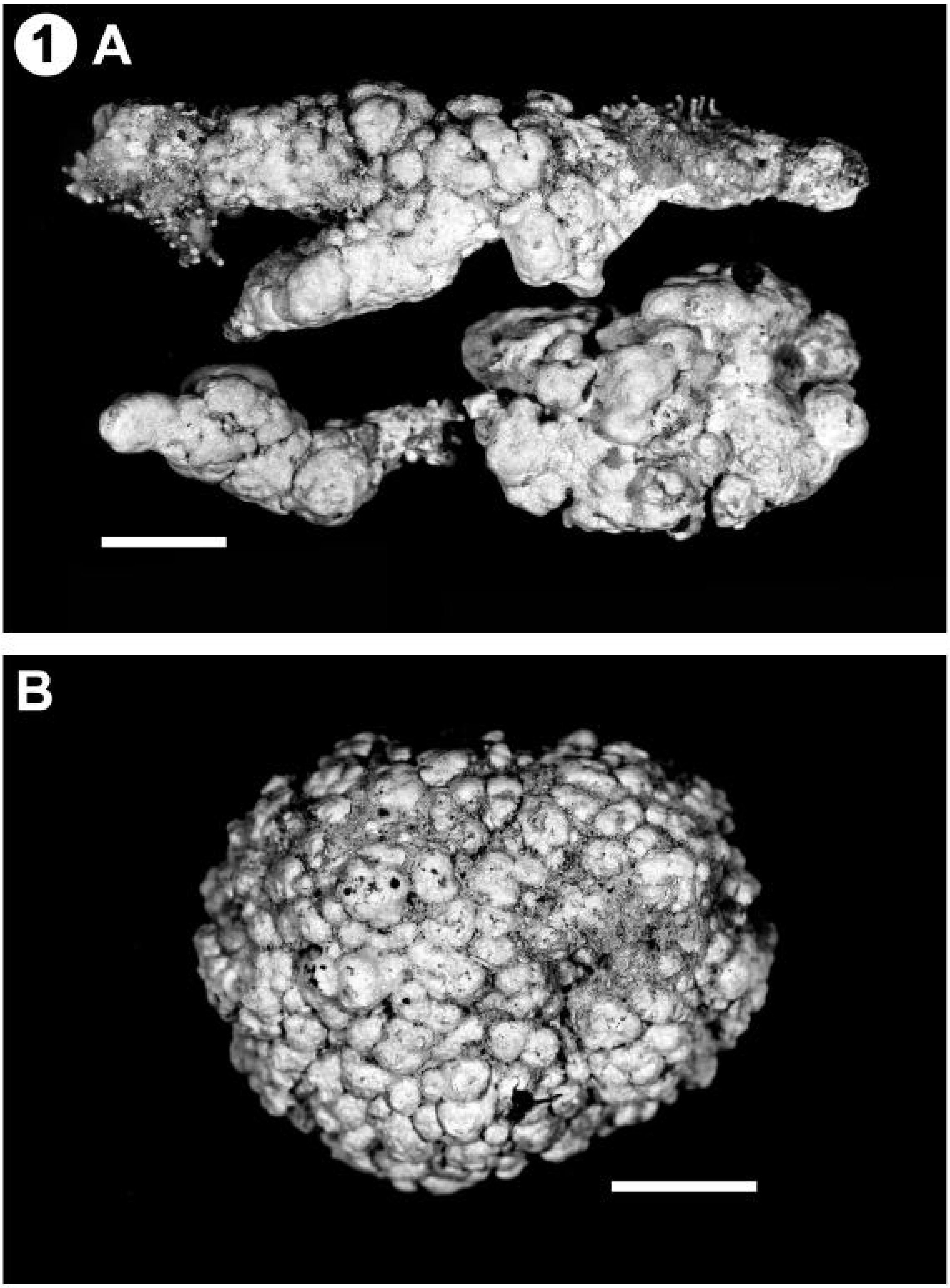
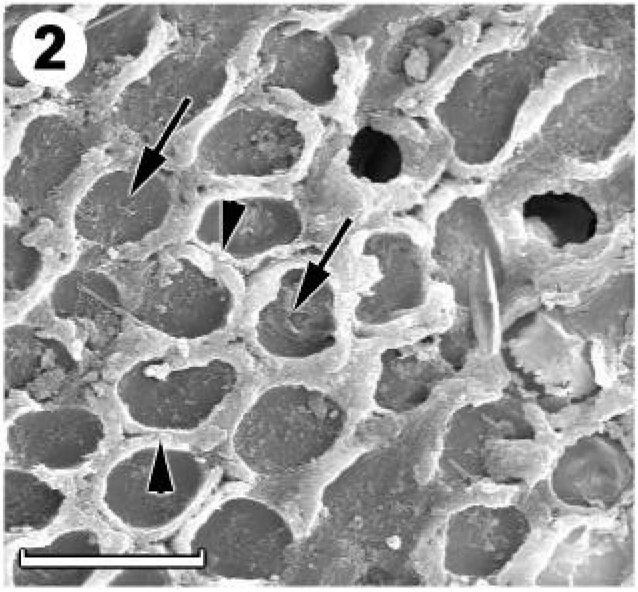


Plate 81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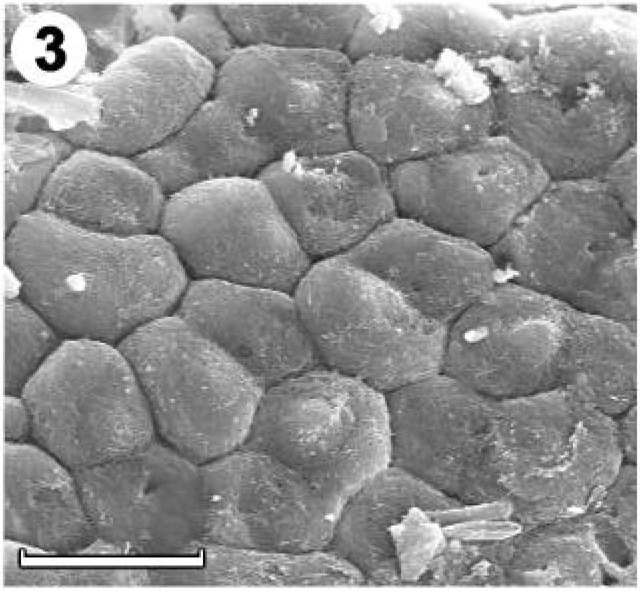
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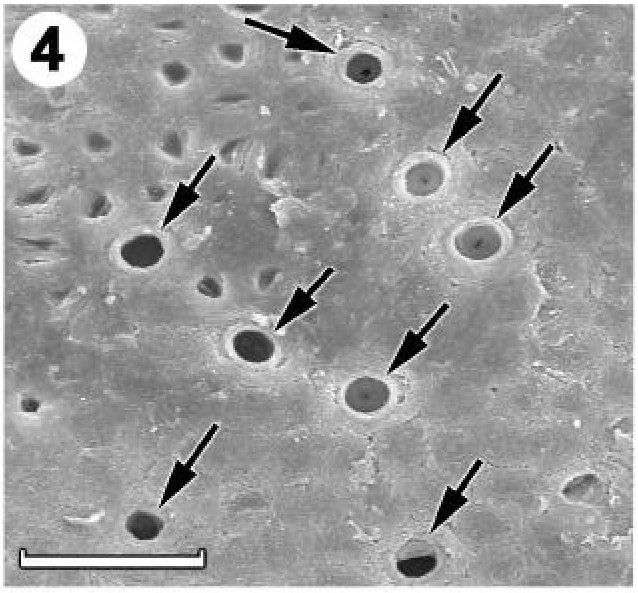
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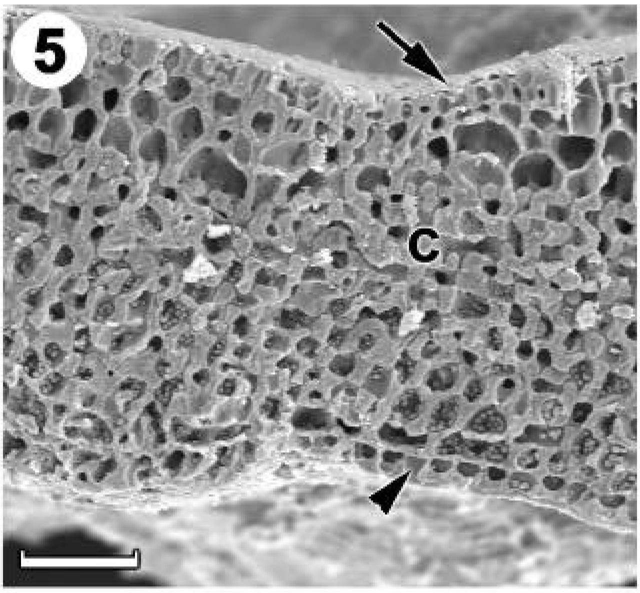
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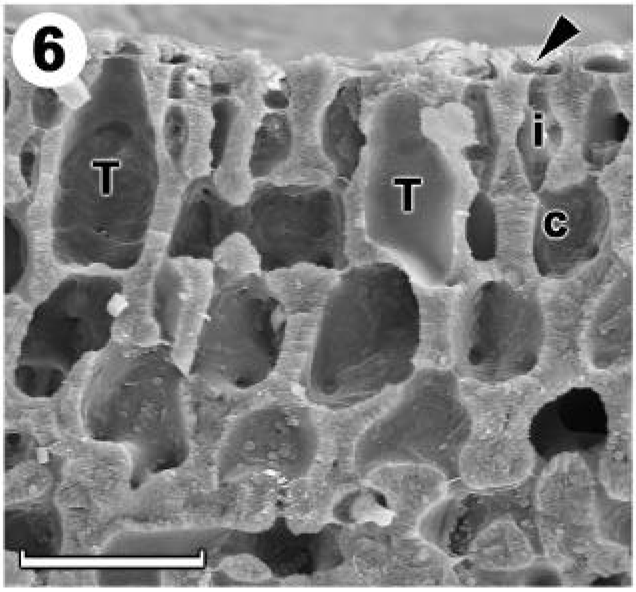
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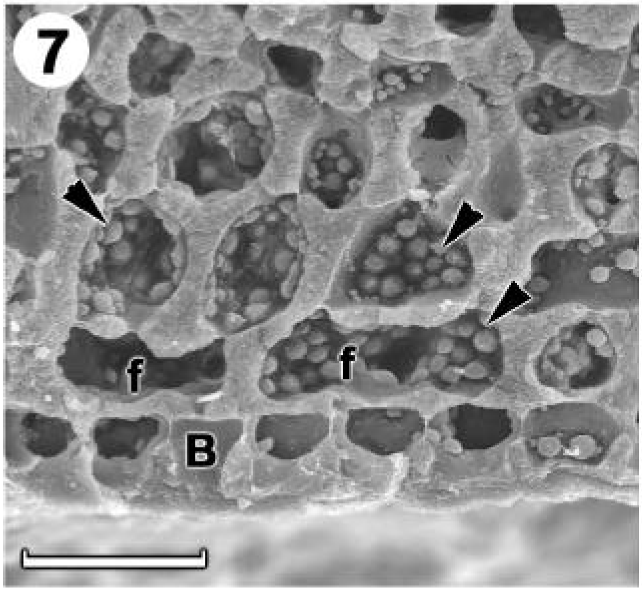
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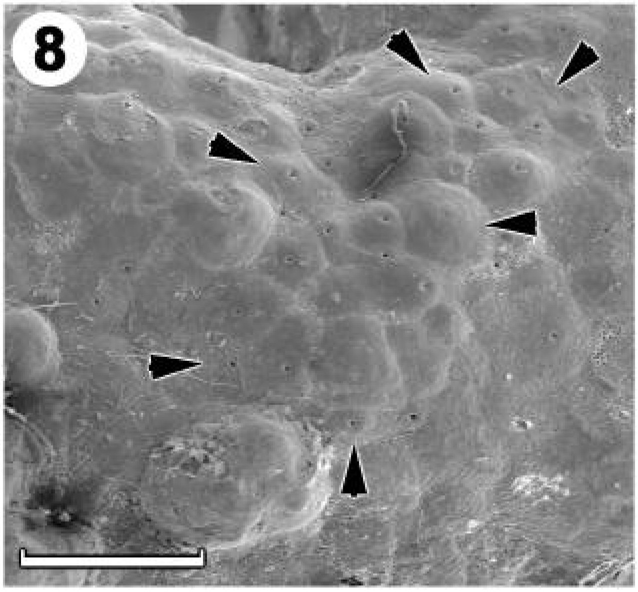
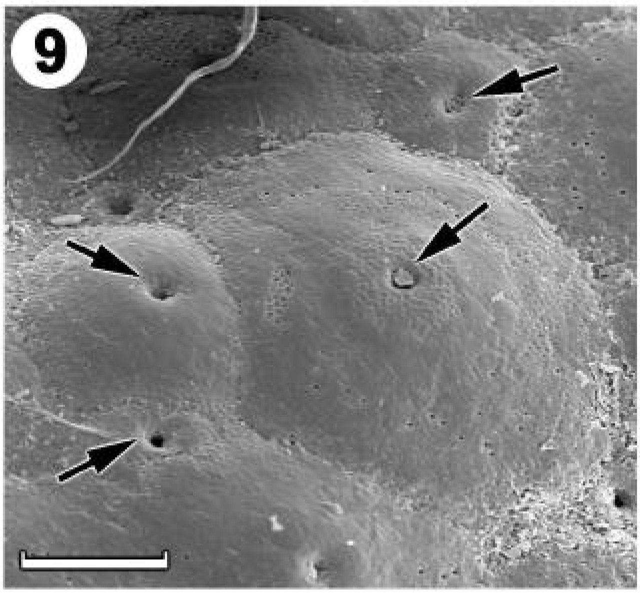
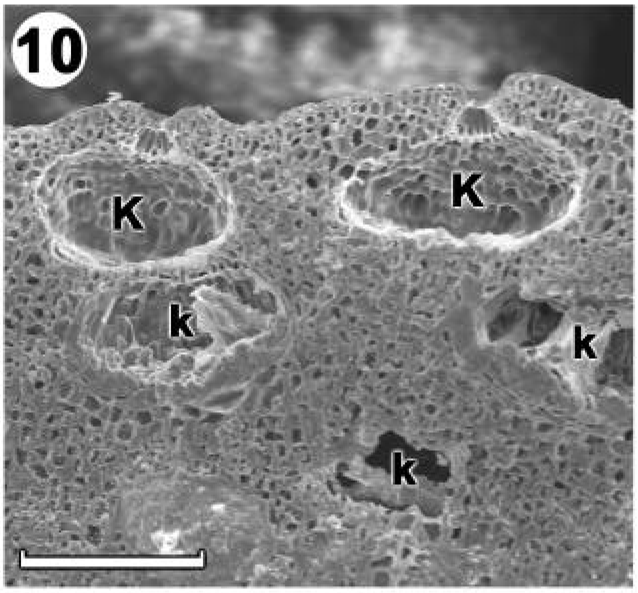
Plate 82







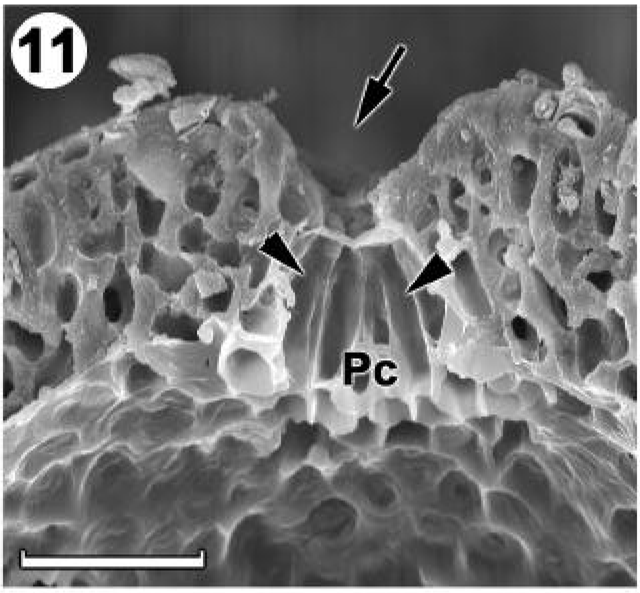
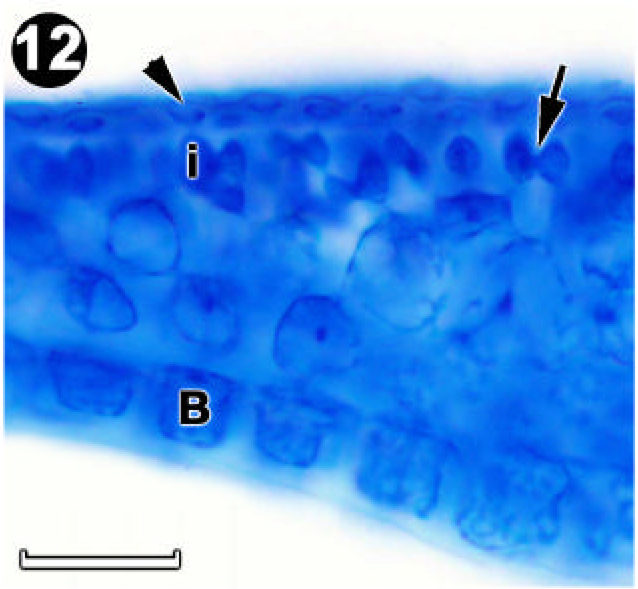
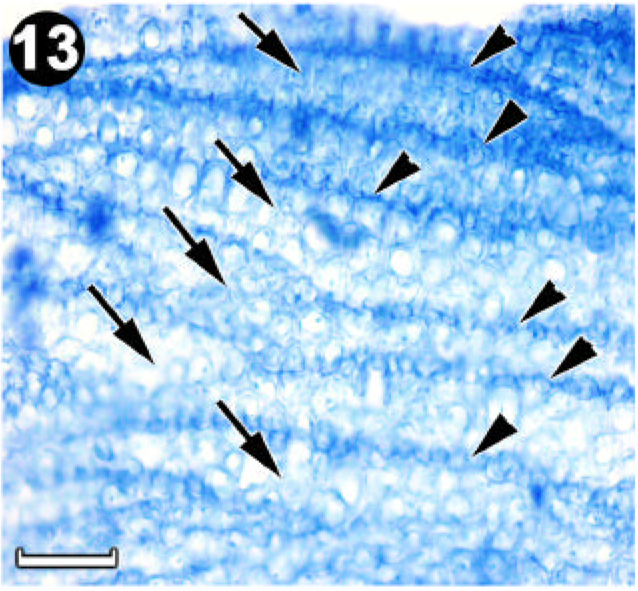
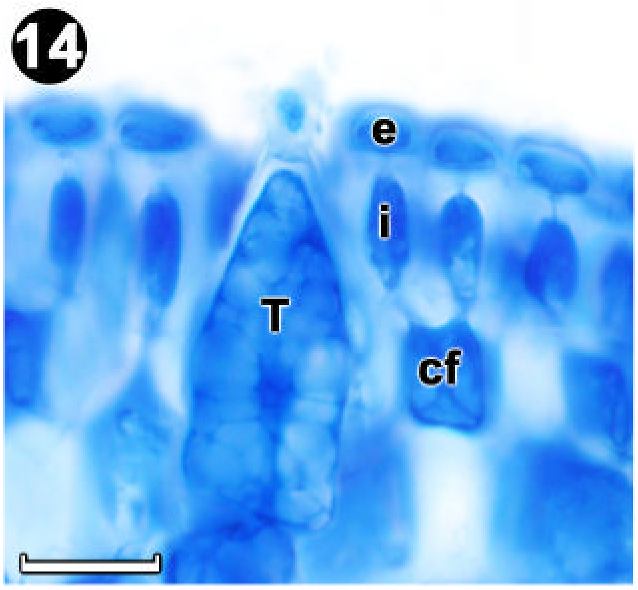
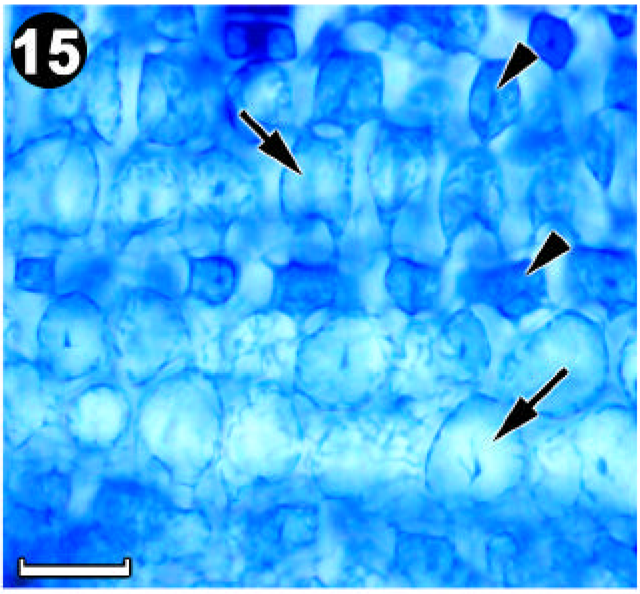


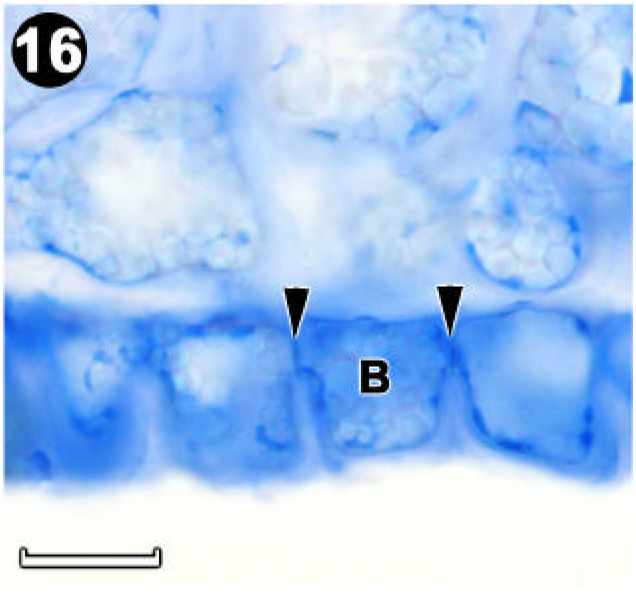
Plate 83











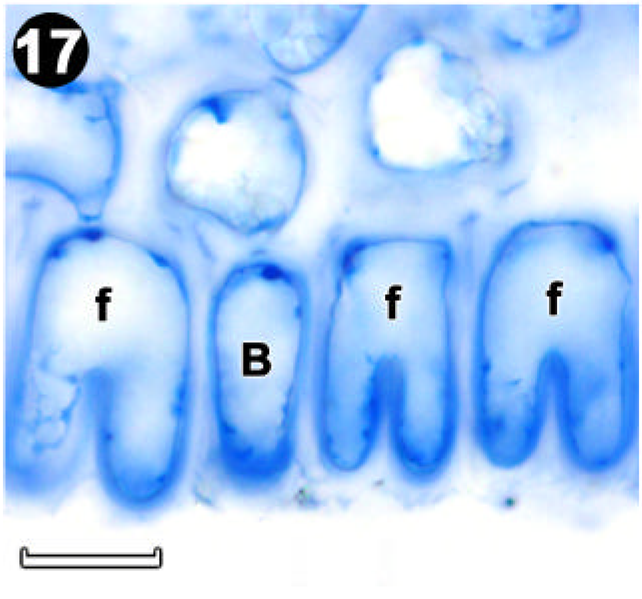
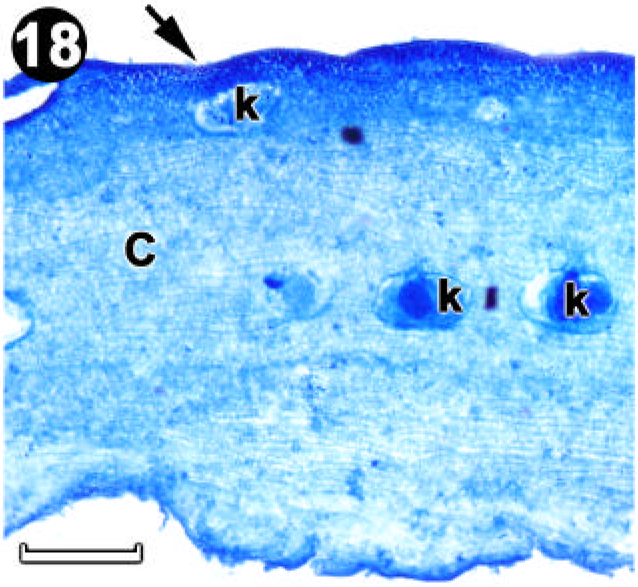
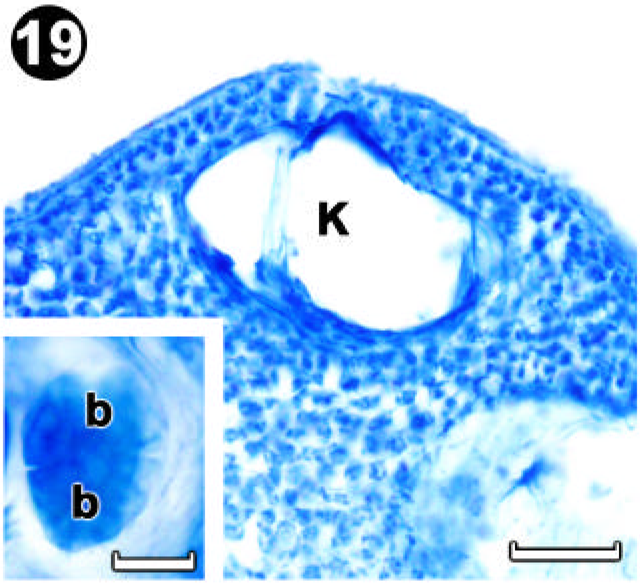
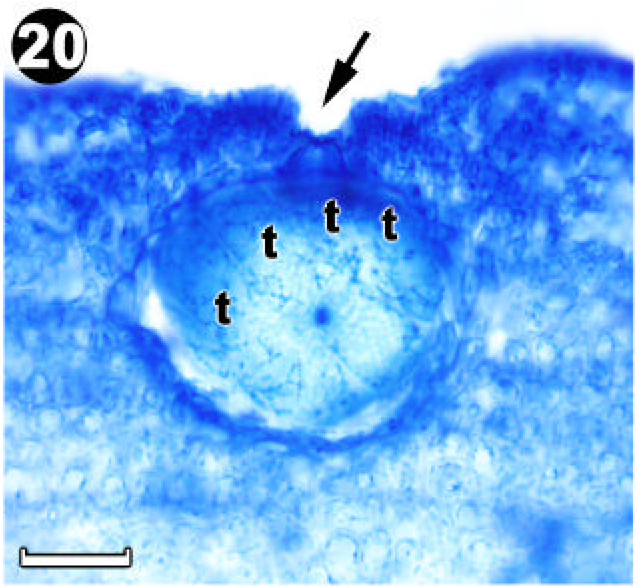
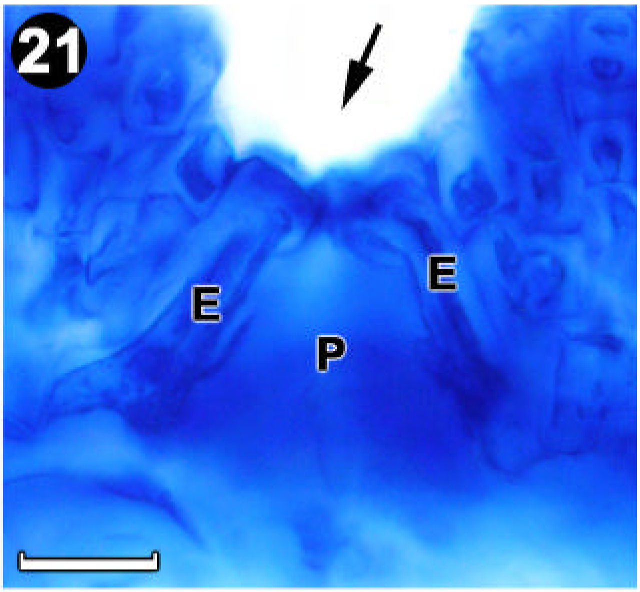


Plate 84









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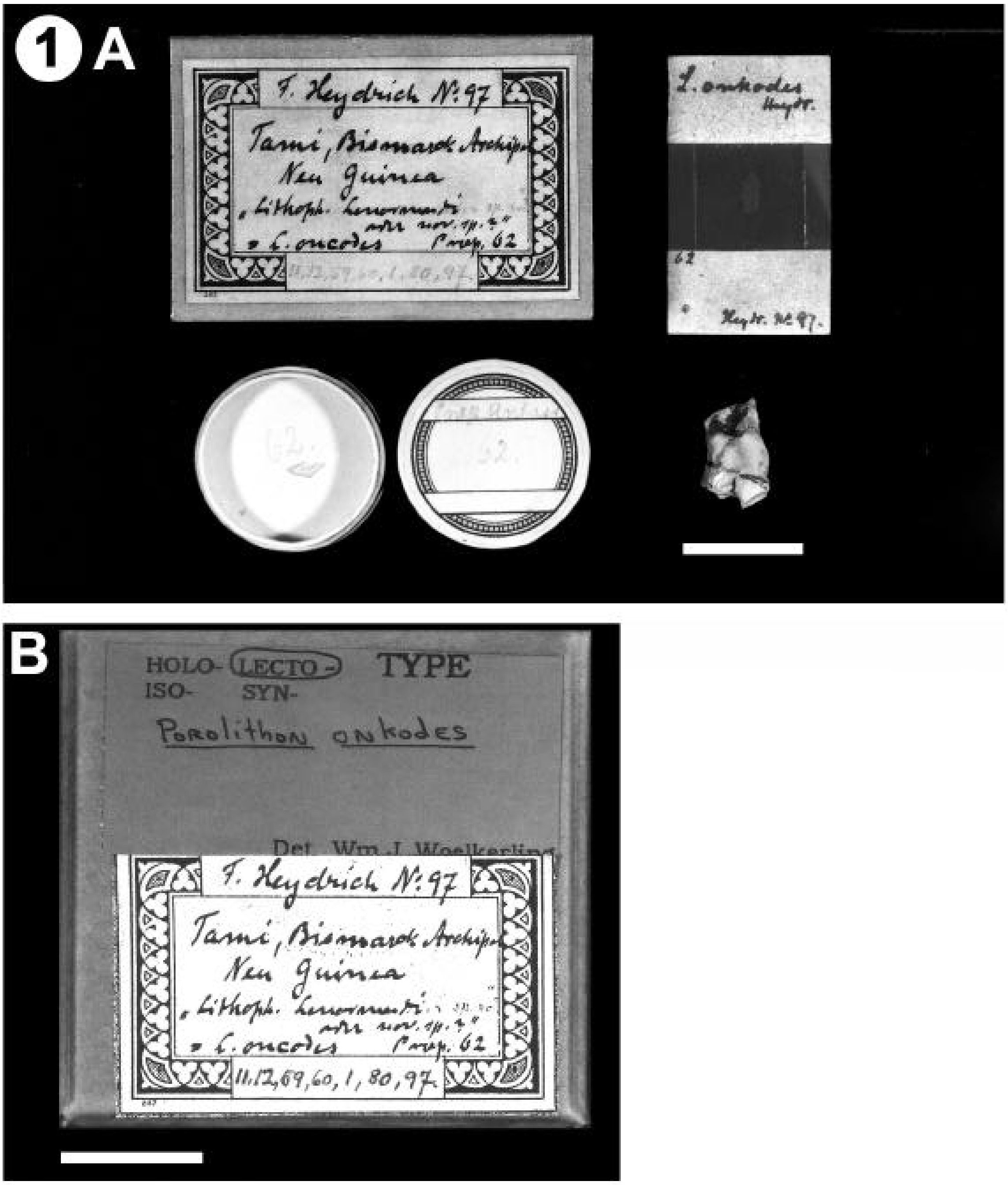
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A
F. Heydrich N:97
Tami, Bismarck Archipel
Neu Guinea
„Lithoph. Lenormandi
oder nov. sp.?"
= L. oncodes Präp. 62
11,12,59,60,1,80,97.
L. onkodes Heydr.
62
Heydr. N:97.
62.
B
HOLO- LECTO- TYPE
ISO- SYN-
Porolithon onkodes
Det. Wm.J. Woelkerling
F. Heydrich N:97
Tami, Bismarck Archipel
Neu Guinea
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oder nov. sp.?"
= L. oncodes Präp. 62
11,12,59,60,1,80,97.

Plate 86

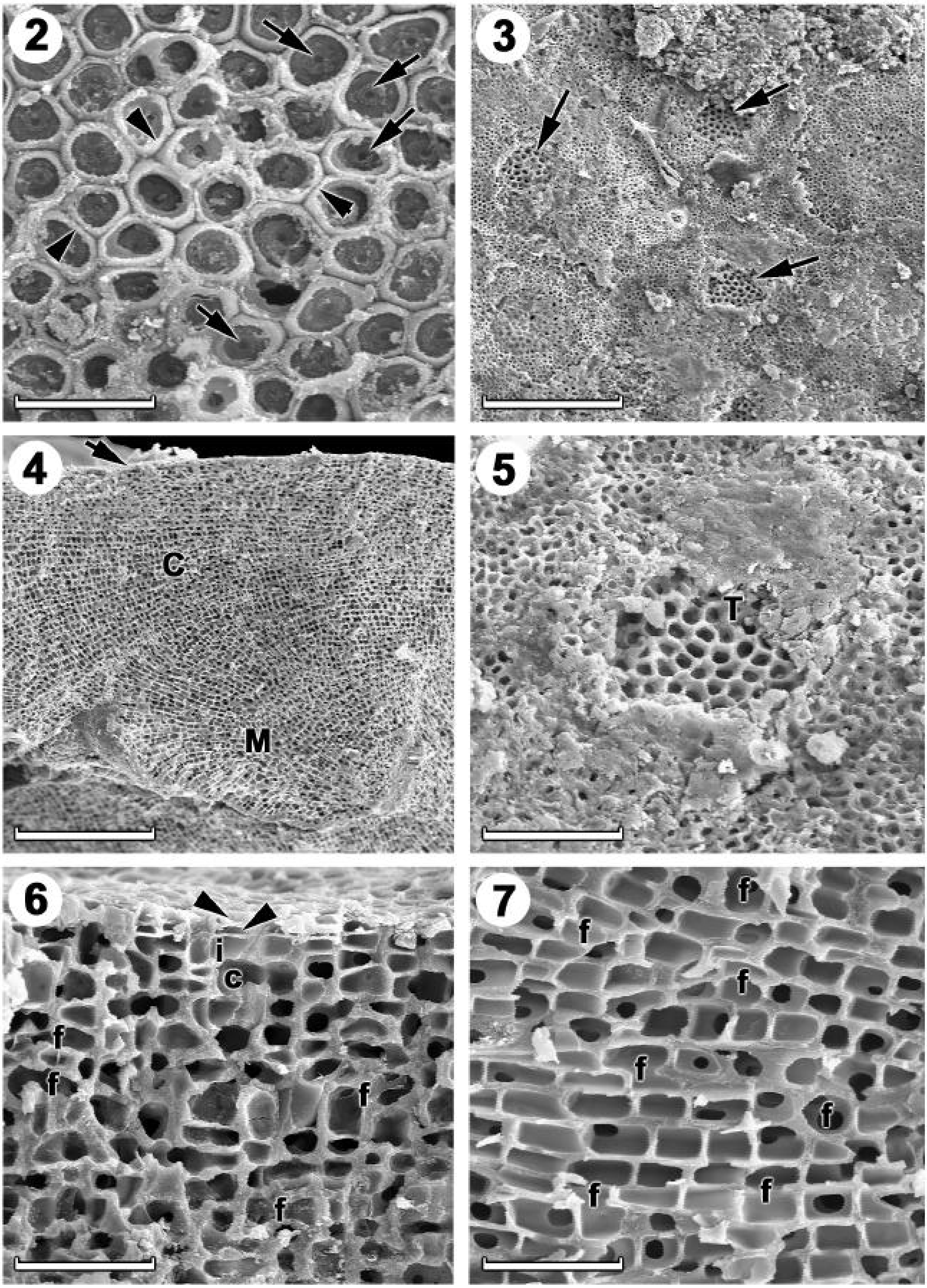


Plate 87

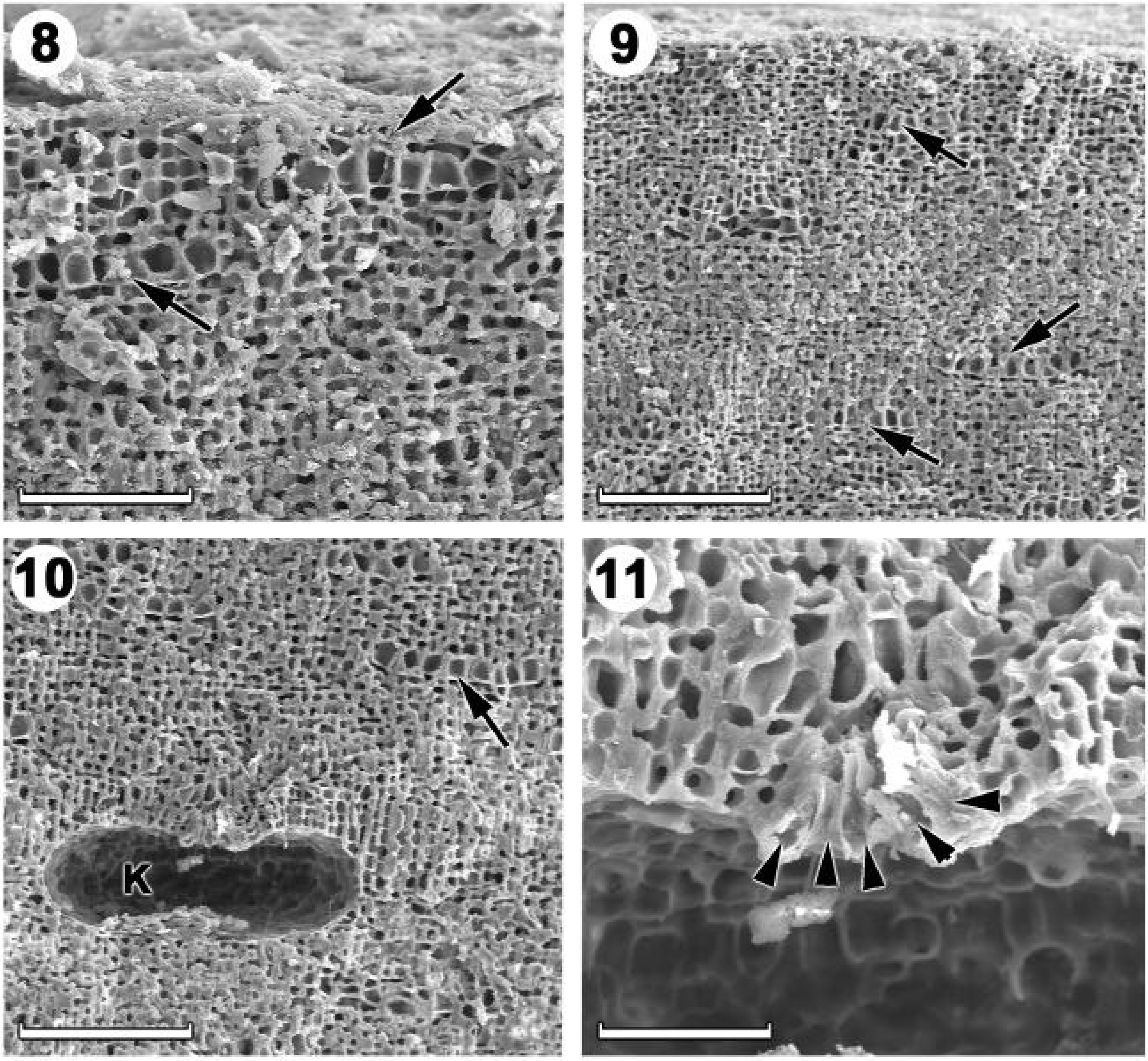
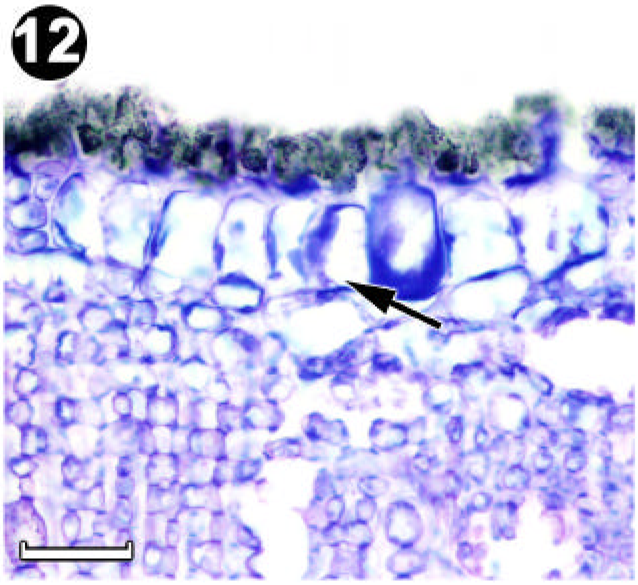
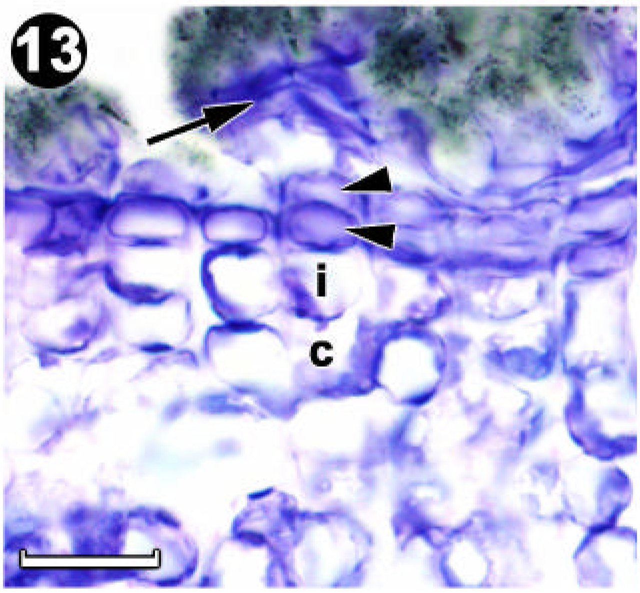
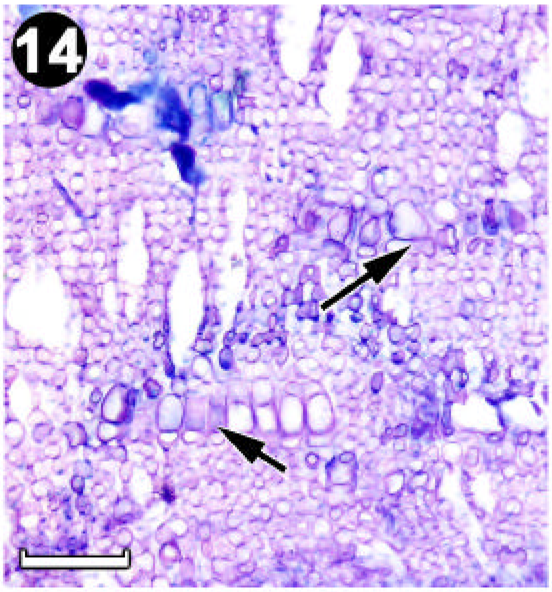
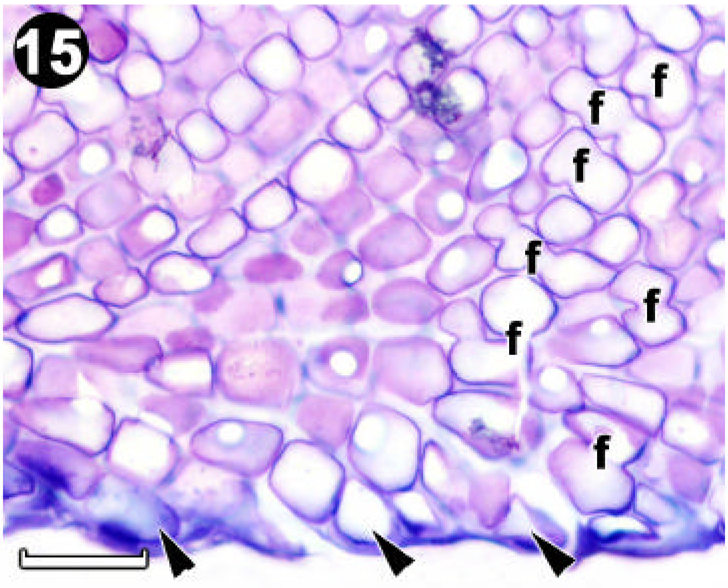


Plate 88









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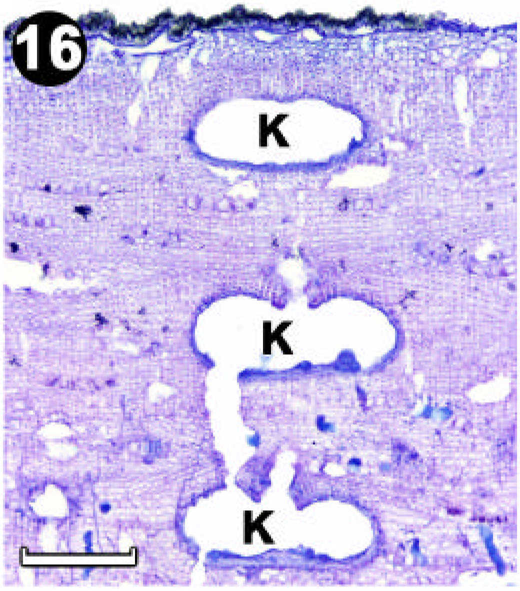

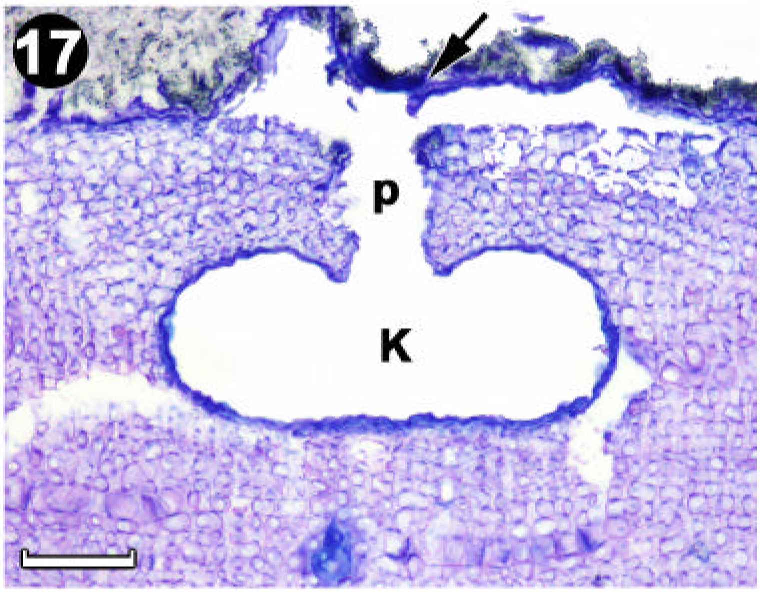

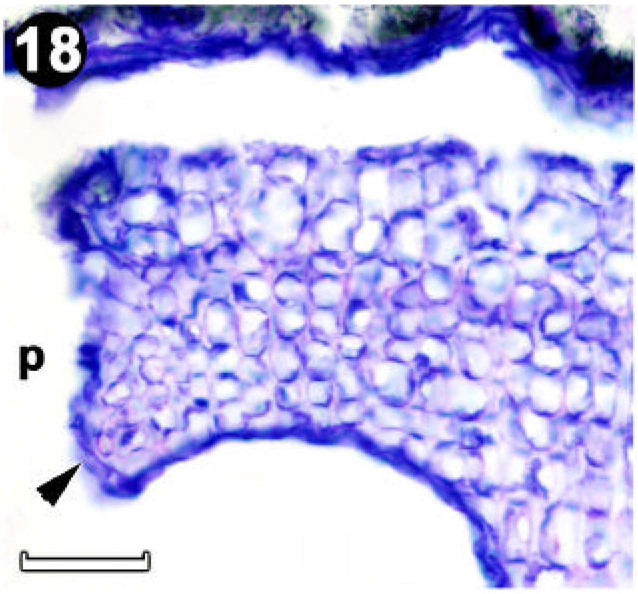

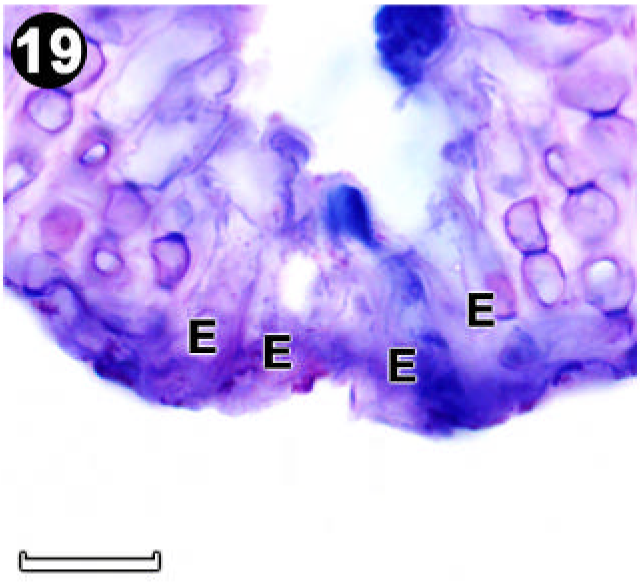

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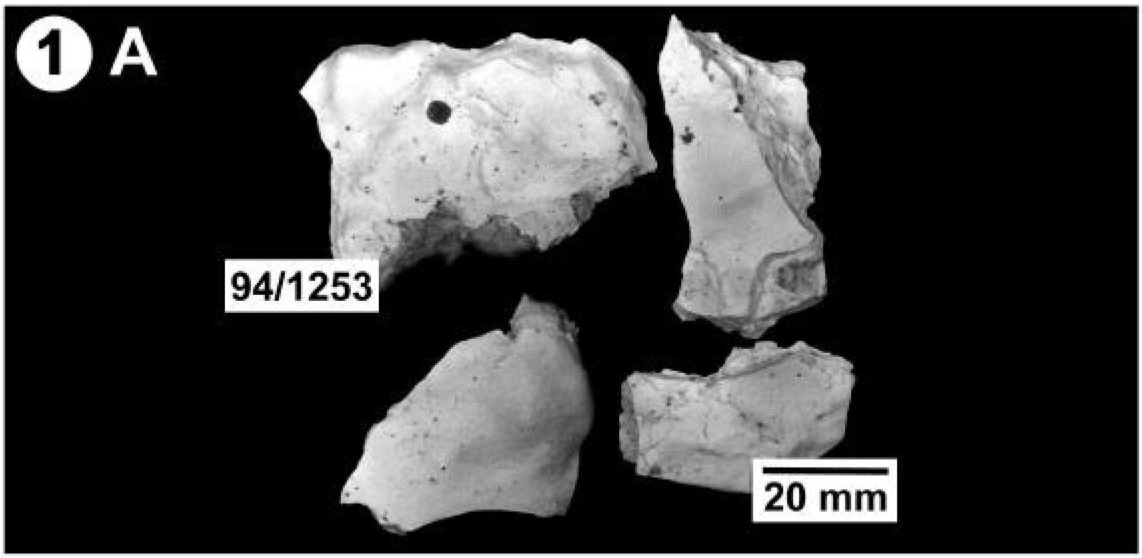

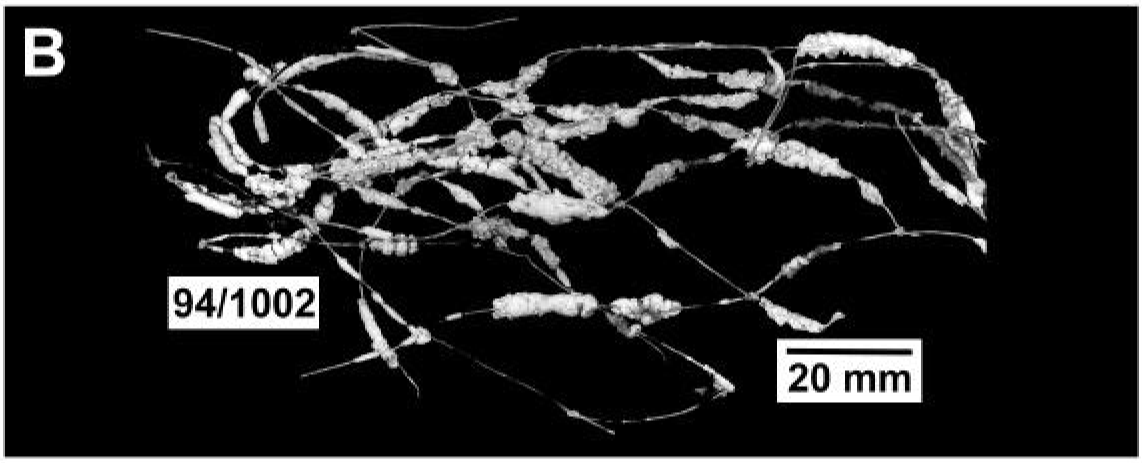

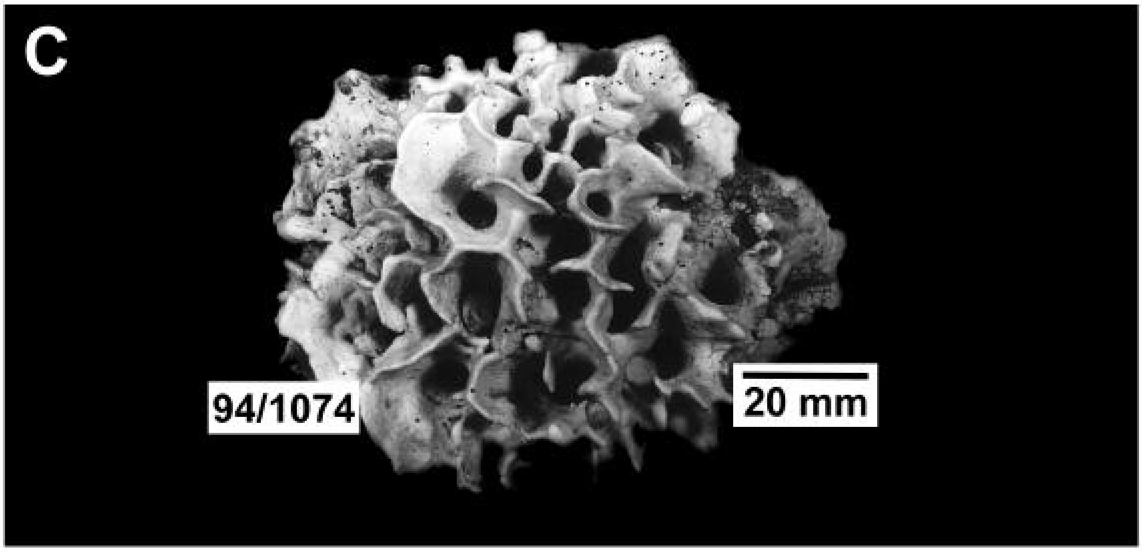

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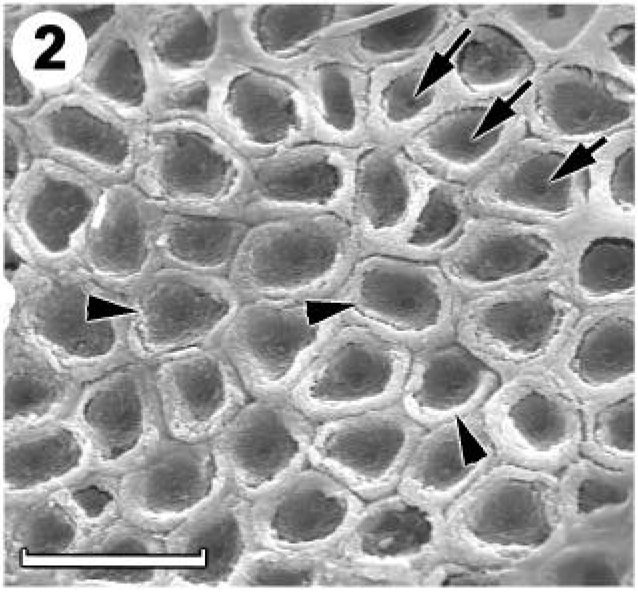

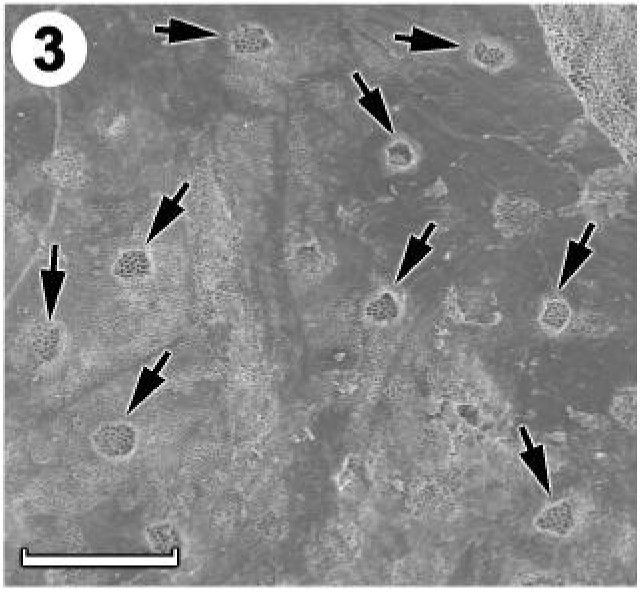

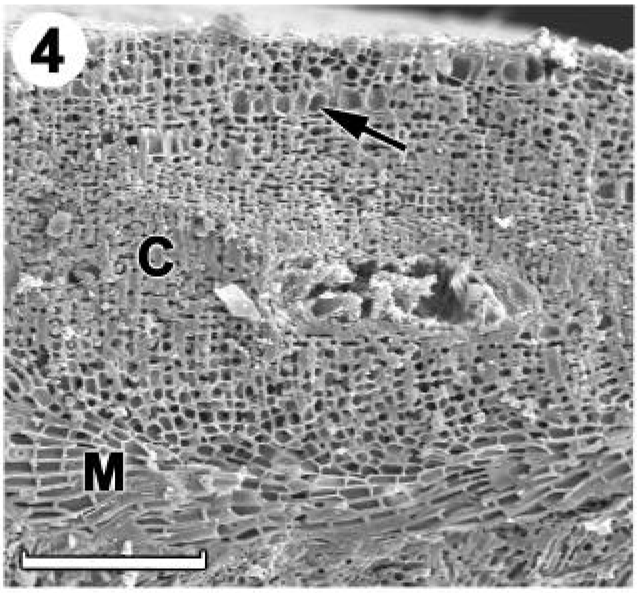

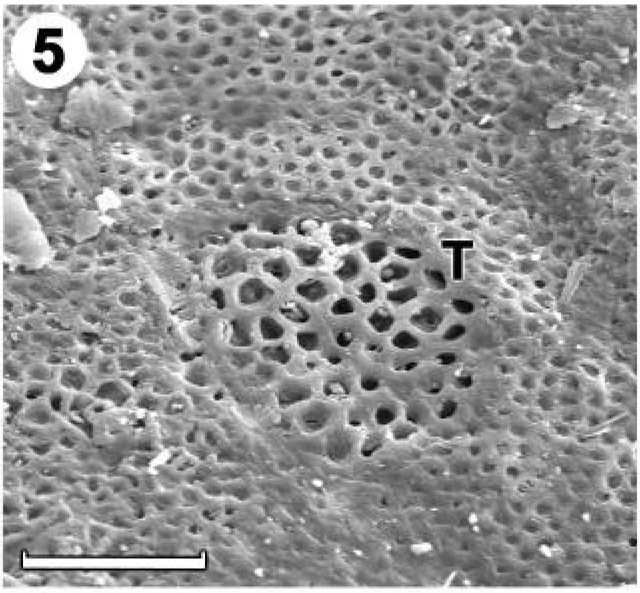

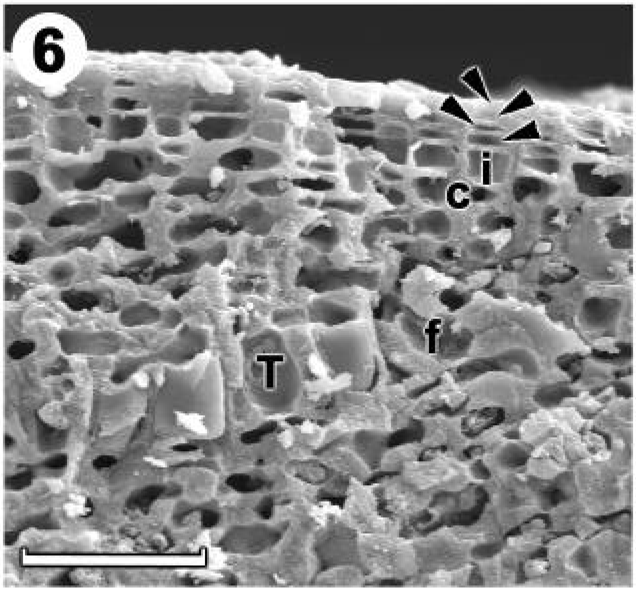

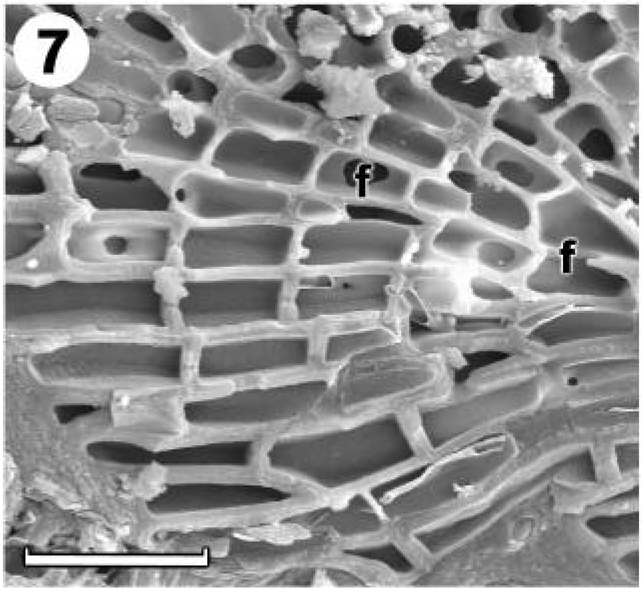

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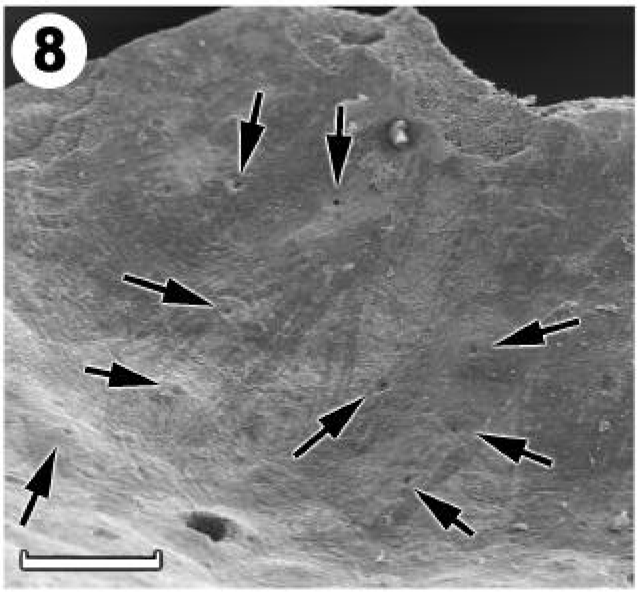

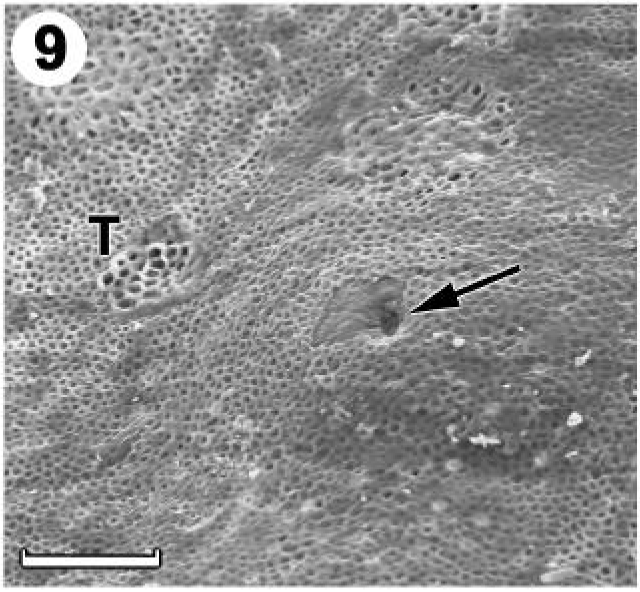

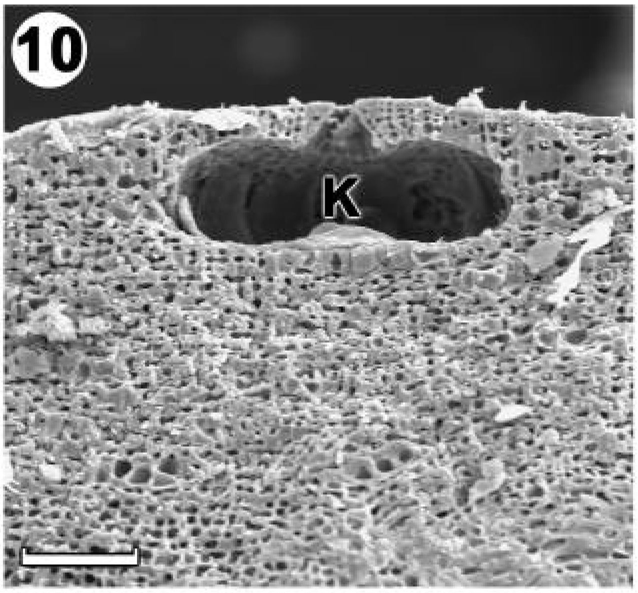

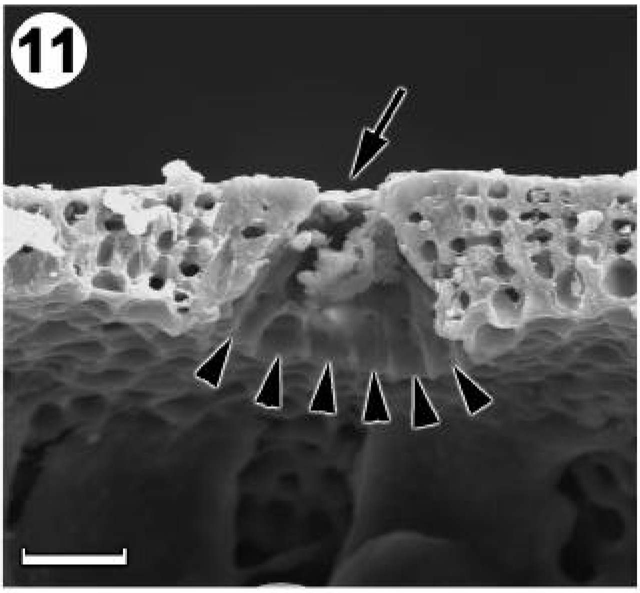

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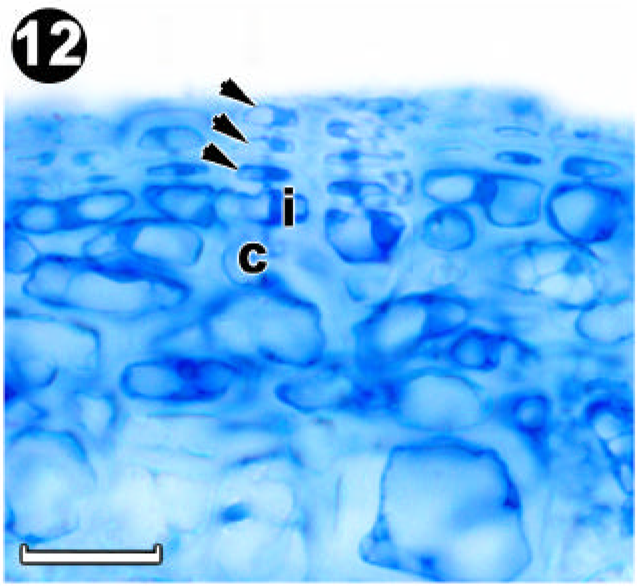
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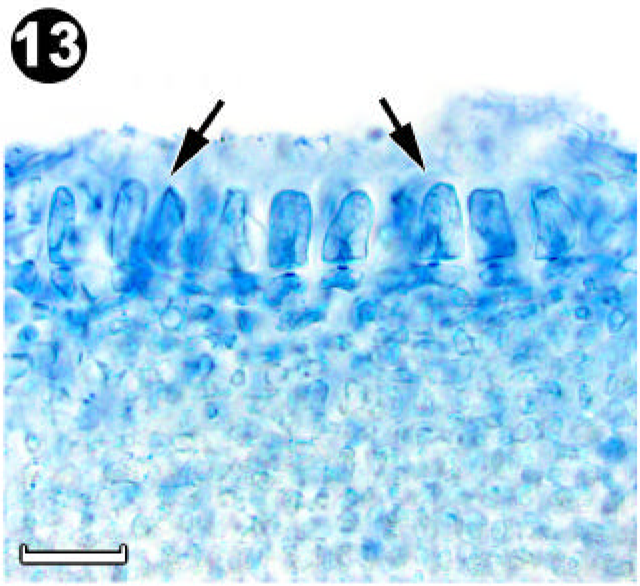
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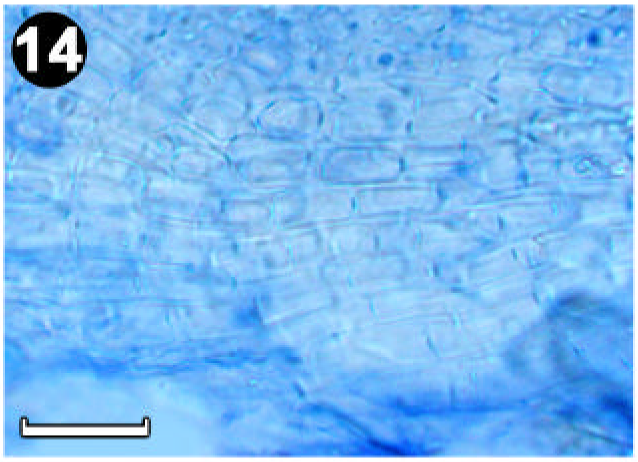
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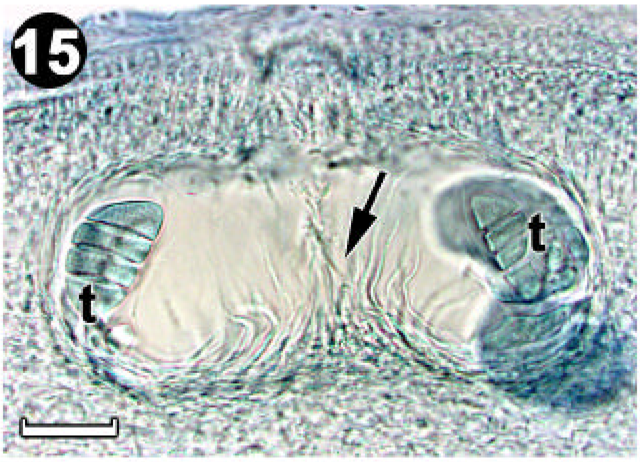
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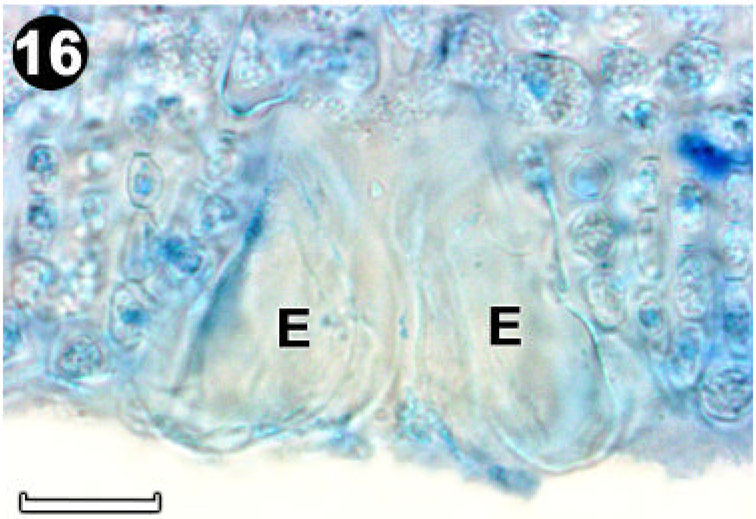
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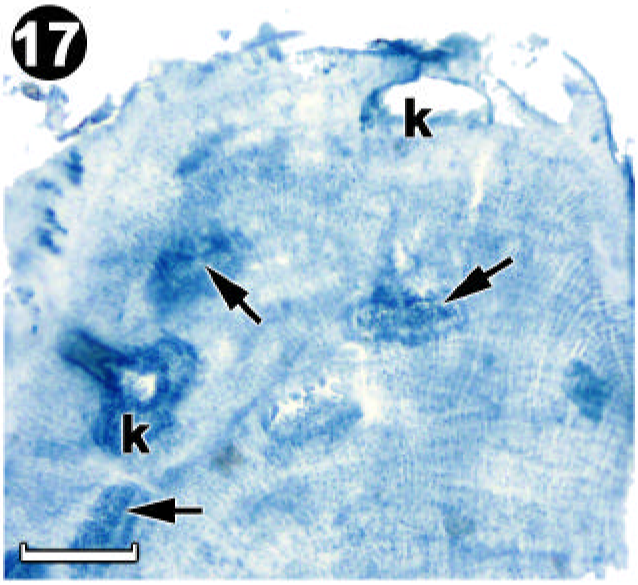
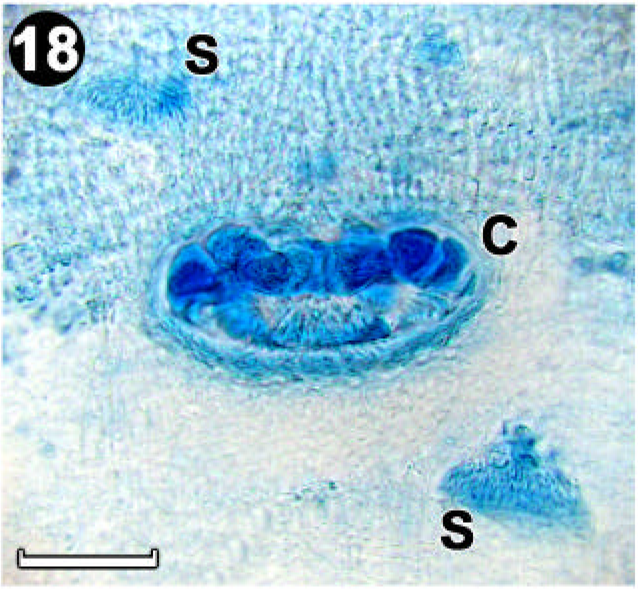




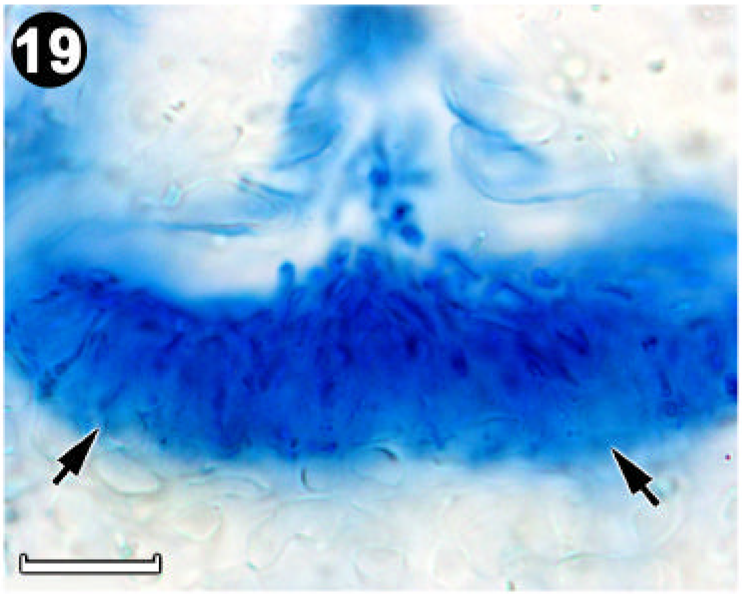
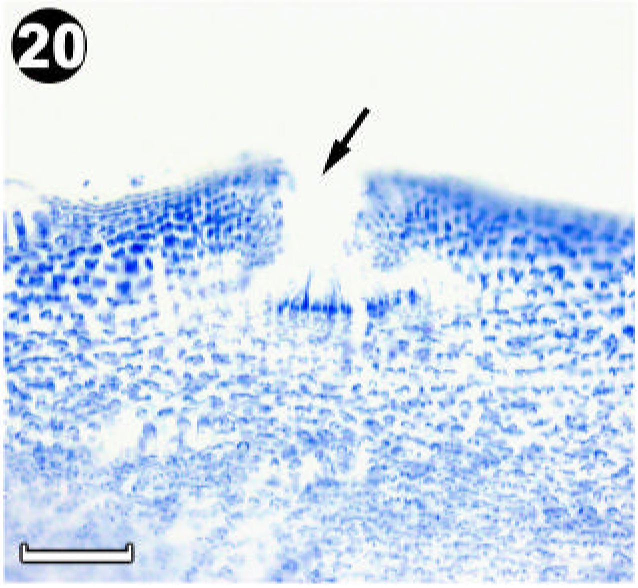
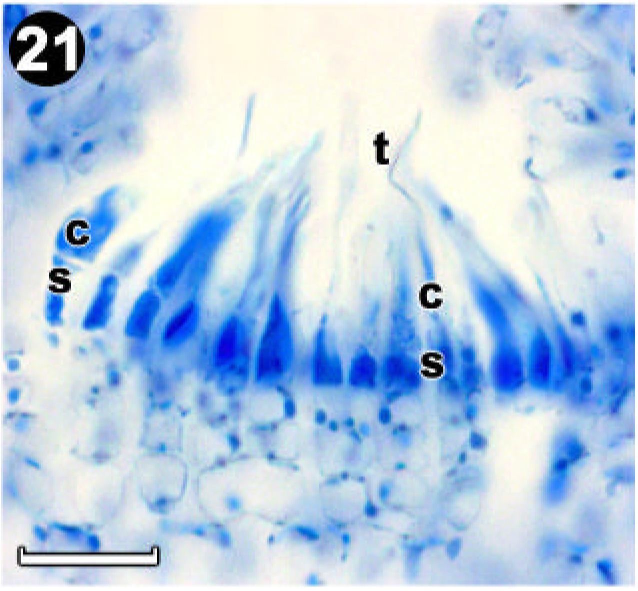
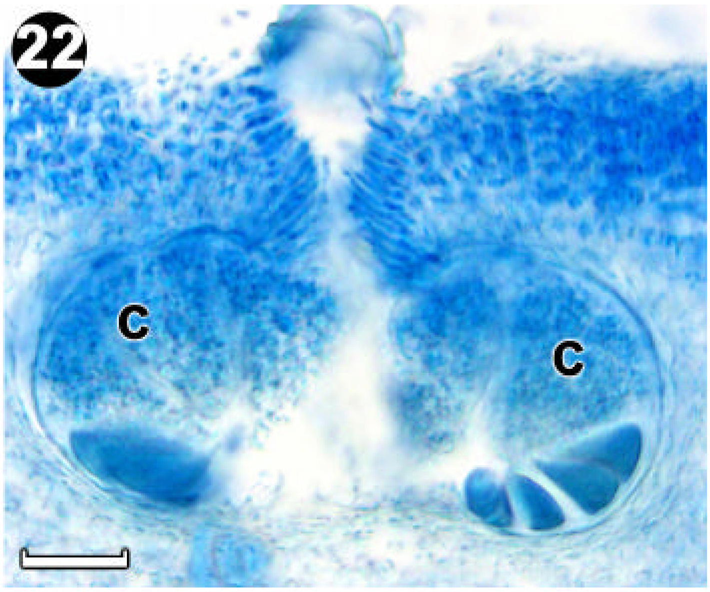


Plate 95







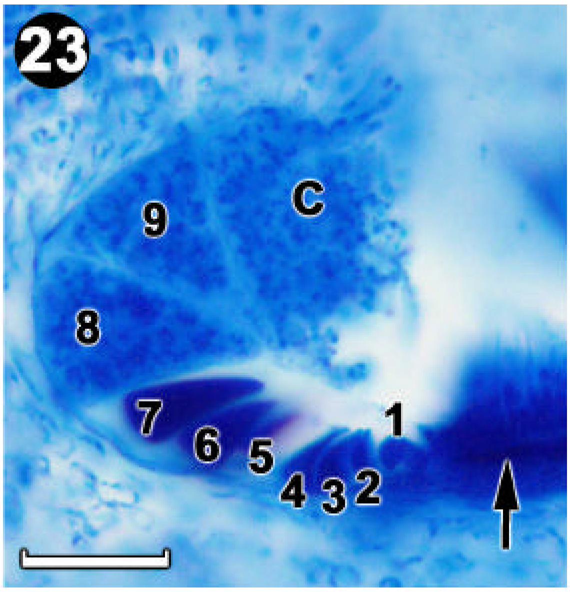
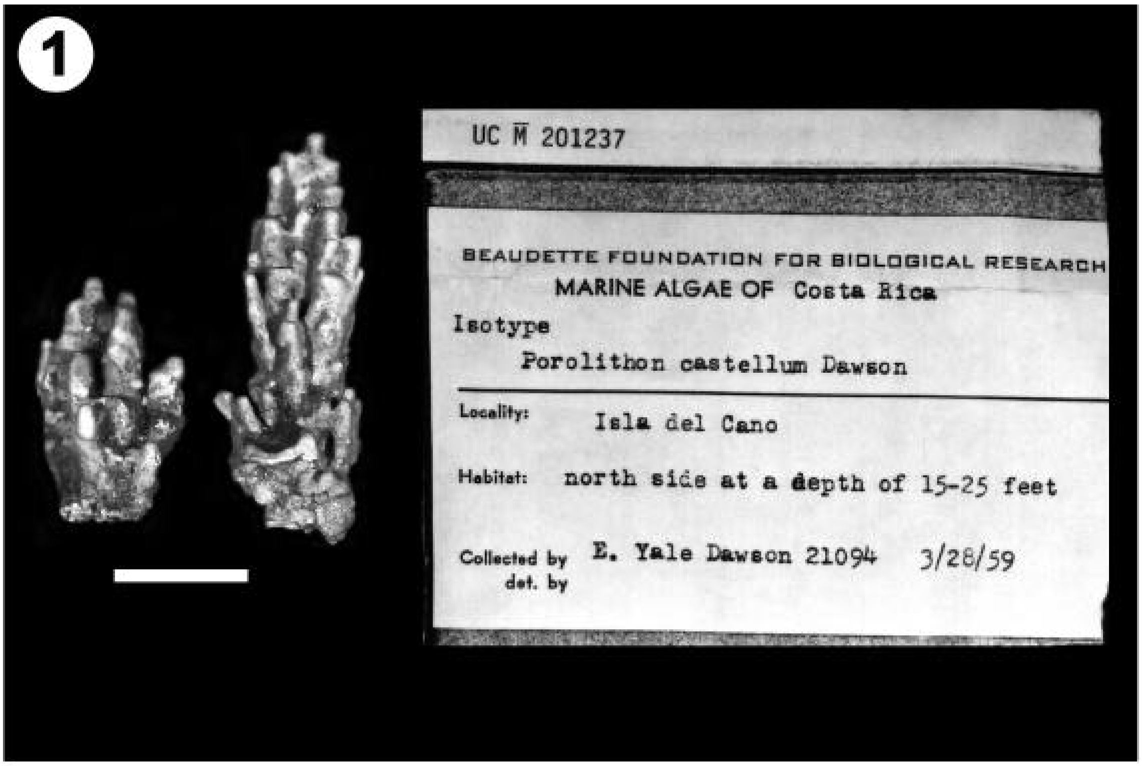


Plate 96



UC M̄ 201237

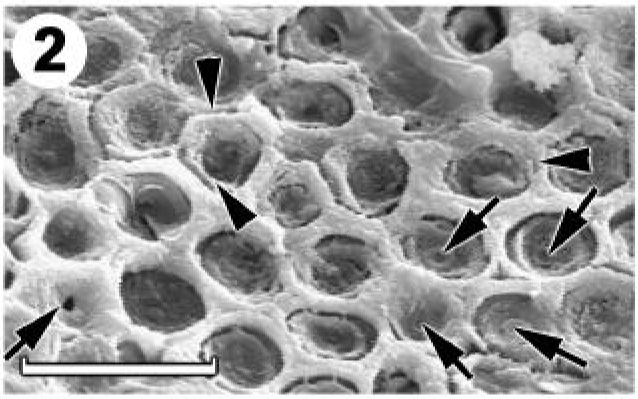
BEAUDETTE FOUNDATION FOR BIOLOGICAL RESEARCH
MARINE ALGAE OF Costa Rica
Isotype
Porolithon castellum Dawson

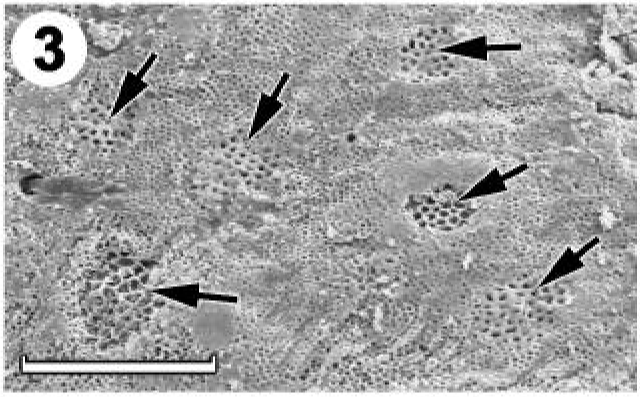
Locality: Isla del Cano

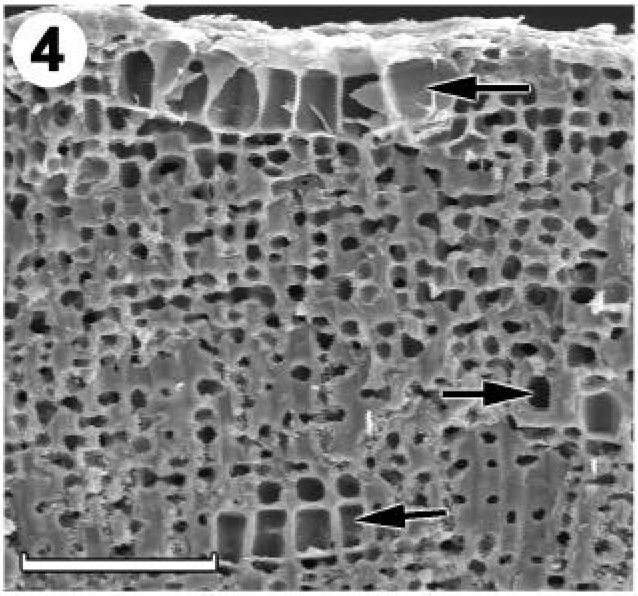
Habitat: north side at a depth of 15-25 feet

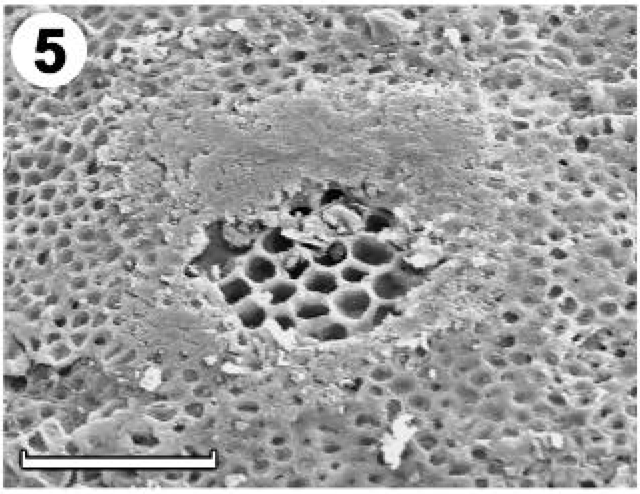
Collected by E. Yale Dawson 21094 3/28/59
det. by

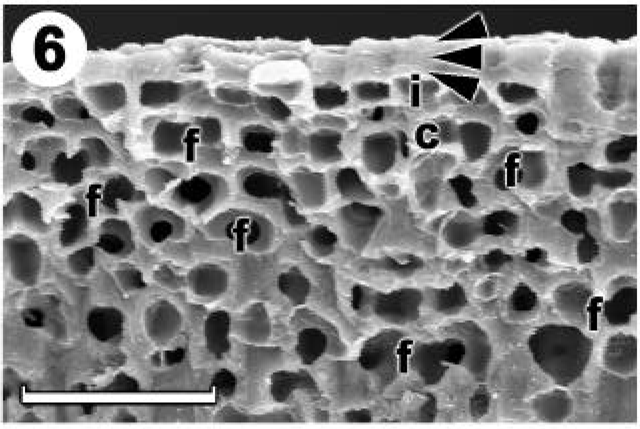
Plate 97

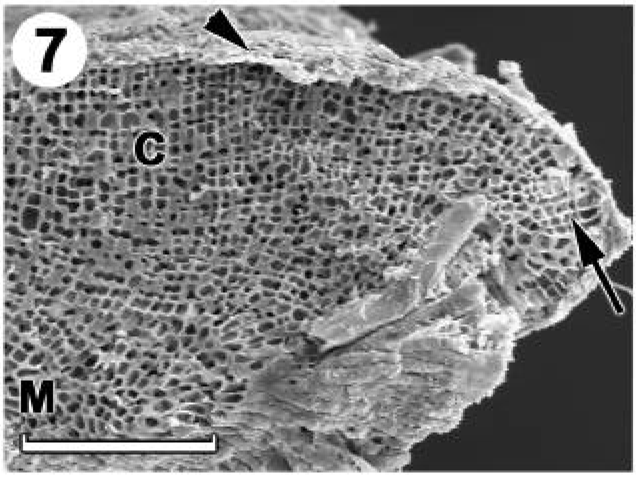


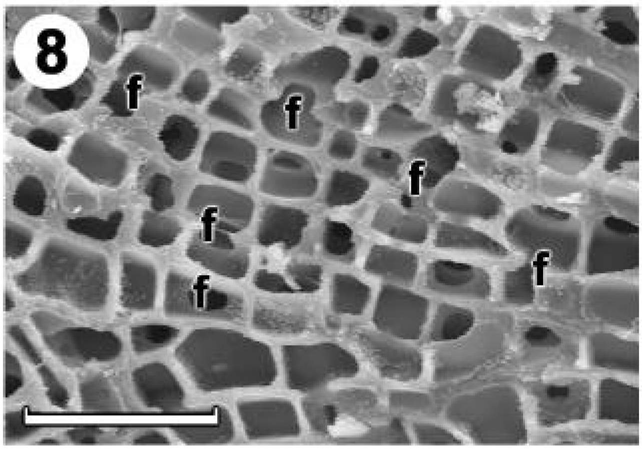












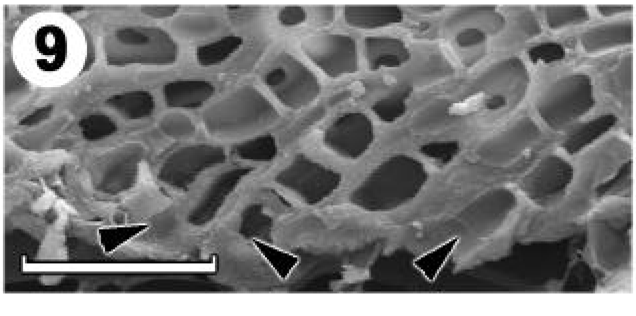
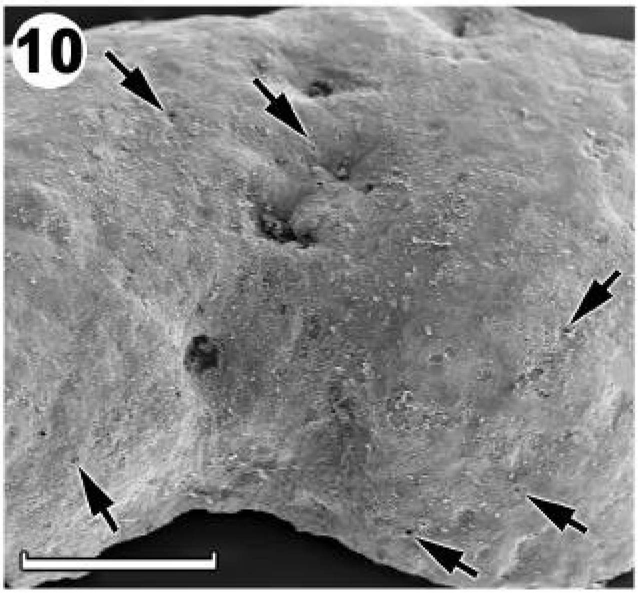
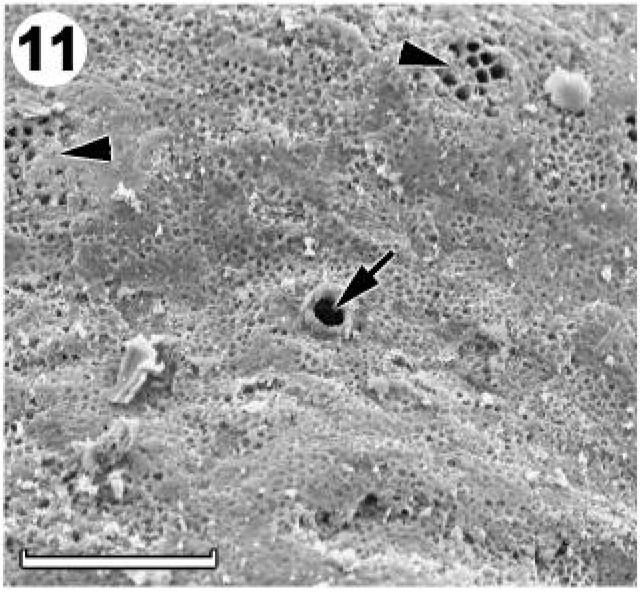
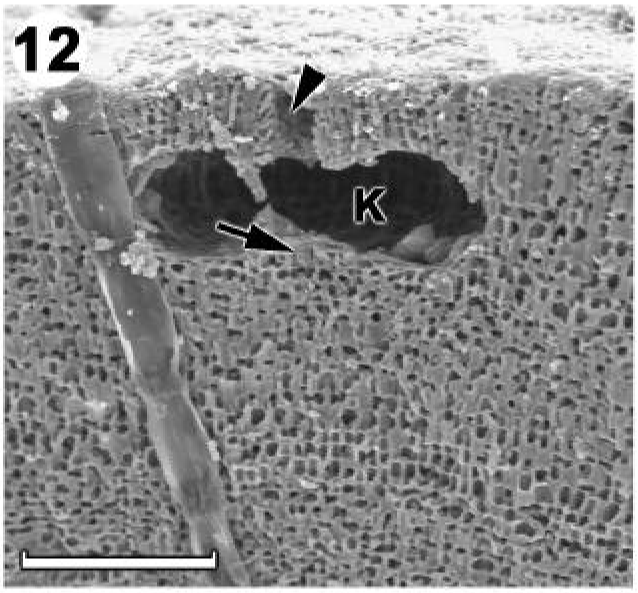
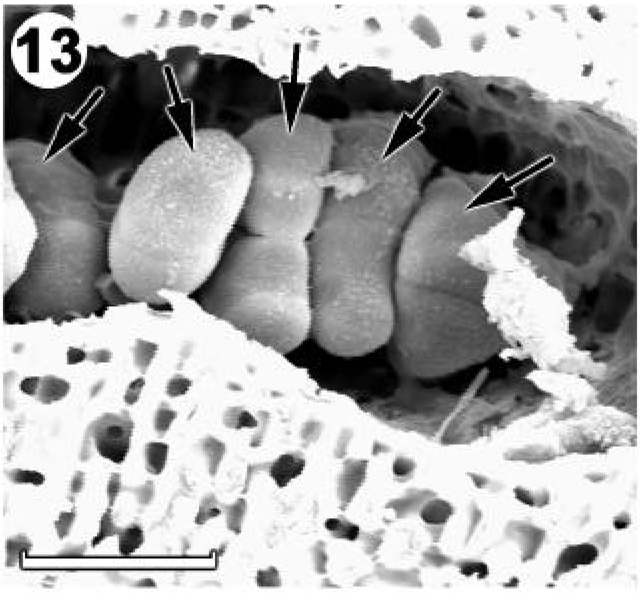


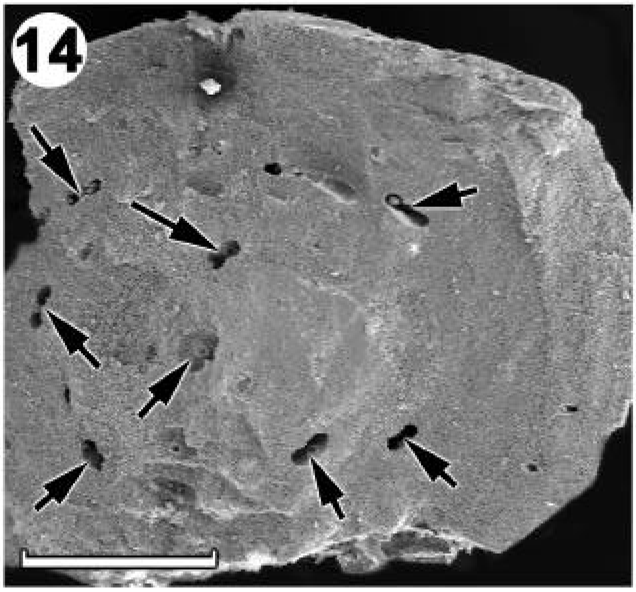
Plate 98











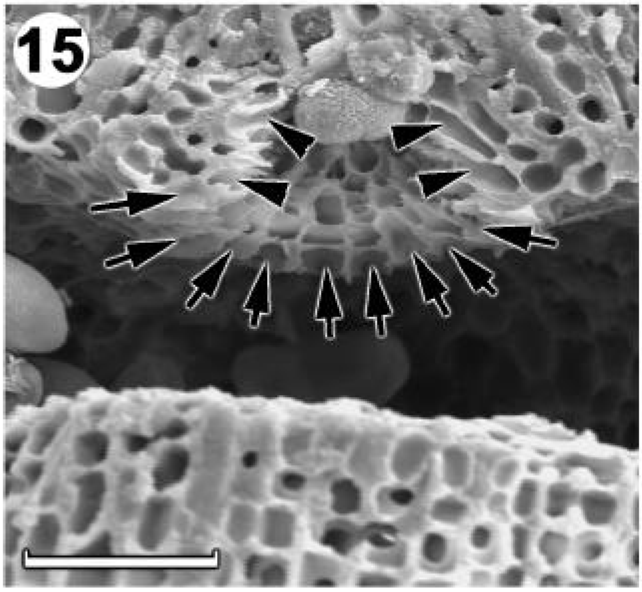
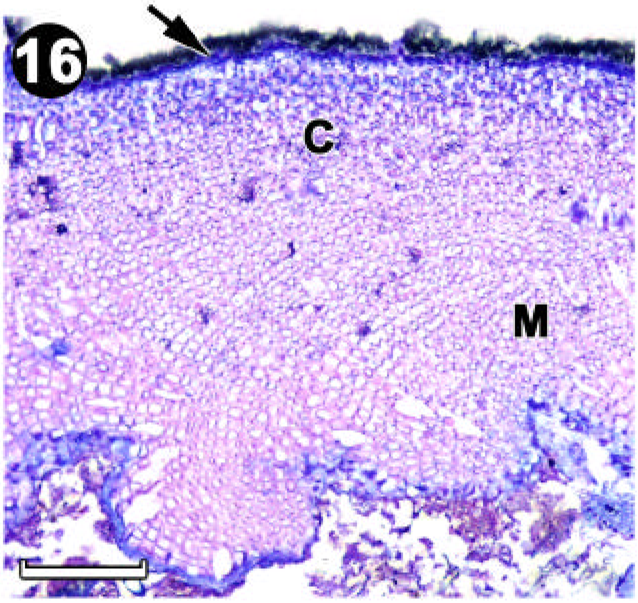
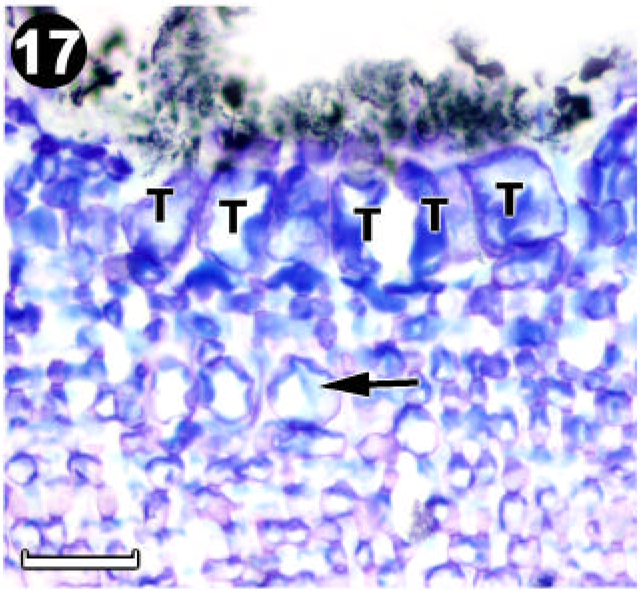
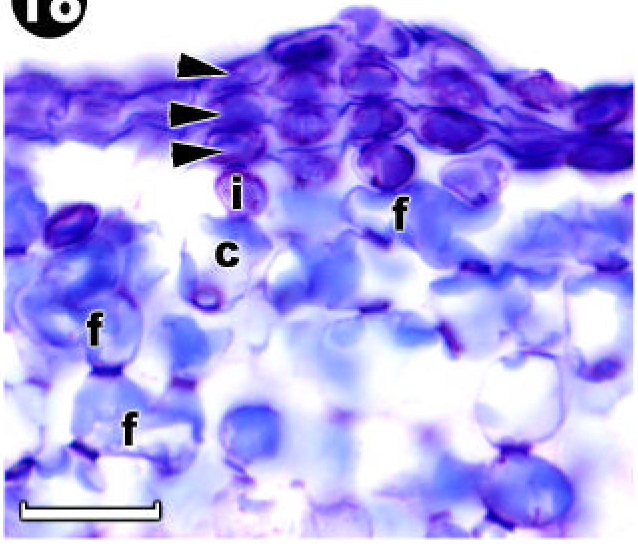
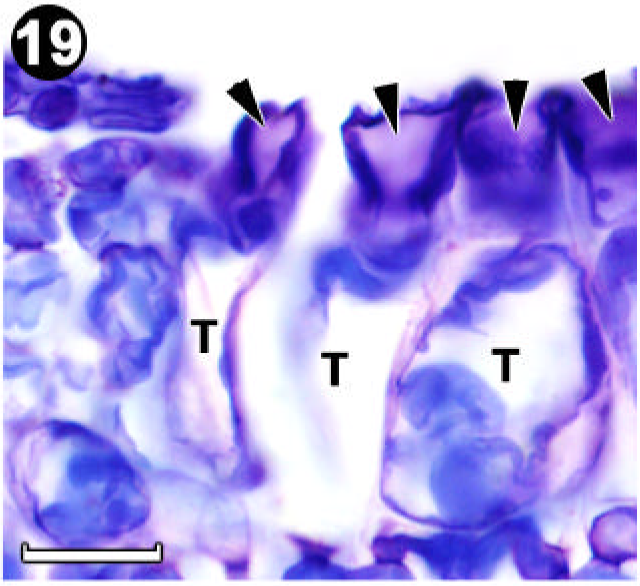


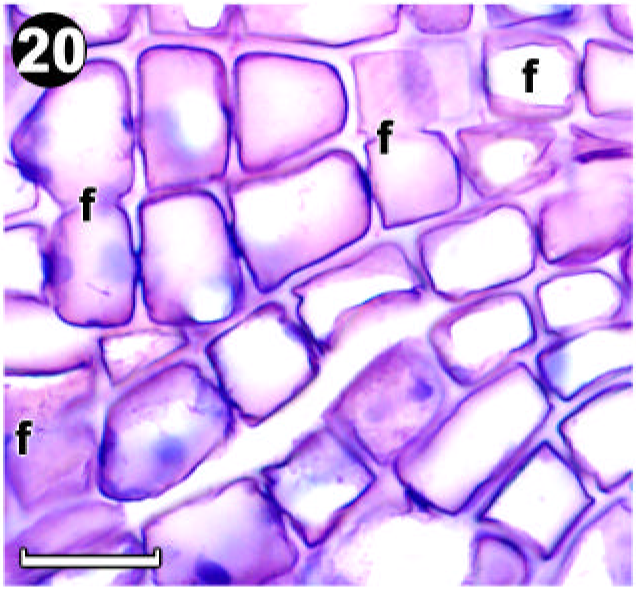
Plate 99

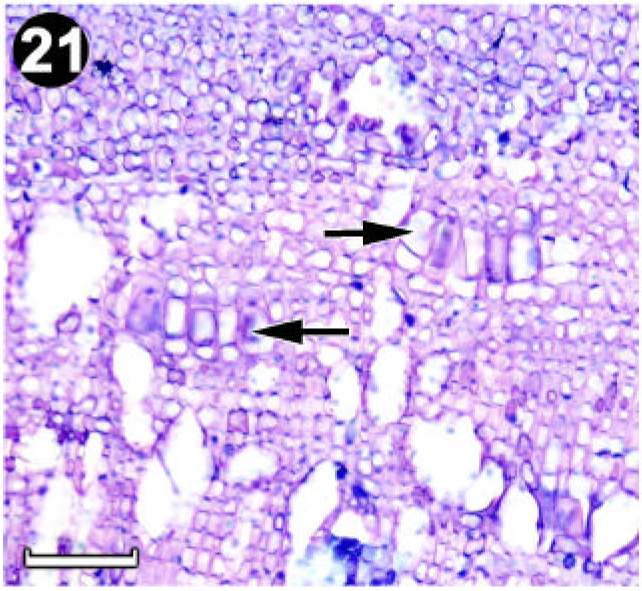












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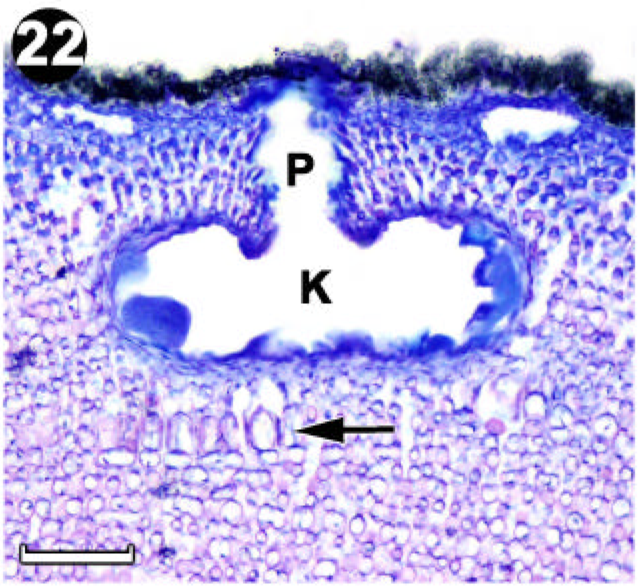

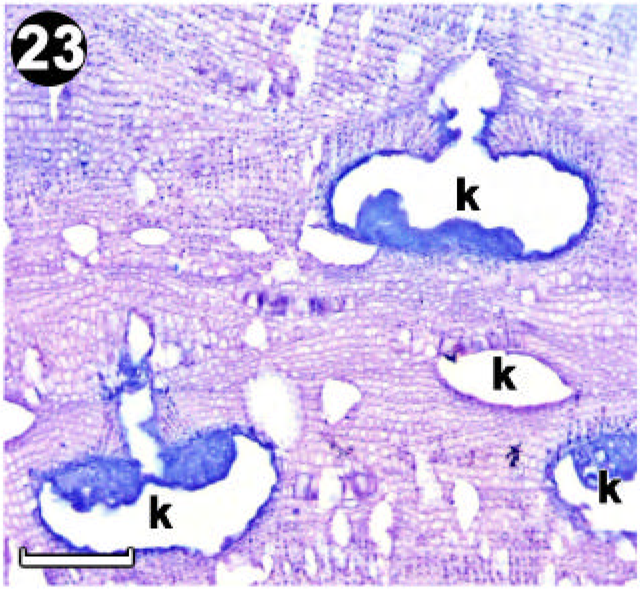

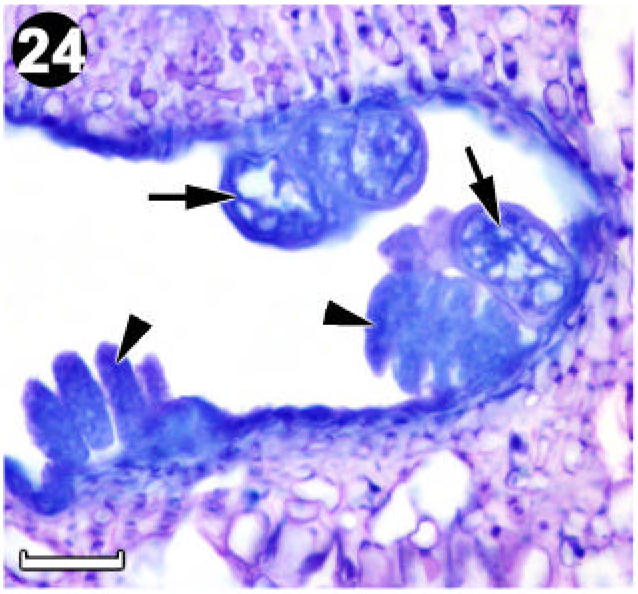

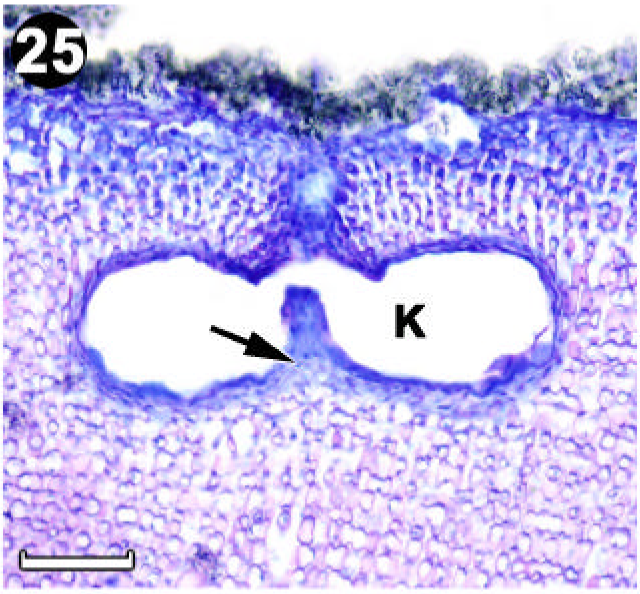

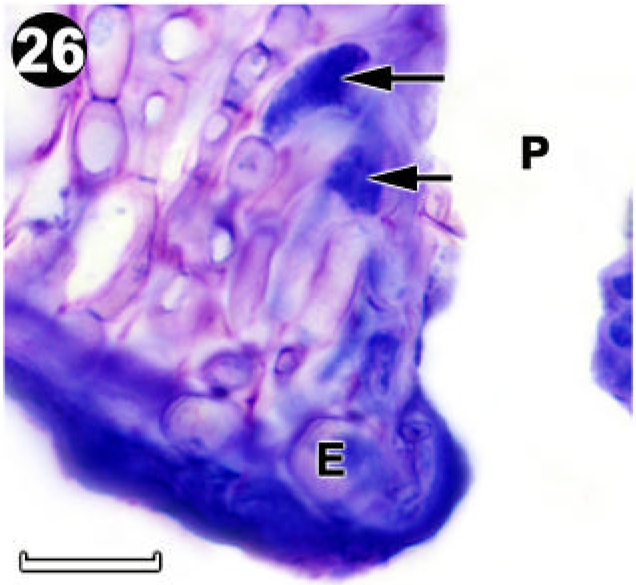

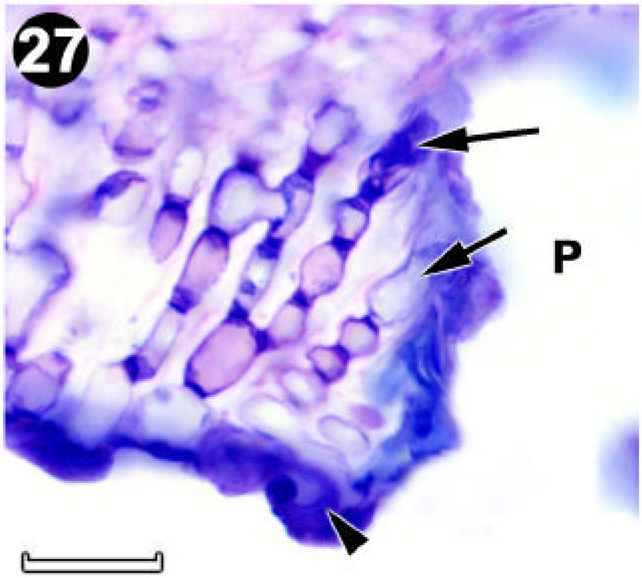

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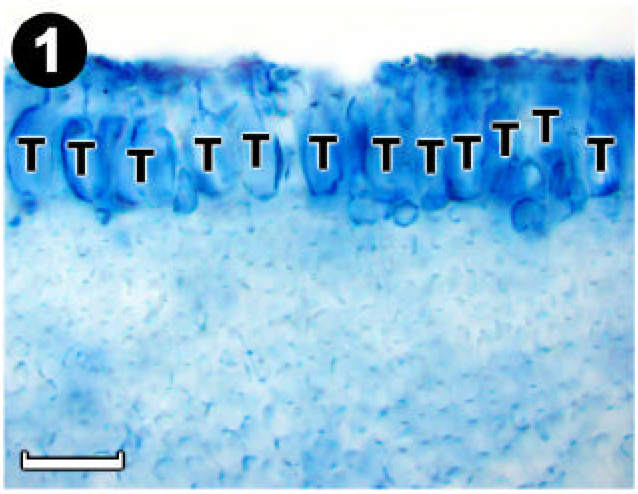

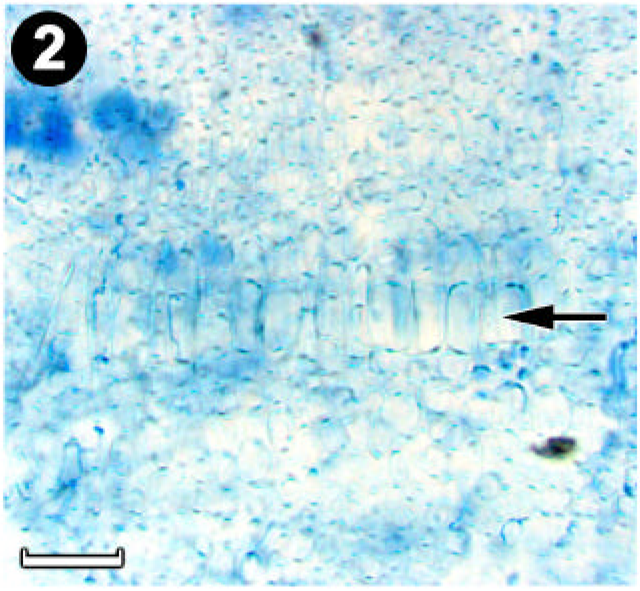

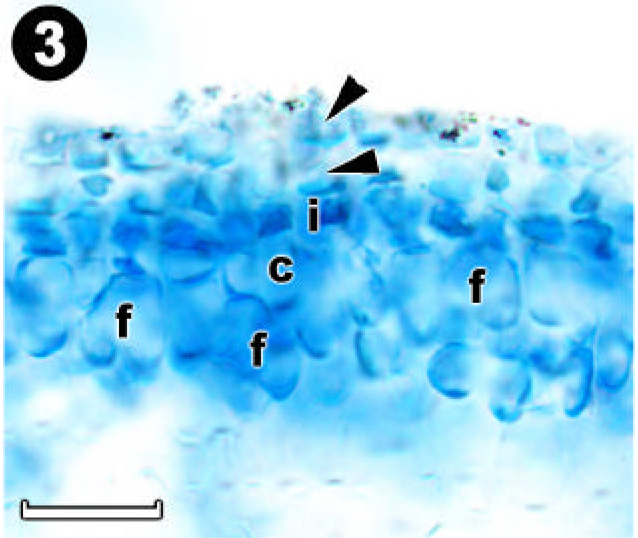

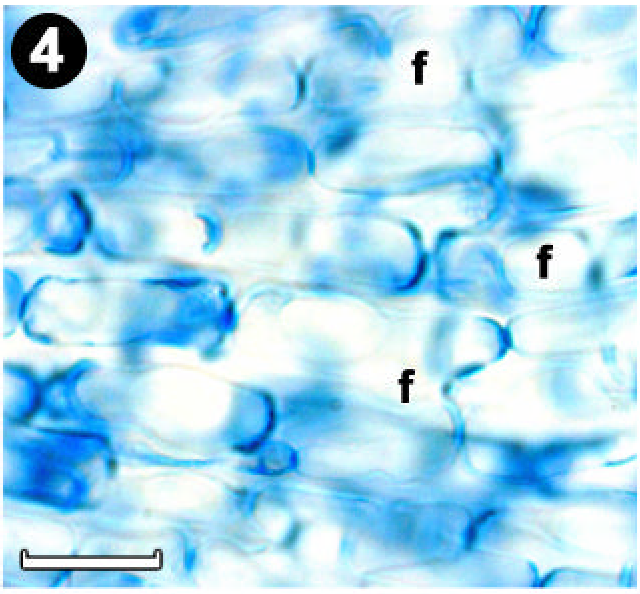

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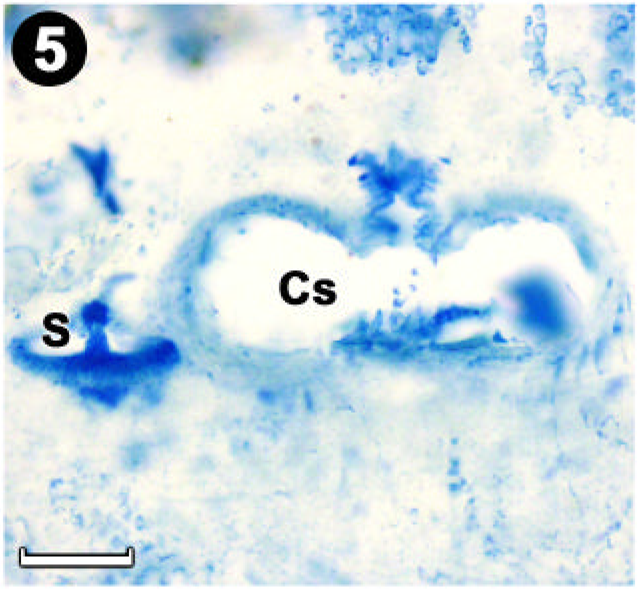

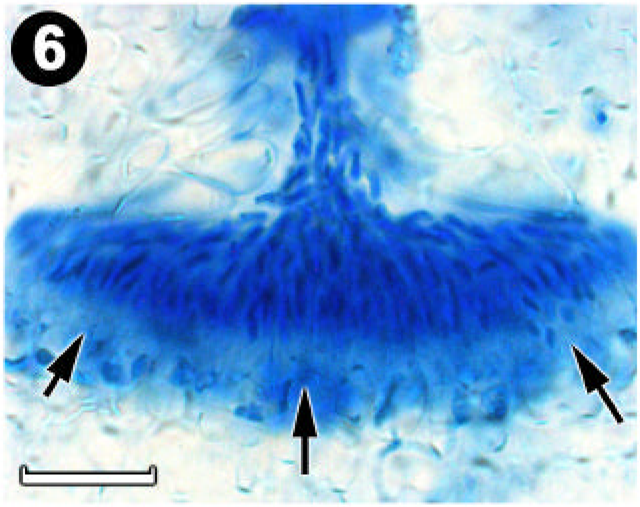

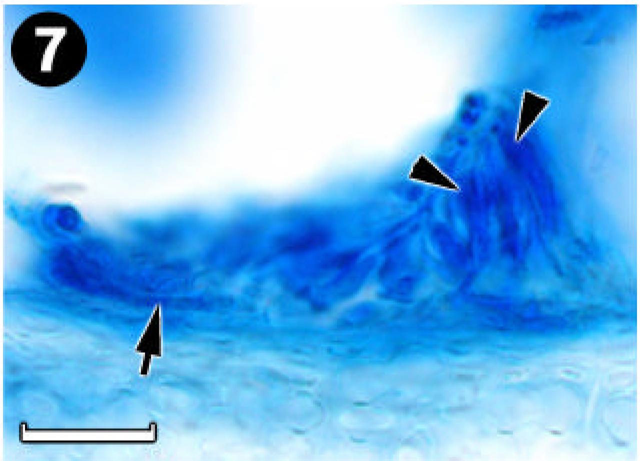

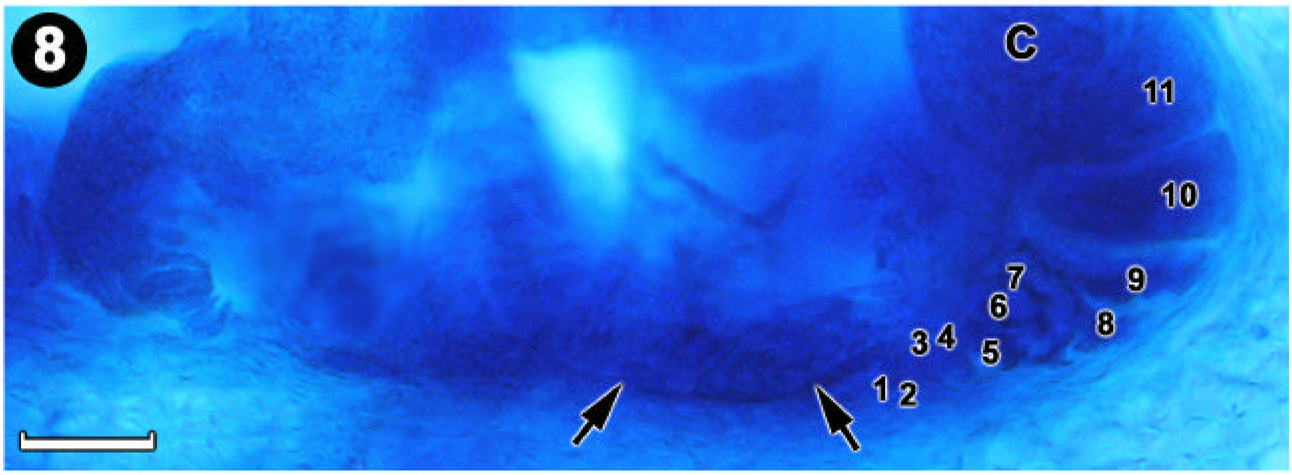

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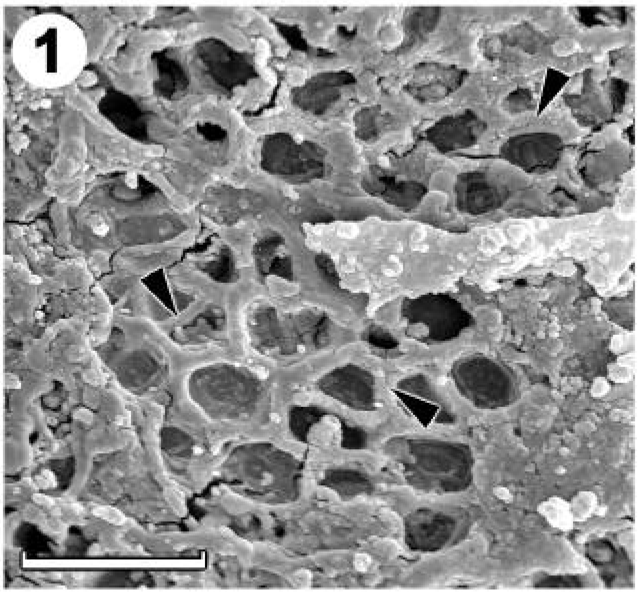

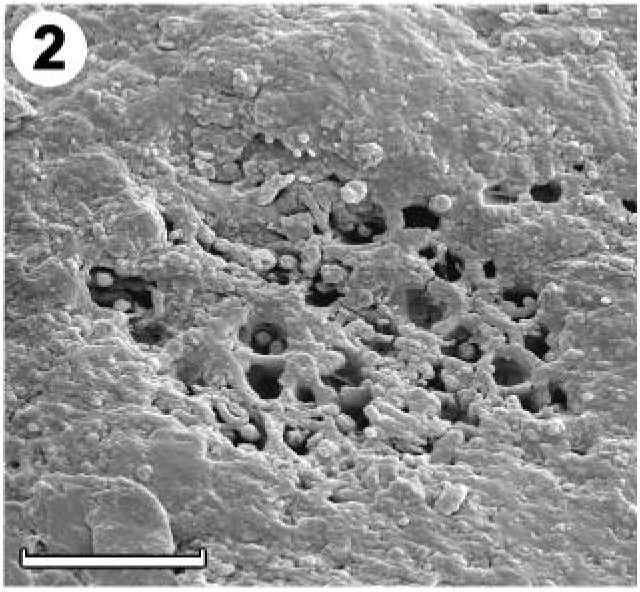

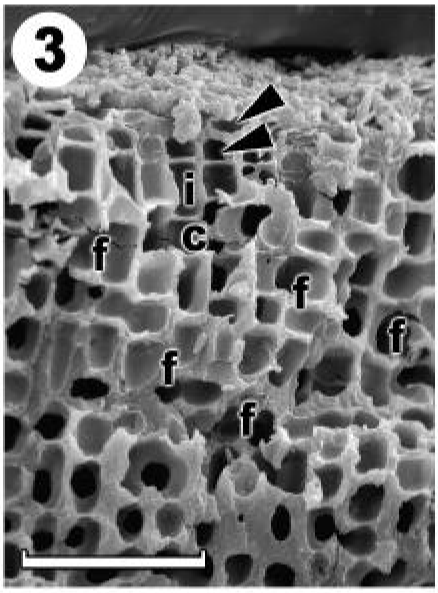

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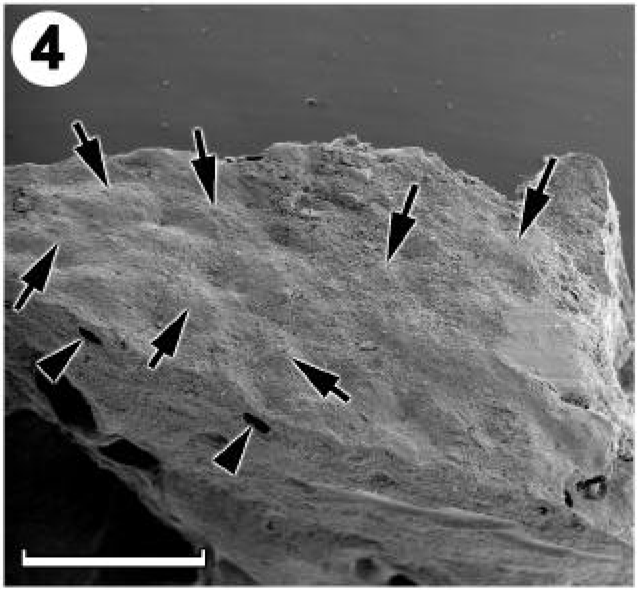

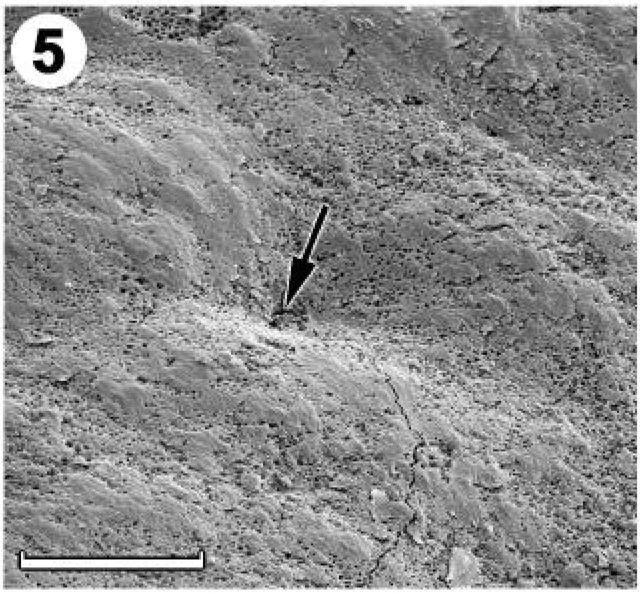

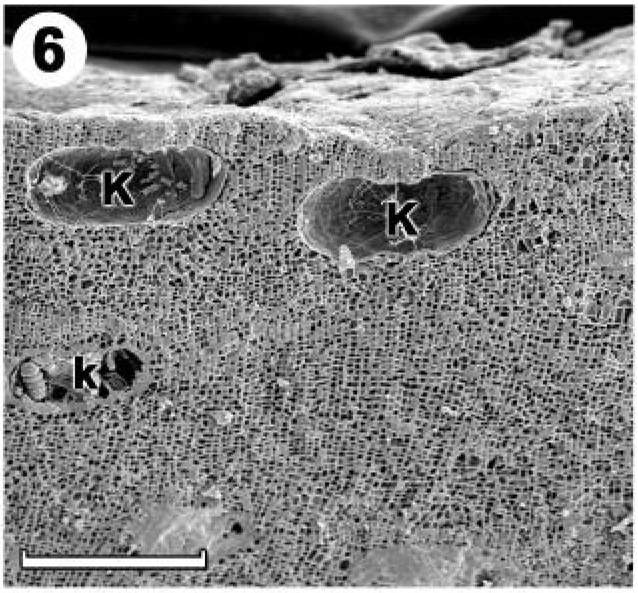

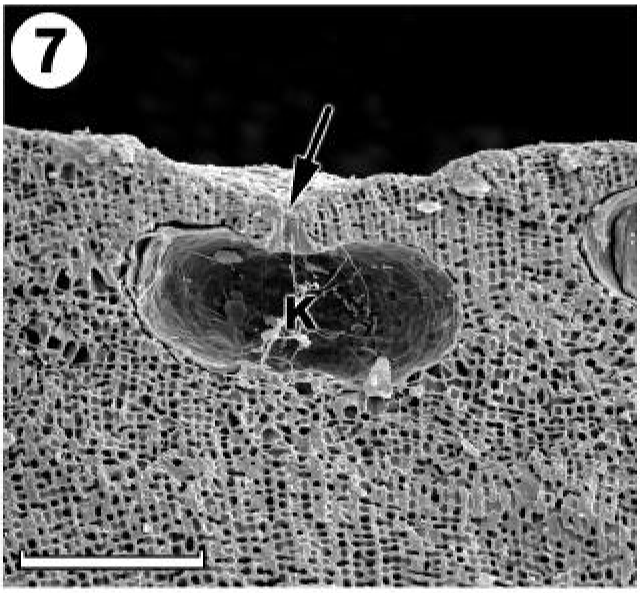

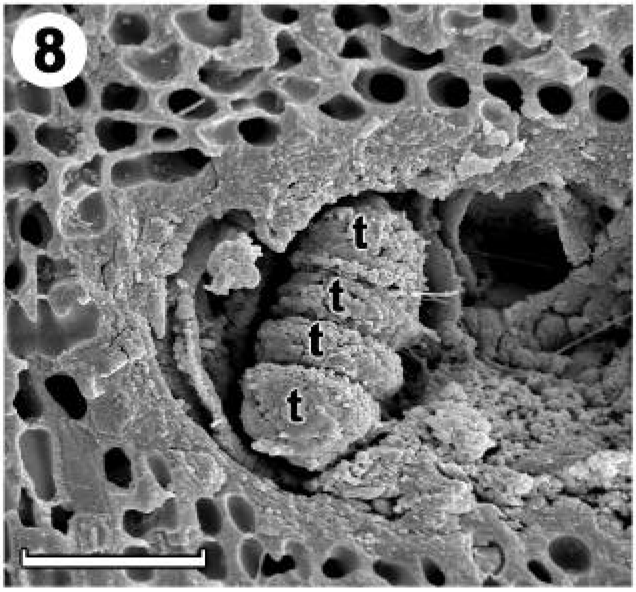

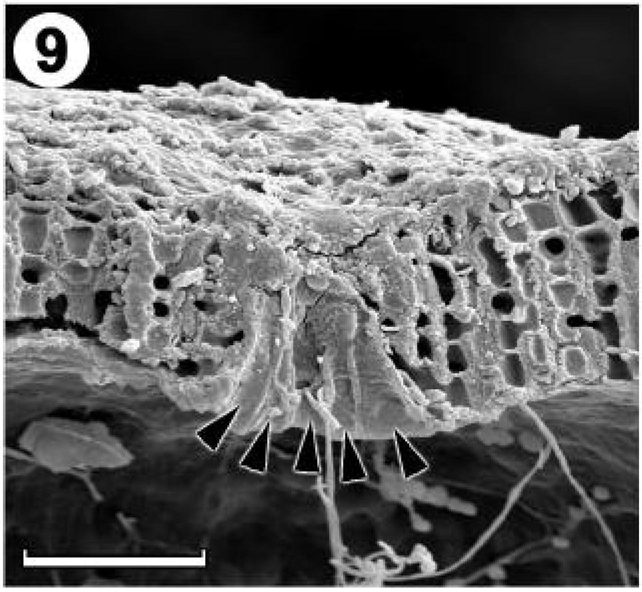

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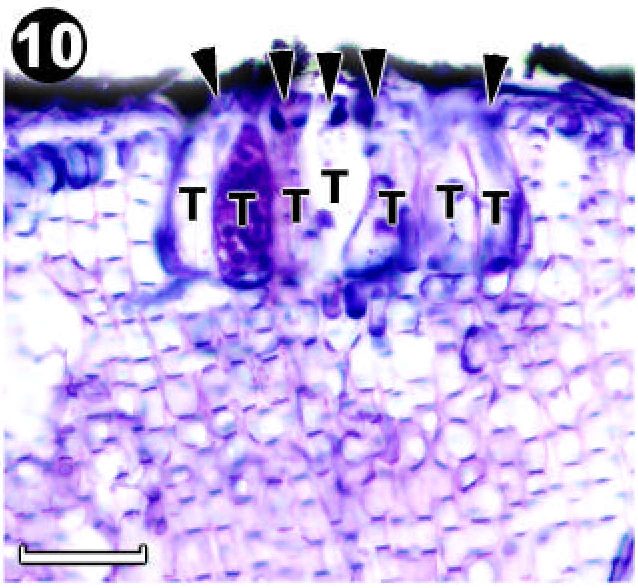

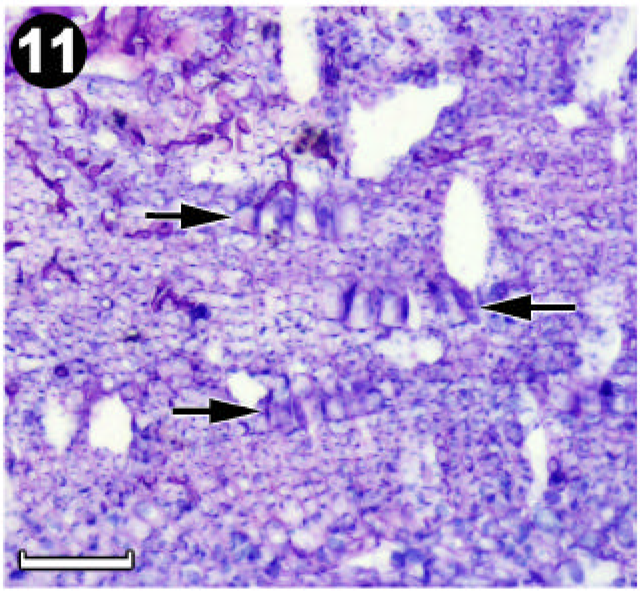

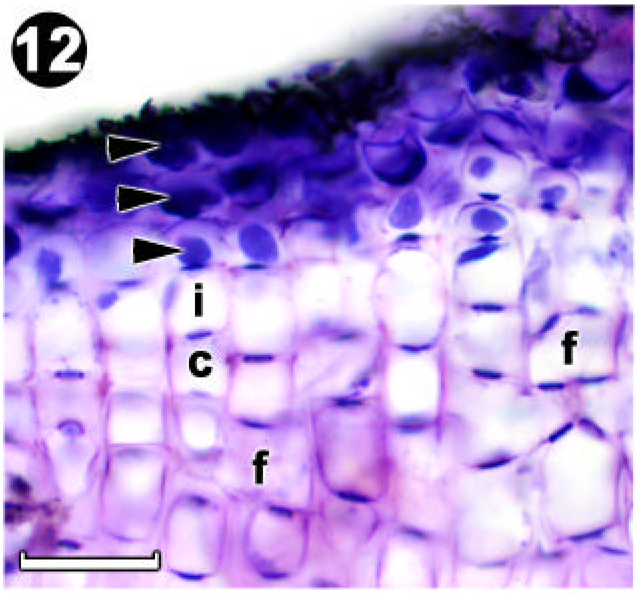

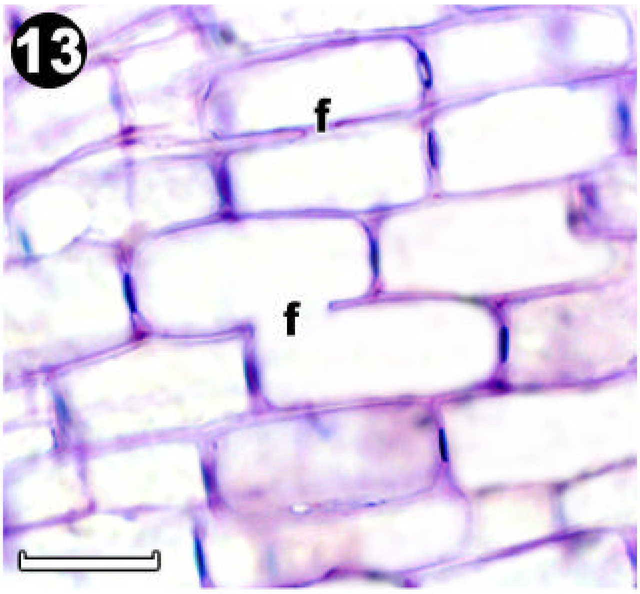

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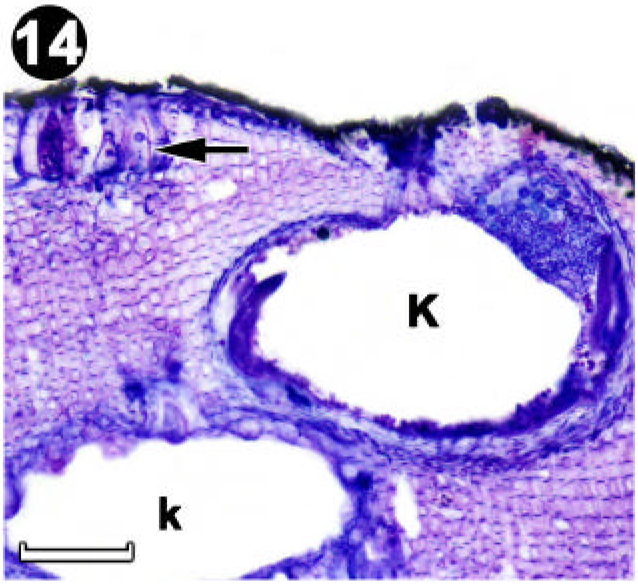

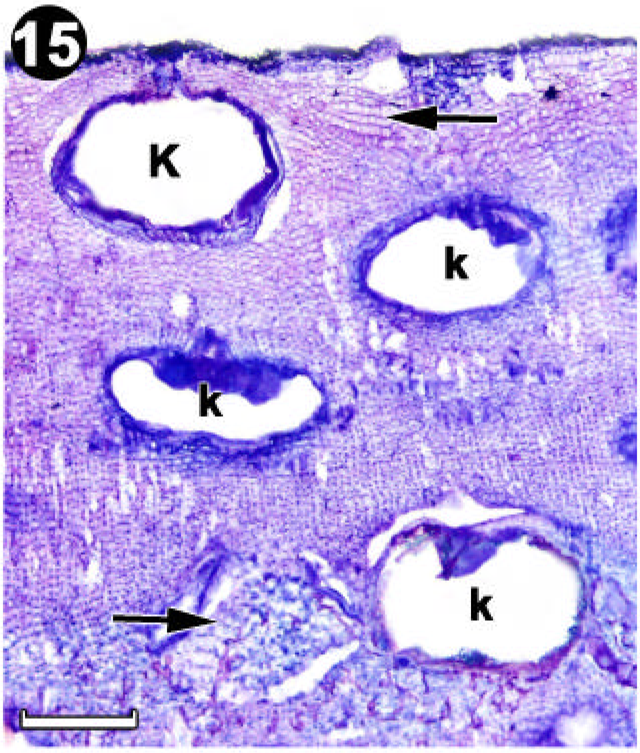

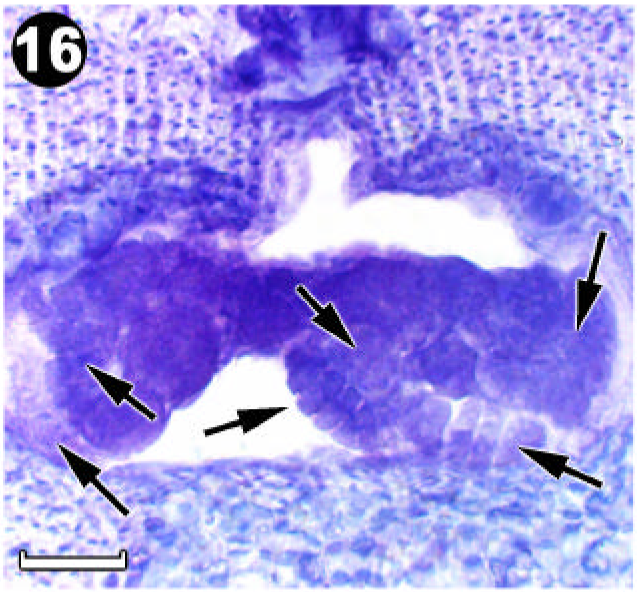

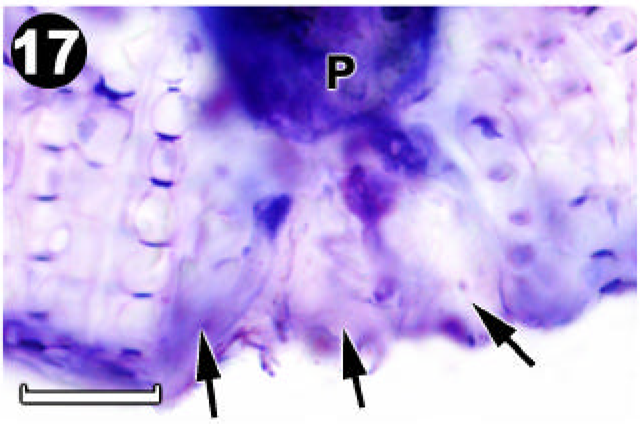

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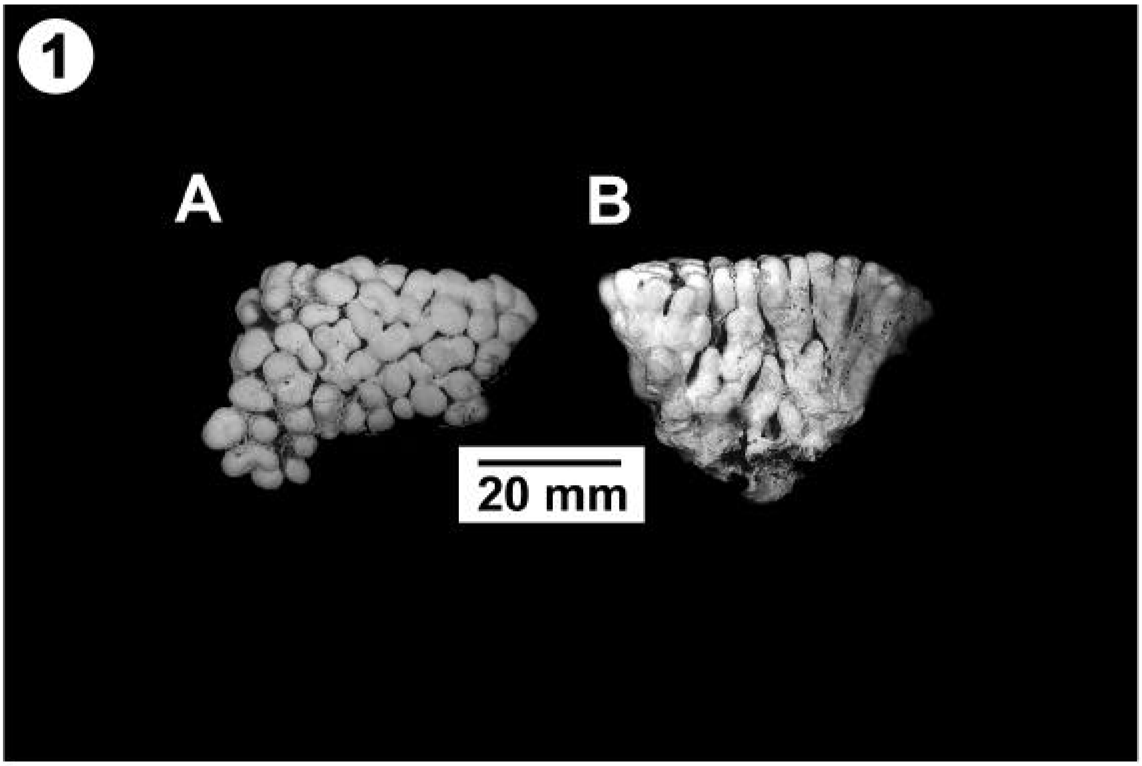

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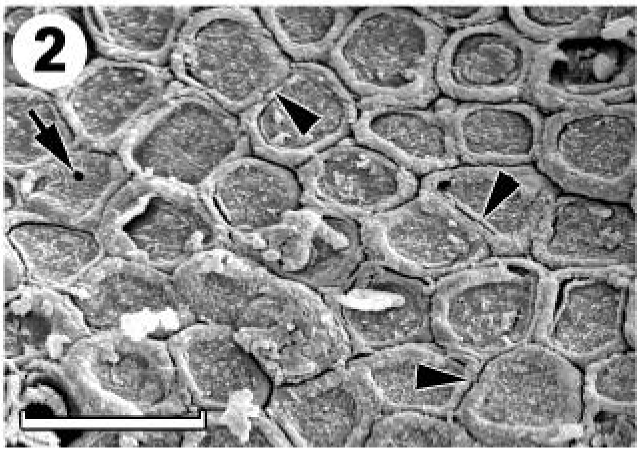

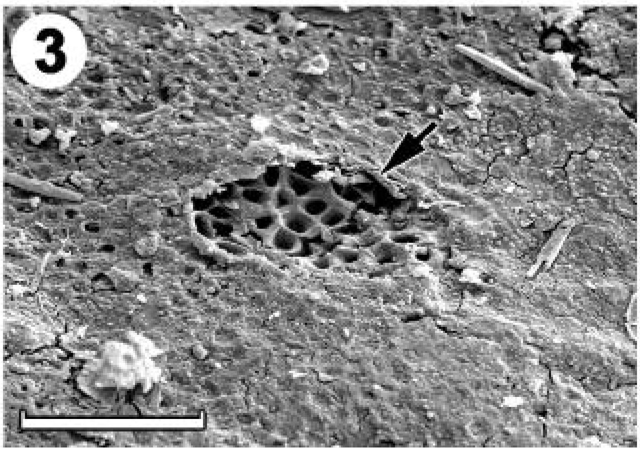

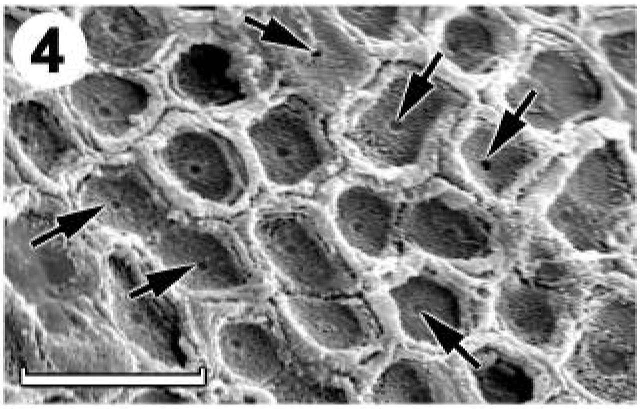

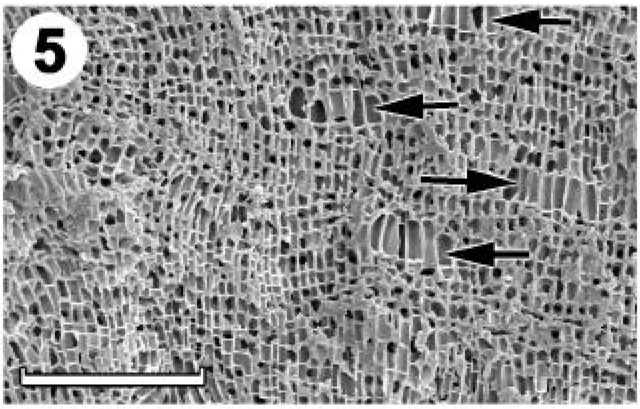

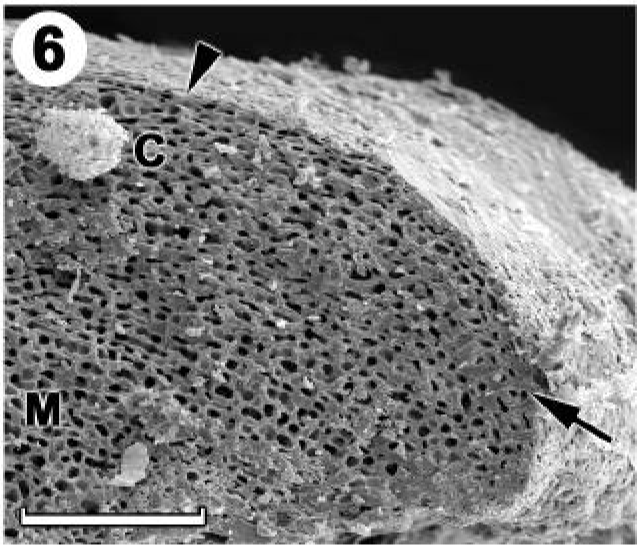

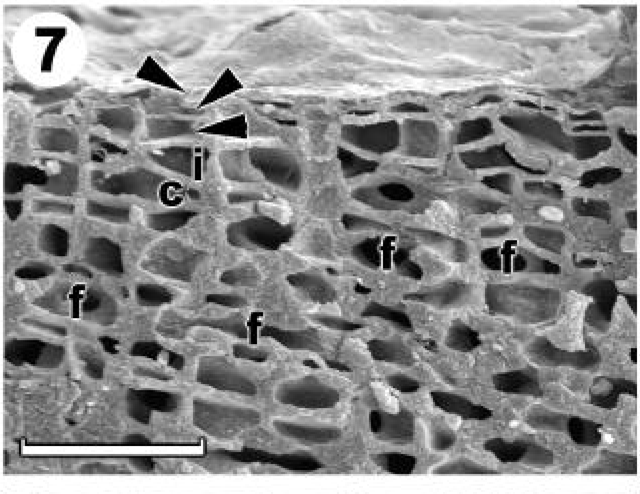

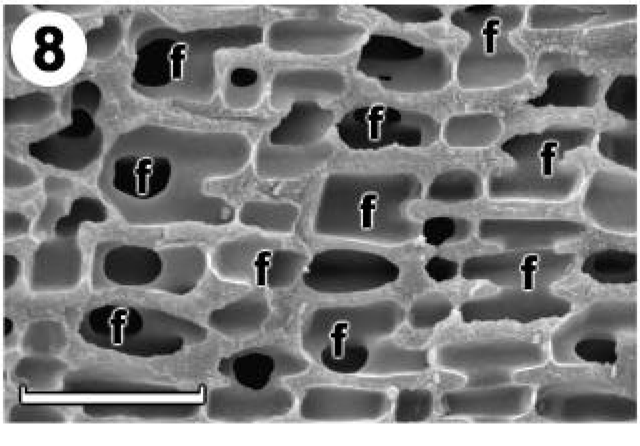

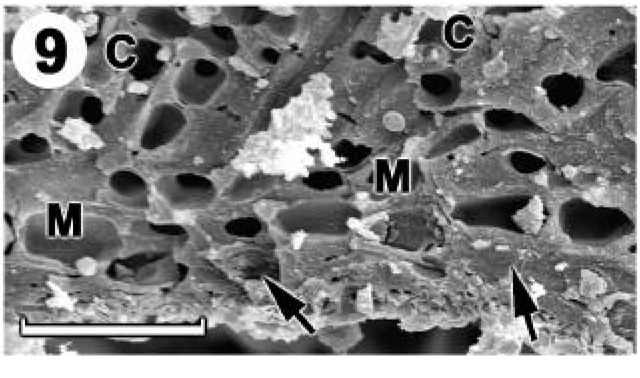

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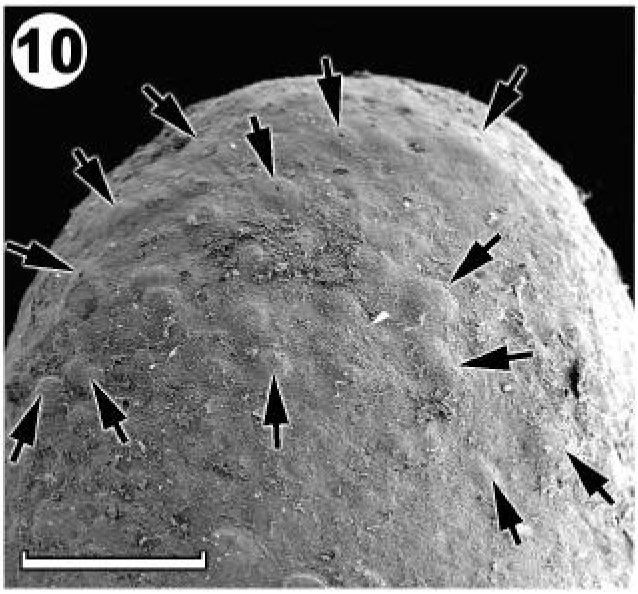

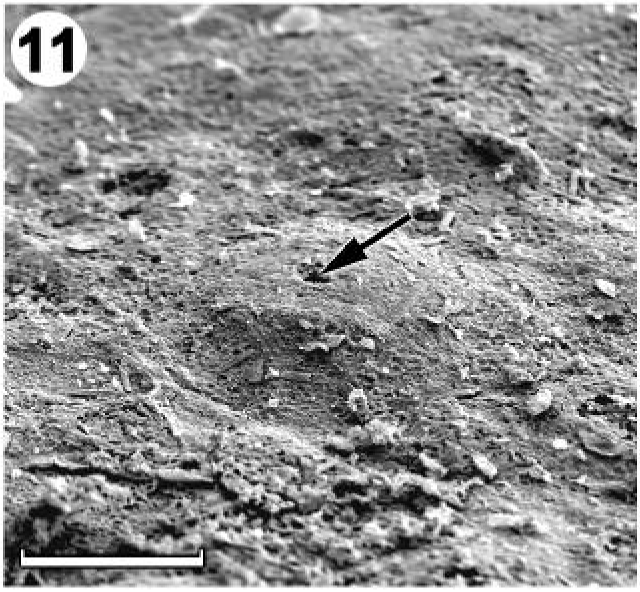

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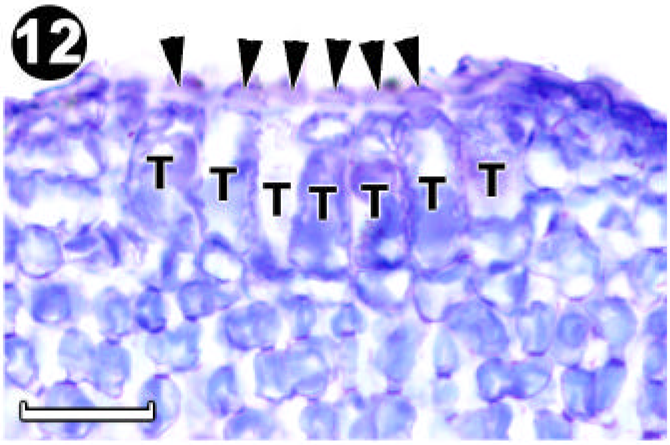

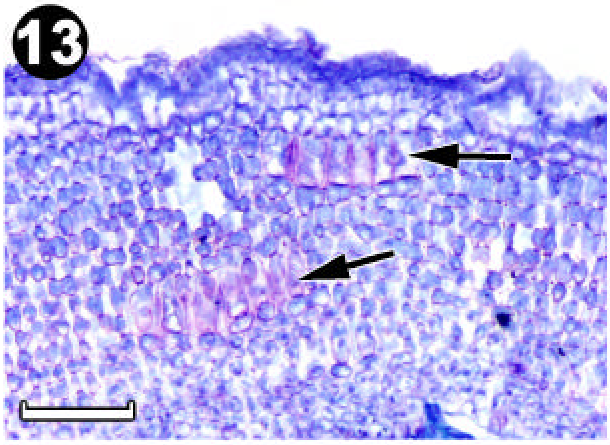

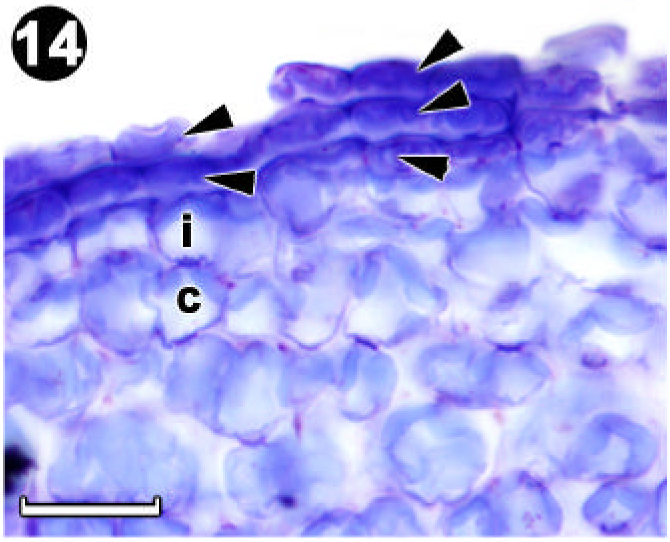

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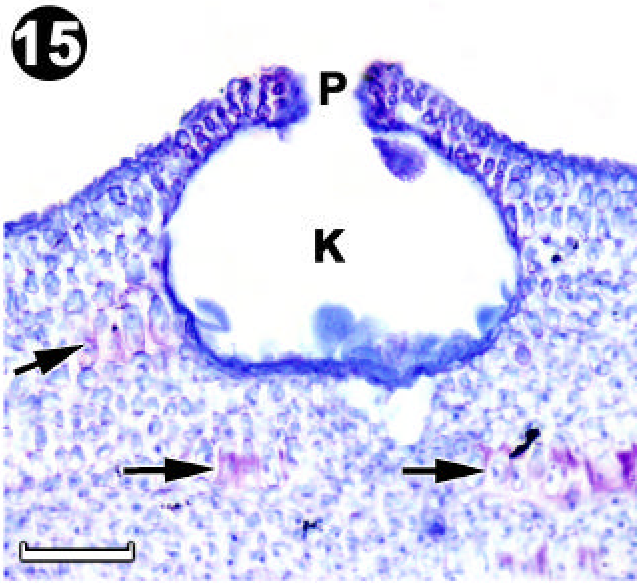

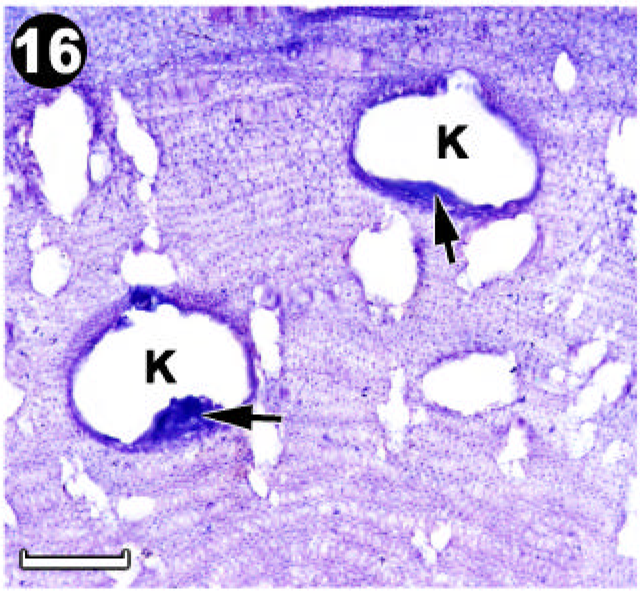

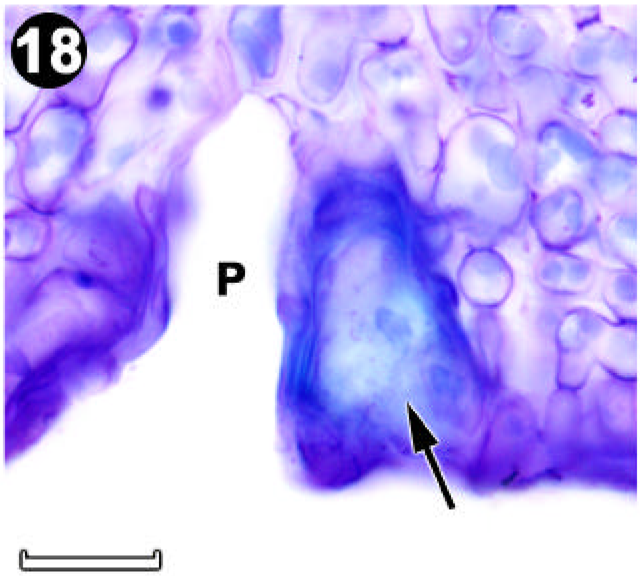

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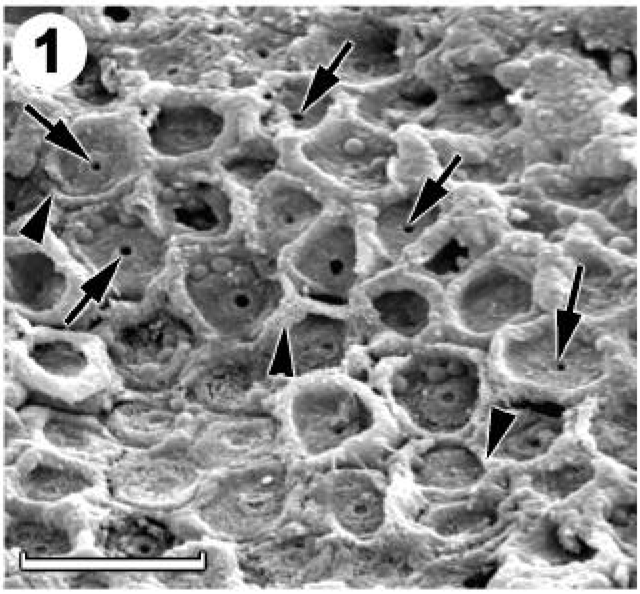

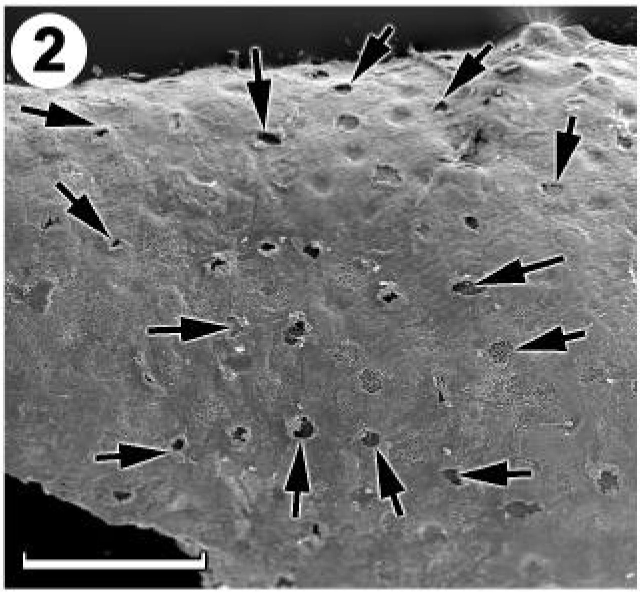

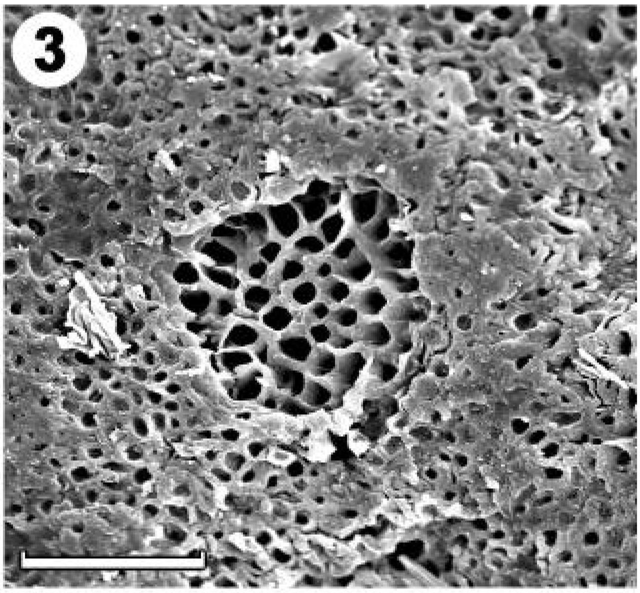

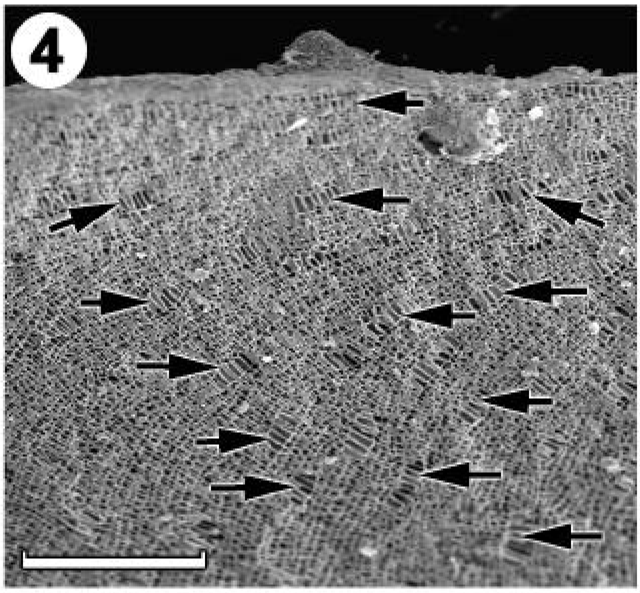

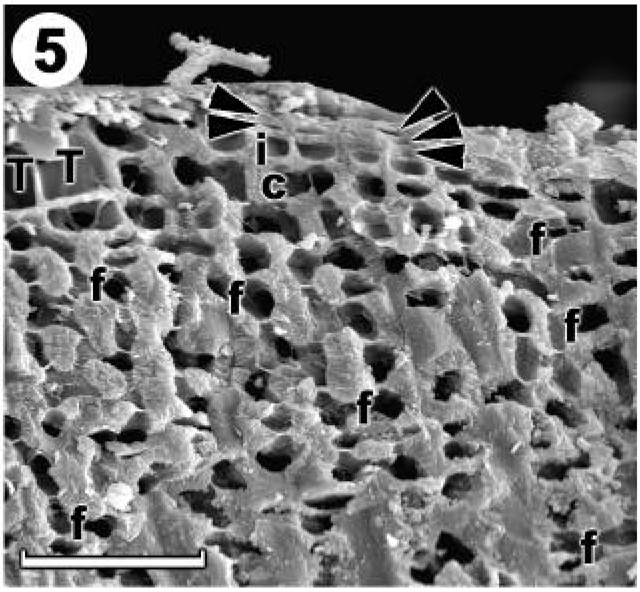

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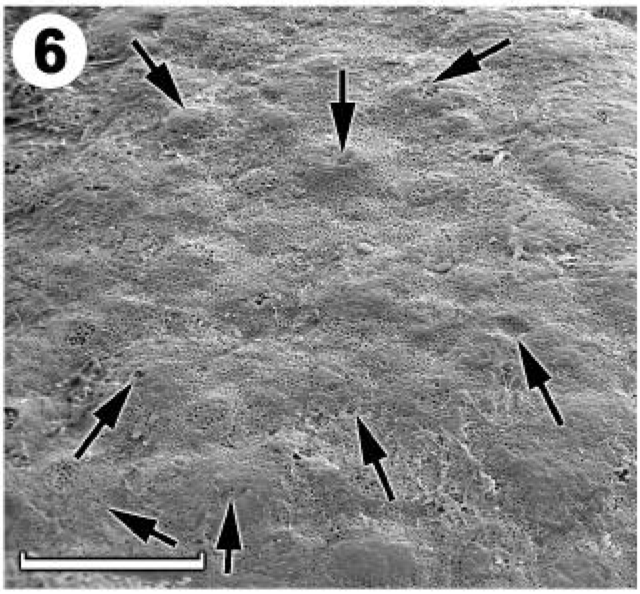

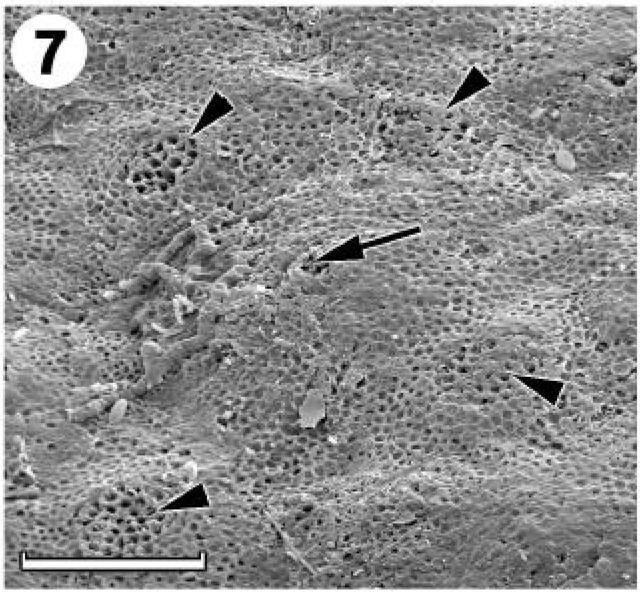

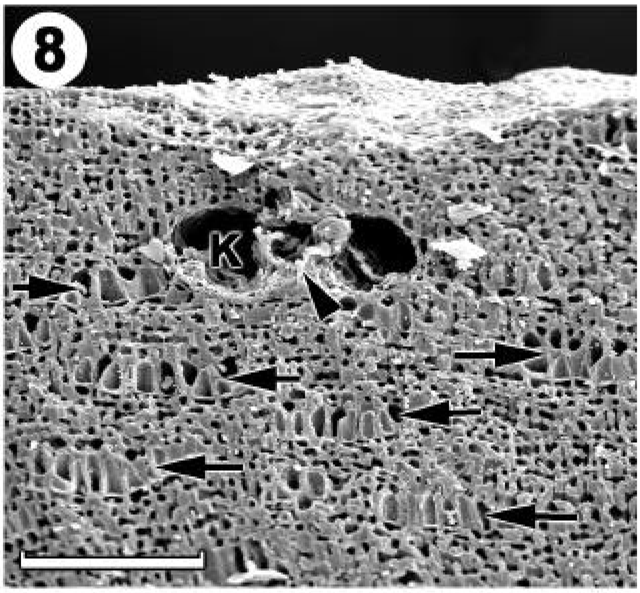

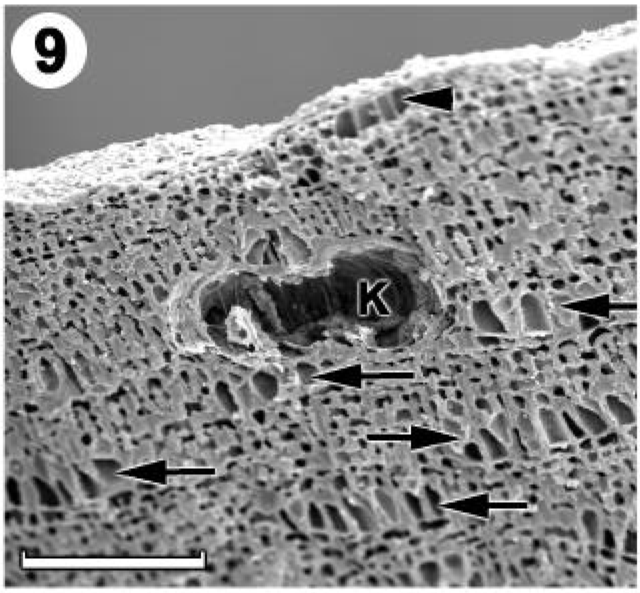

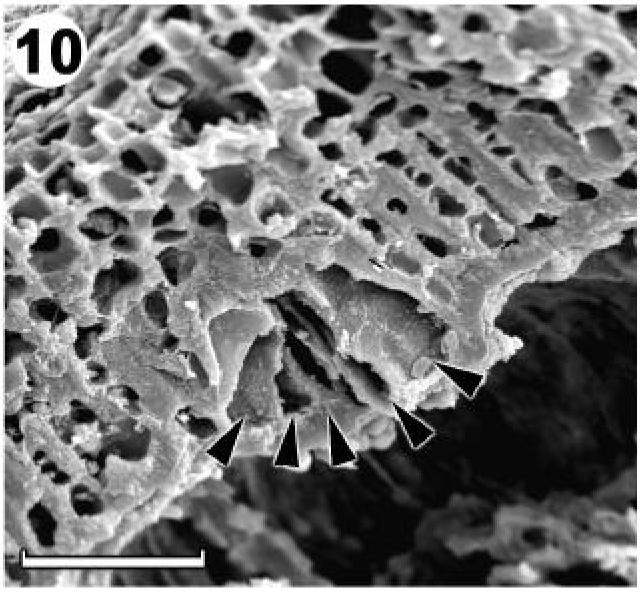

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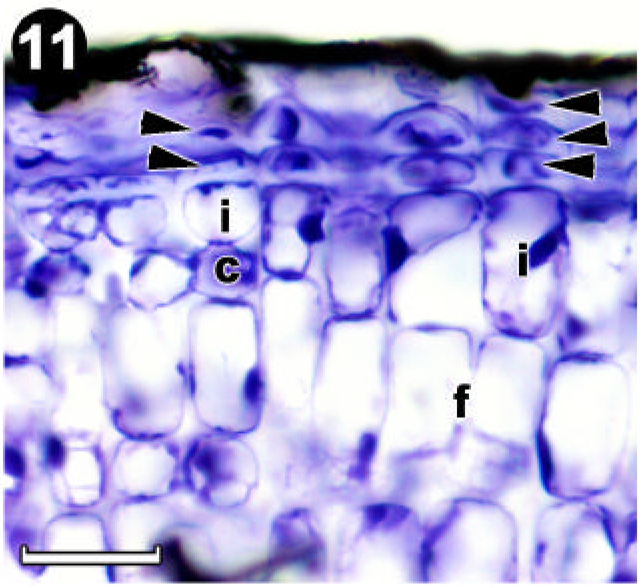

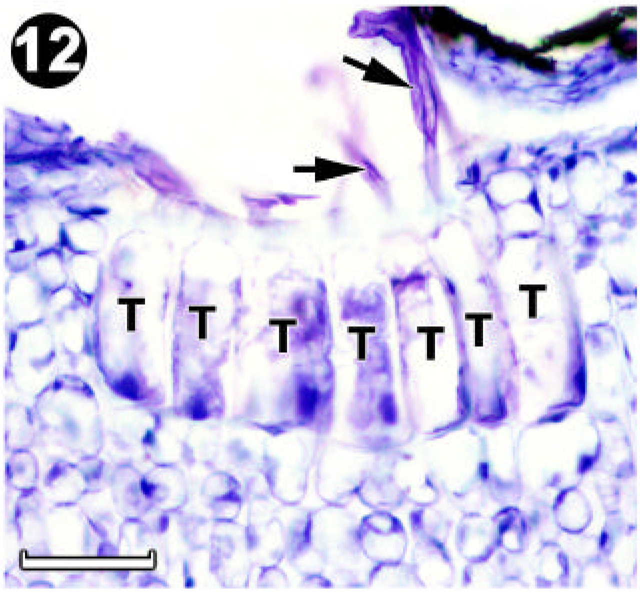

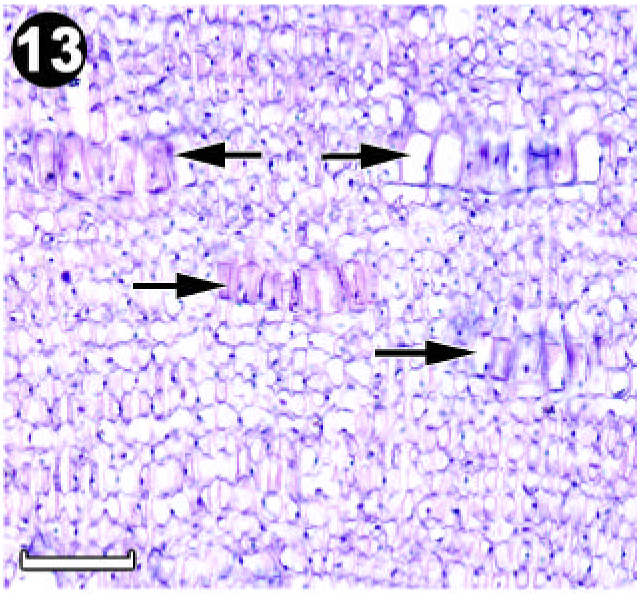

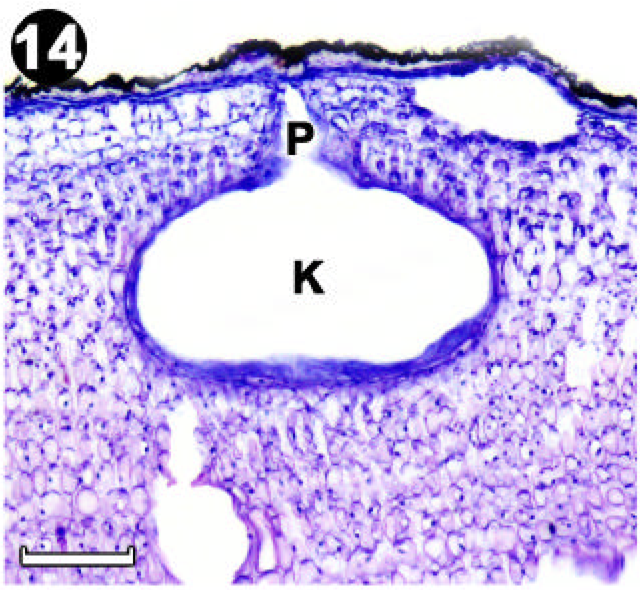

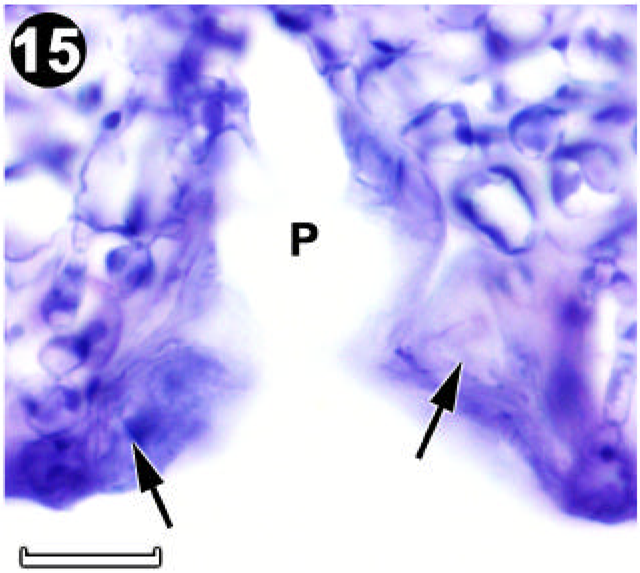

A global revision of the nongeniculate coralline algal genera Porolithon (defunct) and Hydrolithon (Corallinales, Rhodophyta)

Volume 2.

Gavin W. Maneveldt

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South Africa

Supervisor: Derek W. Keats

Co-supervisor: Frans M. Weitz

A thesis submitted in fulfilment of the requirements for the degree PhD in the Department of Biodiversity and Conservation Biology

June 2005

Paper 2.

A modern account of selected taxa from the genus *Hydrolithon* Foslie (Corallinales, Rhodophyta) and descriptions of taxa found to conform to the generic delimitation of *Hydrolithon*

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ABSTRACT

In 1909 Foslie established the genus Hydrolithon to encompass 4 species possessing a dimerous thallus with basal cells that were slightly longer than they were wide, and conceptacles that were like those of Goniolithon (i.e. obviously domed) in which tetrasporangia occurred in uniporate conceptacles that lacked columella. Hydrolithon has undergone substantial revision since 1909 and it is presently characterised by the pattern of its tetrasporangial conceptacle roof development. In Hydrolithon, the pore canals of the tetrasporangial conceptacles are lined by a ring of conspicuous, elongate cells that arise from filaments interspersed among the sporangial initials. These cells do not protrude into the pore canal, but are oriented more-or-less perpendicularly to the roof surface. Based on this feature, Hydrolithon and Porolithon are considered congeneric and Porolithon has been subsumed into Hydrolithon. Porolithon onkodes, the type species of the previous Porolithon, was the only species examined which was formally transferred to Hydrolithon. A few other Porolithon taxa have also been transferred, but without any review; the larger number have still not been formally transferred. In addition, a host of other species have since been included in Hydrolithon. The current research has attempted to reassess as many taxa as possible that have been ascribed to the genus Hydrolithon as well as taxa found to conform to the generic delimitation of Hydrolithon. This has been hampered by a lack of type material supplied from various herbaria, a lack of representative material from type localities, and inadequate descriptions of even recently described taxa. Not-with-standing, the following taxa have been found to conform well to the present-day diagnosis of Hydrolithon; H. boergesenii, H. craspedium, H. gardineri, H. improcerum, H. munitum, H. onkodes, H. reinboldii, H. rupestris and H. superficiale. A number of taxa that have been ascribed to Hydrolithon do not conform to the present-day generic disposition of this genus.

Hydrolithon breviclavium has been found to conform to the genus *Spongites* and is consequently referred to as *Spongites brevicalvius* (Foslie) Maneveldt & Keats comb. nov. *Hydrolithon consociatum* and *H. subantarcticum* are found to be conspecific, the former having nomenclatural priority. Previous research has, however, considered these two taxa synonymous with *Spongites discoideus*. An investigation into the sporangial conceptacle roof development of these two taxa show that they belong within the confines of the genus *Pneophyllum* instead, and should therefore be referred to as *Pneophyllym consociatum* (Foslie) Maneveldt & Keats comb. nov. In addition, this study has found that the following taxa conform to the present-day delimitation of *Hydrolithon*: *Neogoniolithon caribaeum*, *N. erosum* and *N. rugulosum*. These taxa have, however, all been found to be conspecific and subsequently are all referred to as *Hydrolithon erosum* (Foslie) Maneveldt & Keats comb. nov. Similarly, *Hydrolithon samöense* (*Lithophyllum samoënse* Foslie 1906: 20) has also been found to be conspecific with *Hydrolithon erosum* (Foslie) Maneveldt & Keats comb. nov. (*Lithophyllum erosum* Foslie 1906: 20) the latter having nomenclatural priority. *Hydrolithon samoënse* was and still is, however, very widely used and it may be argued that the epithet *samoënse* instead be given priority; this suggestion requires further investigation. The current research has also showed that a number of other taxa are conspecific with *H. munitum* (*H. murakoshii*) and *H. rupestris* (*N. rufum*). Because a number of types could not be obtained, these taxa have been analysed based on previous research.

INTRODUCTION

Non-geniculate coralline algae that have been ascribed to the genus Hydrolithon (Foslie) Foslie are important in the ecology of coral reefs, often forming the major components of many algal reefs (Lee 1967; Littler 1973; Adey 1978; Adey et al. 1982; Littler & Littler 2000, 2003). Foslie (1909: 55) established the genus Hydrolithon to encompass those taxa that possessed a dimerous thallus with basal cells that were slightly longer than they were wide, and conceptacles that were like those of Goniolithon (i.e. obviously domed) in which tetrasporangia occurred in uniporate conceptacles that lacked a columella (Penrose & Wolkerling 1988). Foslie (1909) ascribed four species to Hydrolithon (see Table 1) but did not designate the type specimen. It was not until much later that Mason (1953: 333) designated the lectotype specimen, Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie.

The concept of Hydrolithon has undergone substantial change since 1909 (see Penrose & Woelkerling 1988 for a review of these changes). Woelkerling (1985) and Penrose & Woelkerling (1988) ultimately concluded that the characters used to delineate the type of Hydrolithon were not reliable, as the types of the genera Porolithon and Spongites also possessed these characters. Penrose & Woelkerling (1988) then subsumed both Hydrolithon and Porolithon in Spongites (the oldest available name for the complex) but did note that Spongites (sensu lato) encompassed a broad range of taxa. During their course of study on the southern Australian taxa of Spongites (sensu lato), it became apparent to Penrose & Woelkerling (1992) that two distinct patterns of tetrasporangial conceptacle development occurred. Their conclusion was that Hydrolithon and Spongites were distinct genera.

In Hydrolithon, the pore canals of the tetrasporangial conceptacles are lined by a ring of conspicuous, elongate cells that arose from filaments interspersed among the sporangial initials.

These cells do not protrude into the pore canal and are oriented more-or-less perpendicularly to the roof surface. Based on this new evidence, Penrose & Woelkerling (1992) still considered Hydrolithon and Porolithon to be congeneric and since Hydrolithon was described first, Porolithon was considered to be a heterotypic synonym and thus subsumed into Hydrolithon. In their 1992 reappraisal however, Porolithon onkodes, the type species of the former Porolithon, was the only species examined which was formally transferred to Hydrolithon. Only a few of the remaining taxa ascribed to Porolithon have received varying degrees of taxonomic review in light of these changes; the majority have undergone none. Some have even been transferred without any study e.g. H. craspedium (P. Silva in Silva et al. 1996). Yet other, more modern publications (e.g. Littler and Littler 2003), have not even considered the synonymy of Porolithon to Hydrolithon. Similarly, the host of publications and descriptions pertaining to the Mastophoroideae written prior to 1992 (e.g. Adey 1970) should be reviewed in light of the findings by Penrose & Woelkerling (1992). The purpose of this paper is therefore to provide a modern revision of selected taxa (excluding taxa conforming to the Fosliella-state of Hydrolithon – see Penrose & Chamberlain 1993) from the genus Hydrolithon and also to describe fully taxa found to conform to the generic delimitation of Hydrolithon.

MATERIALS AND METHODS

Type specimens were obtained from **BM**, **PC** and **TRH** (Table 2). Type material was first fixed in 1 part liquid detergent: 4 parts commercial formalin in distilled water (10% ~ 4% formaldehyde) for at least 48 hours prior to examination. This method was found useful for rehydrating most of the material. For representative material, 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.

For scanning electron microscopy (SEM), air-dried material was fractured using either finger nails, forceps, diagonal cutters, or a small hammer & cold chisel. Wherever possible a fracture 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 gold for 4-6 min in an Edwards S150B sputter coater, and examined with a Hitachi X650 scanning electron microscope, equipped with a Mamiya 6X7 camera at an accelerating voltage of 20 or 25 kV.

Formalin-preserved specimens were decalcified in 10% nitric acid. After decalcification all specimens were immersed in 70%, 90% and 100% ethanol solutions respectively for a minimum of 30 minutes each. Specimens were then immersed in Leica Historesin filtration medium (50ml basic resin [liquid] and 1 packet [0.5g] activator) until completely infiltrated. Infiltration is complete when the specimen appears slightly translucent and sinks to the bottom of the infiltration vessel. A hardening solution was added to the infiltration medium (15 ml infiltration solution + 1 ml hardener) and the specimens orientated in this final solution until set. Gelling of the hardener usually occurred within about 15mins; some specimens were placed in an oven to allow more rapid hardening. All specimens were sectioned at 12 –15 µm thickness using a Bright 5030 microtome. Each individual section was removed from the microtome blade using a fine sable hair brush, and transferred to a slide covered with distilled water. All slides were then placed on a slide warmer until dry. Slides were then stained with toluidine blue (0.25 g borax/100ml and 0.06g toluidine blue/100ml), left to dry and covered with cover slips using a mounting medium. Photographs were taken from prepared slides using an Olympus microscope equipped with a digital camera. In some instances, when good sections were not obtained, drawings were made directly from prepared slides using a Zeiss microscope equipped with a drawing tube.

Conceptacle outside diameter and pore diameter was measured directly from the SEM. All other measurements were made using a calibrated eyepiece micrometer. In cell measurements for monomerous thalli, length denotes the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. For dimerous thalli, the dimensions of the cells of basal filaments are given as follows: height denotes the dimension at right angles to the substratum (technically diameter as defined for monomerous thalli), while width denotes the dimension between successive primary pit connections parallel to the substratum (technically length as defined for monomerous thalli). Conceptacle measurements follow the system of Adey & Adey (1973). Thallus terminology follows Chamberlain (1990). Growth-forms terminology follows Woelkerling et al. 1993 unless otherwise stated. Typification data follow Woelkerling (1993) unless otherwise stated.

Preparation of the plates (digitisation) was made using the graphics software package Adobe® Photoshop® and were constructed at 300dpi. The plates are arranged in alphabetical order of the species basionym firstly for previously described species followed by that of newly described species.

Herbarium material is decreasing due to sampling for study. Therefore, although many species are well known (e.g. *H. onkodes*), I have illustrated all material in detail for all specimens studied to provide a detailed record and reduce the need to refer to dwindling type material. Also, many previous publications that have reported studies of type material have not presented detailed analyses of the types.

OBSERVATIONS

The genus Hydrolithon

Hydrolithon (Foslie) Foslie (1909: 55) (see Adey 1970: 11), emend Penrose and Woelkerling (1992: 87)

Goniolithon Foslie subgenus Hydrolithon Foslie 1905a: 7

Foslie (1905a: 7) originally described Hydrolithon as a subgenus of Goniolithon Foslie comprising only two taxa; Goniolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie (as Gonioithon Reinboldii), and Goniolithon boergesenii Foslie (as Goniolithon Börgesenii). Later Foslie (1909: 55) raised Hydrolithon to genus status and included an additional two taxa; H. improcerum (Foslie) Foslie, and H. breviclavium (Foslie) Foslie. A type species for the genus Hydrolithon Foslie was not designated by Foslie and it was not until much later that Mason (1953: 333) designated the lectotype specimen, Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie. Later, Kylin (1956: 208) also designated a lectotype specimen, Hydrolithon improcerum (Foslie) Foslie, but this designation is invalid as Mason's (1953) designation was published first and thus holds priority.

Heterotypic synonyms

Heteroderma Foslie (1909: 56)

Porolithon Foslie (1909: 57)

Fosliella Howe (1920: 587)

Spongites Kützing (1841: 30) (see Penrose & Woelkerling 1988: 173-174)

Etymology

'Hydrolithon' from Greek hydor (water) and lithos (stone).

Description

Thallus non-geniculate, non-endophytic, and lacking haustoria; of varying growth forms; anchored ventrally to the substratum by cell adhesion or growing unattached. Thallus occasionally unconsolidated, but usually pseudoparenchymatous. Plants monomerous and/or dimerous, more-or-less radial. When dimerous, thalli lack a basal layer of palisade cells throughout. Cells of contiguous filaments joined by cell fusions; secondary pit connections unknown. Germination disc 4-celled.

Sporangial conceptacles uniporate. Sporangia zonately divided, lacking apical plugs. Pore canals of tetrasporangial conceptacles lined by a ring of conspicuous, enlarged cells that arise from filaments interspersed among sporangial initials; these cells do not protrude into the pore canal, and are oriented more-or-less perpendicularly to the roof surface.

Gametangial plants monoecious or dioecious. Spermatangial conceptacles with simple spermatangial systems borne only on the floor of the chamber. Gonimoblast filaments developing from the periphery of a central fusion cell (see Penrose 1991, 1992; Penrose & Woelkerling 1988, 1992; Penrose & Chamberlain 1993).

Type species

Basionym

Lithophyllum reinboldii Weber van Bosse & Foslie in Foslie 1901b: 5

Pl. 31-35, Figs 1-21.

Current Placement/Name

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie 1909: 55 (see Penrose and Woelkerling (1992: 83).

Pl. 36-40, Figs 1-21.

Lectotype

TRH. Moearas Reef, east coast of Borneo (East Kalimantan), Indonesia; Siboga Expedition collection 38. Type designated by Adey in Adey & Lebednik (1967: 32). Previous references to typification were by Dawson 1960: 28 (as Hydrolithon), Adey & Lebednik 1967: 32 (as Goniolithon), Adey 1970: 11 (as Hydrolithon), Adey et al. 1982: 26 (as Hydrolithon), Penrose & Woelkerling 1988: 161, 1992: 83 (as Hydrolithon) and Verheij & Woelkerling 1992: 284 (as Lithophyllum). Isolectotype material also exists in TRH (Siboga Expedition collections 57 and 74) and L (see Woelkerling 1993).

Synonyms

Homotypic synonyms:

Goniolithion reinboldii (Weber van Bosse & Foslie in Foslie) Foslie 1905a: 7 (see also Weber-van Bosse 1904: 5; De Toni 1905: 1801; Mazza 1917: 194-197; Printz 1929: 31; Hackett 1977: 18).

Porolithon reinboldii (Weber van Bosse & Foslie in Foslie) Lemoine 1911: 166.

Spongites reinboldii (Weber van Bosse & Foslie in Foslie) Penrose & Woelkerling 1988: 173 (see also Kalugina-Gutnik et al. 1992: 17; Titlyanova et al. 1992: 43 [as *Spongines reindoldii*]).

Etymology

'*reinboldii*', named after German phycologist T. Reinbold.

Description of Type

Habit and Vegetative Structure

The isolectotype material from TRH (Siboga Expedition collections 57 and 74) was examined during this study (Pl. 31, Fig. 1). Both specimens are free-living rhodoliths. The fragment marked S.E. 57 is the smaller of the two and measures roughly 50-55 mm in diameter. The larger of the two fragments (marked S.E. 74) measures roughly 70-85 mm in diameter. The specimens are both lumpy with more-or-less rounded, knobbly protuberances that measure up to 7 mm in length X 12 mm in diameter. Protuberances are dense and tightly packed. The thallus is adherent, measuring 1700-2400 µm thick in crustose areas. No margins have been observed. The cell surface (SEM) is neither of the *Phymatolithon*- nor the *Leptophytum*-type (Pl. 32, Fig. 2), but differs from both in that the outer surface is thick and rounded, possessing a minute central pore does exist (see Chamberlain 1990).

The thallus is dimerous, consisting of a single layer of basal filaments from which arise the erect filaments that make up most of the thallus (Pl. 32, Fig. 5; Pl. 34, Figs 14-17). Cells of the basal filaments are book-shaped (Pl. 34, Figs14-17). In primary-filament view, cells of the basal filaments are more-or-less square, and measure 16-41 µm long X 12-36 µm in diameter. In filament cross sections, basal cells are rectangular to elongate, and measure 16-41 µm long X 6-12 µm in diameter.

Cells of erect filaments are strongly horizontally arranged (Pl. 34, Fig. 13) due to extensive connections by broad cell fusions. This phenomenon appears to increase with depth in the thallus. In their unfused, uninflated state, cells of the erect filaments are square to elongate and measure 7-24 µm long X 5-11 µm in diameter. When the cells of the erect filaments fuse, they are typically spherical to elongate, and measure 16-50 µm long X 12-29 µm in diameter. Secondary pit connections were not seen. Subepithallial initials are square to elongate (Pl. 32, Figs 3 & 4; Pl. 34, Fig. 12), and measure 10-21 µm long X 6-14 µm in diameter. Epithallial cells (Pl. 32, Figs 3 & 4; Pl. 34, Fig. 12) are squat to elliptical, occur singly, and measure 5-7 µm long X 7-14 µm in diameter. Trichocytes are bottle-shaped and common at the thallus surface and occur singly or paired (Pl. 32, Fig. 4; Pl. 34, Fig. 11). Trichocytes (except pairs) are separated from one another by the cells of one or generally more, normal erect filaments and trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes measure 25-50 µm long X 17-26 µm in diameter. They are often overgrown and buried within the thallus.

Reproduction

The type lacks gametangial material.

Sporangial conceptacles are slightly raised above the thallus surface, measuring 270-650 µm in external diameter (Pl. 33, Figs 7-9; Pl. 35, Figs 18 & 19). Their chambers (Pl. 33, Figs 6 & 9; Pl. 35, Figs 18 & 19) are elliptical and measure 200-270 µm in diameter X 125-175 µm high, with the roof 43-68 µm (4-5 cells; incl. epithallial cell) thick (Pl. 33, Fig. 10; Pl. 35, Figs 20 & 21). The conceptacle floor is flush with the surrounding thallus surface to 9 cells below the thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 33, Fig. 10; Pl. 35, Figs 20 & 21). The pore is slightly sunken dorsally (Pl. 33, Fig. 10; Pl. 35, Fig. 21) and the pore canal also narrows dorsally, and is lined by a single elongate cell (oriented more-or-less vertically) plus an epithallial cell that tilts slightly into the pore, giving it its tapered appearance. The pore-canal is typically funnel-shaped measuring c. 18 µm at its apex and c. 31 µm at its base. There were no signs of a central columella. Zonately divided tetrasporangia are plump (Pl. 35, Fig. Insert), and become spherical and almost fill the chamber when mature, measuring 94-140 µm long X 34-94 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 33, Fig. 6; Pl. 35, Fig. 18), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Description of representative specimens

Representative specimens examined

Fiji: Dravuni, Great Astrolabe Reef (D Keats, 2.vi.1994, UWC: 94/1041); Fish Patch, Suva Barrier Reef (D Keats, 5.viii.1994, UWC: 94/1150; 5.x.1994, UWC: 94/1244, 3.xii.1995, UWC: 95/1560); Nukalau Island, Suva Lagoon (D. Keats, 8.xi.1994, UWC: 94/1264; 5.xii.1994, UWC: 94/1382); Suva Lagoon (D Keats, 13.xi.1999, UWC: 99/FJ-01).

Habitat and Phenology

Hydrolithon reinboldii occurs attached to coral reef substrata on the outer side of windward reefs, leeward reefs, and lagoonal patch reefs, but is most abundant encrusting shells, pieces of coral, and forming rhodoliths in the rubble zone of windward reefs at c. 10-15 m depth. It also occurs intertidally on wave-exposed areas of some reefs (Keats pers. comm.).

Distribution

Australia (Penrose & Woelkerling 1992; Verheij 1993, 1994; Ringeltaube & Harvey 2000; Littler & Littler 2003), Borneo (Lemoine 1911; Adey et al. 1982), Caroline Islands (Lemoine 1911), Comores (Segonzac 1984; Silva et al. 1996), China (Zhang & Zhou 1978), Djibouti (Segonzac 1984), El Salvador (Adey et al. 1982), French Polynesia (Payri et al. 2000, Littler & Littler 2003), Fiji (Littler & Littler 2003; This study), Guam (Gordon et al. 1976; Adey et al. 1982), Hawaii (Adey et al. 1982), India (Adey et al. 1982; Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Indonesia (Foslie 1901b, 1909; Penrose & Woelkerling 1992; Verheij 1993, 1994; Silva et al. 1996), Japan (Baba 1987; Iryu & Matsuda 1988; Yoshida 1998), Kenya (Silva et al. 1996), Laccadive Islands (Lemoine 1911; Adey et al. 1982; Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Maldives (Lemoine 1911; Adey et al. 1982; Krishnamurthy & Jayagopal 1987; Silva et al. 1996), Mauritius (Lemoine 1911; Segonzac 1984; Silva et al. 1996), Réunion (Segonzac 1984; Silva et al. 1996), Mexico (Revillagigedo Islands - Pacific) (Dawson 1960; Adey et al. 1982), Papua New Guinea (Lemoine 1911), Philippines (Adey et al. 1982), Seychelles (Segonzac 1984; Silva et al. 1996; Kalugina-Gutnik et al. 1992; Titlyanova et al. 1992), Samoa (Foslie 1901b; Lemoine 1911), South Sandwich Islands (Lemoine 1911), Sri Lanca (Segonzac 1984; Silva et al. 1996), Tanzania (Zanzibar) (Foslie 1901b; Lemoine 1911; Segonzac 1984; Silva et al. 1996), Timor (Adey et al. 1982), Viet Nam (Adey et al. 1982).

Habit and Vegetative Structure

Plants are generally adherent on coral rock, dead coral skeletons, shells, or form free-living rhodoliths (Pl. 36, Fig. 1) (Keats pers. comm.). Thalli measure up to at least 100 mm in diameter and 5 mm thick. Thalli are generally lumpy with more-or-less rounded, knobbly protuberances that measure up to 9 mm in length X 10 mm in diameter. Protuberances are dense and tightly packed. The margin is adherent, entire to lobed, and it lacks orbital ridges. The surface is irregularly tesselate, and commonly has white scales of sloughing epithallial cells. The cell surface (SEM) is neither of the Phymatolithon- nor the Leptophytum-type (Pl. 37, Figs 2 & 3). It often, however, appears Leptophytum-type after sloughing has occurred (Pl. 37, Fig. 2). Plants are usually deep lavender, with a matt and chalky texture.

The thallus is dimerous, consisting of a single layer of basal filaments from which arise the erect filaments that make up most of the thallus (Pl. 37, Figs 5 & 7; Pl. 39, Figs 12, 16 & 17). Cells of the basal filaments are book-shaped (Pl. 37, Fig. 7; Pl. 39, Figs 12, 16 & 17). In primary-filament view, cells of the basal filaments are more-or-less square, and measure 10-42 µm long X 12-36 µm in diameter. In filament cross sections, basal cells are rectangular to elongate, and measure 10-42 µm long X 6-12 µm in diameter. Cell fusions are common (Pl. 37, Fig. 7; Pl. 39, Fig. 17). Thalli rarely become secondarily monomerous, and when they do it is probably in response to wound healing.

Cells of erect filaments are strongly horizontally arranged (Pl. 37, Fig. 5; Pl. 39, Figs 13 & 15) due to extensive connections by broad cell fusions. This phenomenon appears to increase with depth in the thallus. In their unfused, uninflated state, cells of the erect filaments are square to elongate and measure 7-24 µm long X 5-12 µm in diameter. When the cells of the erect filaments fuse, they are typically spherical to elongate, and measure 16-50 µm long X 12-31 µm in diameter. Secondary pit connections were not seen. Subepithallial initials are square to elongate (Pl. 37, Fig. 6; Pl. 39, Fig. 14), and measure 9-24 µm long X 6-14 µm in diameter. Epithallial cells (Pl. 37, Fig. 6; Pl. 39, Fig. 14) are squat to elliptical, occur singly (sometimes 2 when shedding), and measure 5-8 µm long X 6-14 µm in diameter. Trichocytes are bottle-shaped and common at the thallus surface and occur singly or in pairs (Pl. 37, Figs 4 & 6; Pl. 39, Fig. 14). Trichocytes (except pairs) are separated from one another by the cells of one or generally more, normal erect filaments and trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes measure 25-50 µm long X 15-26 µm in diameter. They are often overgrown and buried within the thallus.

Protuberances are radially organised, with a central core of filaments composed of elongate cells, from which radiate out filaments composed of cells similar to those of the erect filaments of crustose areas. Cells of filaments within protuberances commonly show strong layering.

Reproduction

Gametangial material have not been seen.

Sporangial conceptacles are slightly raised above the thallus surface, measuring 190-900 µm in external diameter (Pl. 38, Figs 8-10; Pl. 40, Figs 18 & 19). Their chambers are elliptical (Pl. 38, Fig. 10; Pl. 40, Figs 18 & 19) and measure 160-500 µm in diameter X 90-175 µm high, with the roof 37-68 µm (4-5 cells; incl. epithallial cell) thick (Pl. 38, Fig. 11; Pl. 40, Fig. 19). The conceptacle floor is flush with the surrounding thallus surface to 9 cells below the thallus surface. The roof is formed from filaments interspersed among the sporangia and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 38, Fig. 11; Pl. 40, Fig. 21). The pore canal narrows dorsally, and is lined by a single elongate cell (oriented more-or-less vertically) plus an epithallial cell that tilts slightly into the pore, giving it its tapered appearance. The pore is sunken and the pore-canal is typically funnel-shaped (Pl. 38, Fig. 11; Pl. 40, Fig. 21) measuring c. 18 μm at its apex and c. 31 μm at its base. There were no signs of a central columella. Zonately divided sporangia develop across the conceptacle floor. Tetrasporangia are plump, and become spherical and almost fill the chamber when mature (Pl. 40, Fig. 20), measuring 68-161 μm long X 27-143 μm in diameter. Bisporangia, measuring 62-124 μm long X 43-105 μm in diameter, were also seen (Pl. 40, Fig. insert). Sporangial conceptacles often become buried in the thallus (Pl. 38, Fig. 10; Pl. 40, Fig. 18), and often contain apparently viable sporangia. Although not common, infilled conceptacles have been observed.

Key features

Hydrolithon reinboldii is characterised by the following **combination** of characters: 1) thallus thick, adherent, often protuberant, also occurring as free-living rhodoliths with an obviously tesselate surface; 2) primary thallus dimerous; 3) has a single basal layer of non palisade cells; 4) cells of erect filaments are strongly horizontally arranged due to extensive connections by broad cell fusions; 5) sporangial conceptacles that are only slightly raised above the thallus surface; 6) trichocytes present, both at the surface and immersed in the thallus, commonly occurring singly and in pairs; 7) trichocytes quite often separated by the cells of normal erect filaments; 8) the sporangial conceptacle pore is sunken; 9) the base of sporangial conceptacle pore canals consistently lined by a ring of conspicuous, enlarged, domed cells; 10) the enlarged cell in the sporangial pore canal subtends a single epithallial cell that tilts slightly into the pore and gives it a tapered appearance in vertical section i.e. the sporangial conceptacle pore canal is more-or-less funnel shaped; 11) the sporangial conceptacle roof is formed from filaments interspersed among the sporangia and *not* peripheral to them; 12) the sporangial pore canal *not* usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 13) the tetrasporangial conceptacle roof is commonly 4-5 cells thick; 14) the sporangial conceptacle floor is commonly 0-9 cells below the surrounding thallus surface.

Remarks

Hydrolithon reinboldii, the type of the genus *Hydrolithon*, has been the subject of a number of studies (e.g. Dawson 1960; Gordon et al. 1976; Adey et al. 1982; Krishnamurthy & Jayagopal 1987; Penrose & Woelkerling 1988). All earlier reports of this species, however, generally dealt only with vegetative characters. It was not until Penrose & Woelkerling's (1992) reappraisal, that the sporangial conceptacle anatomy and roof development in *Hydrolithon reinboldii* was seen as an important character separating *Hydrolithon* (sensu stricto) from *Spongites* (sensu stricto). Similarly, this study has opted to describing all features possible in case they too would be useful as diagnostic features.

Descriptions of taxa in alphabetical order of their basionym

Basionym

Goniolithon boergesenii Foslie 1901a: 19

Current Placement/Name

Hydrolithon boergesenii (Foslie) Foslie 1909: 56

Refer to Paper 1 [*A revision and characterization of the species of nongeniculate coralline algae previously ascribed to the now defunct genus* Porolithon *(Corallinales, Rhodophyta)*] for the description of Hydrolithon boergesenii.

Basionym

Goniolithon breviclavium Foslie 1907a: 20

Pl. 1-4, Figs 1-16.

Current Placement/Name

H. breviclavium (Foslie) Foslie 1909: 56 (see also Adey 1970: 11; Adey et al. 1982: 26)

Holotype

TRH. Honolulu, Oaha, Hawaii, USA; unnumbered. Previous references to typification were by Adey & Lebednik 1967: 30 (as Goniolithon), Adey 1970: 11 (as Hydrolithon), Adey et al. 1982: 26 (as Hydrolithon), Woelkerling 1993: 44 (as Goniolithon).

Synonyms

Homotypic synonyms:

Spongites breviclavius ("Spongines braviclavium") Titlyanova et al. 1992: 43

Etymology

"breviclavium", brevi = short + clavi = club (Stearn 1973). Foslie (1907a) did not explain the origin of the epithet, but it presumably makes reference to the short, knobbly to warty protuberances that characterises this specimen.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype material housed at TRH (Pl 1, Fig. 1). The type fragments are adherent, measuring up to at least 950 µm thick. Thalli are warty to lumpy, bearing protuberances that are up to 9 mm long X up to 5 mm in diameter. Margins have not been seen. The cell surface (SEM) is both of the Phymatolithon- and the Leptophytum-type (Pl. 2, Figs 2 & 3). Fragments examined comprised of superimposing layers of thalli (Pl. 4, Fig. 14).

The thallus is dimerous, consisting of a single layer of basal filaments from which arise the erect filaments that make up most of the thallus (Pl. 2, Figs 4 & 7; Pl. 4, Figs 11 & 13). Cells of the basal filaments are squat to square (non-palisade) and measure 6-15 µm long X 10-29 µm in diameter. Cells of erect filaments are squat to rectangular, and measure 6-34 µm long X 6-30 µm in diameter. Secondary pit connections were not seen. Subepithallial initials are square to rectangular (Pl. 2, fig 5; Pl. 4, Fig. 12), and measure 11-24 µm long X 7-15 µm in diameter. Epithallial cells (Pl. 2, fig 5; Pl. 4, Fig. 12) are squat to elliptical, occur singly, and measure 5-10 µm long X 6-15 µm in diameter. Trichocytes are rare at the thallus surface and occur singly or in groups of 2-3 (Pl. 4, Fig. 12). Trichocytes (except groups) are separated from one another by the cells of one or generally more, normal erect filaments and trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes measure 19-37 µm long X 12-19 µm in diameter. Trichocytes become overgrown and buried within the thallus. Cell fusions are common throughout the thallus (Pl. 2, Figs 5 & 6; Pl. 4, Fig. 12).

Reproduction

Type fragments lacked gametangial material.

Sporangial conceptacles are raised well above the thallus surface (Pl. 3, Figs 7 & 8; Pl. 4, Figs 14 & 15), and typically occur along the sides and apexes of the protuberances. Sporangial conceptacles are huge and measure 950-1150 µm in external diameter. Their chambers are elliptical to bean-shaped (Pl. 3, Fig. 8; Pl. 4, Figs 14 & 15) and measure 400-575 µm in diameter X 175-235 µm high, with the roof 90-135 µm (8-9 cells, 13-15 along the pore; incl. epithallial cell) thick. The conceptacle floor is flush with the surrounding thallus surface to only 3 cells below the thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from peripheral roof filaments (Pl. 4, Fig. 16). These cells protrude into the pore canal as papillae, and are oriented more-or-less parallel to the roof surface (Pl. 3, Fig 9). There is a small central columella present (giving the conceptacle chamber its bean-shape) (Pl. 4, Fig. 15). Zonately divided tetrasporangia are located peripherally in the conceptacle chamber and measure 78-134 µm long X 28-53 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 4, Fig. 14), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Distribution

Hawaiian Islands (Foslie 1907a; Adey et al. 1982), Seychelles (Titlyanova et al. 1992; Silva et al. 1996), Tropical Pacific and Indian Ocean (Littler & Littler 2003).

Key features

Goniolithon breviclavium is characterised by the following **combination** of characters: 1) thallus thick, adherent, possessing warty to lumpy protuberances; 2) thallus dimerous; 3) has a single basal layer of non palisade cells; 4) tetrasporangial conceptacles that are raised well above the rest of the thallus surface; 5) trichocytes rare, occurring both at the surface and immersed in the thallus, occurring singly or in groups of 2-3; 6) trichocytes quite often separated by the cells of normal erect filaments; 7) the base of tetrasporangial conceptacle pore canals not lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments peripheral to the conceptacle chamber and not from filaments interspersed among the sporangia; 9) the tetrasporangial pore canal is lined by narrow filaments that tilt into the pore canal, are orientated more-or-less parallel to the roof surface, and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is commonly 8-9 cells thick (13-15 cells along the pore); 11) the tetrasporangial conceptacle floor is commonly flush with the surrounding thallus surface.

Remarks

In their description of Hydrolithon breviclavium, Adey et al. (1982: 26) make no mention as to why Goniolithon breviclavium was transferred to the genus Hydrolithon. They do, however, make mention of the apparent differences in the epithallial cell anatomy between the genus Hydrolithon and Neogoniolithon arguing that taxa belonging to Hydrolithon bear thickenings on the outer tangential walls of their epithallial cells, and lack internal cells wall projections. Adey (1970: 8) also considered Neogonioithon to be characterised by, among other features, the presence of a monomerous ("multilayered hypothallium") thallus in contrast with the dimerous ("single-layered hypothallium") thallus of Hydrolithon (Adey 1970: 11). It is possible that both the epithallial cell anatomy and the thallus construction (although not specifically stated) may have led Adey et al. (1982) to the conclusion that Goniolithon breviclavium should be classified as Hydrolithon breviclavium.

The tetrasporangial roof development in Goniolithon breviclavium appears to be that of the type found in Spongites rather than Hydrolithon (sensu Penrose & Woelkerling 1992). Titlyanova et al. (1992: 43), studying the algae of the Seychelles, had already come to this conclusion. Their intended combination, however, is invalid since they did not cite the basionym and therefore failed to satisfy Art 33.2 of the Code. This taxon should therefore be referred to as Spongites breviclavius (Foslie) Maneveldt & Keats comb. nov.

Basionym

Goniolithon improcerum Foslie & Howe in Foslie 1907b: 24

Current Placement/Name

Hydrolithon improcerum (Foslie & Howe) Foslie 1909; 55 (see also Townsend & Adey 1990: 99; Penrose 1996: 258)

Refer to Paper 1 [*A revision and characterization of the species of nongeniculate coralline algae previously ascribed to the now defunct genus Porolithon (Corallinales, Rhodophyta)*] for the description of Hydrolithon improcerum.

Basionym

Lithophyllum consociatum Foslie 1905b: 15 (see also Adey & Lebednik 1967: 24)

Pl. 5-8, Figs 1-15.

Current Placement/Name

Spongites discoideus (Foslie) D. Penrose & Woelkerling (1988: 173)(as "discoidea") (see also Chamberlain 1994b: 148)

Holotype

TRH. Royal Sound, Kerguelen; unnumbered. Previous references to typification were by Adey & Lebednik 1967: 24 (as Lithophyllum), Adey 1970: 12 (as Pseudolithophyllum), Mendoza & Cabioch 1986: 178 (as Hydrolithon), Ricker 1987: 178 (as Pseudolithophyllum), Woelkerling 1993: 62 (as Lithophyllum).

Synonyms

Homotypic synonyms:

Lithophyllum consociatum forma connata Foslie 1907b: 28 (see also Printz 1929: Pl. 59);

Pseudolithophyllum consociatum (Foslie) Lemoine 1913: 48 (see also Adey 1970: 12; Ricker 1987: 178)

Hydrolithon consociatum (Foslie) Mendoza 1979: 8 (see also Mendoza & Cabioch 1986: 178; Mendoza et al. 1996: 28)

Heterotypic synonyms:

Lithophyllum discodeum Foslie 1900b: 73

Pseudolithophyllum discoideum (Foslie) Lemoine 1913: 46

Hydrolithon discoideum (Foslie) Mendoza & Cabioch 1984: 148 (see also Mendoza & Cabioch 1986: 173)

Lithophyllum decipiens f. subantarcticum Foslie 1906: 18 (‘subantarctica’)

Lithophyllum subantarcticum (Foslie) Foslie 1907a: 23 (see also Adey & Lebednik 1967: 17; Printz 1929: Pl. 53)

Pseudolithophyllum subantarcticum (Foslie) Adey 1970: 14

Hydrolithon subantarcticum (Foslie) Mendoza & Cabioch 1986: 180

Lithothamnion mangini Lemoine 1913: 18

Lithophyllum atalayense Lemoine 1920a: 13

Hydrolithon atalayense (Lemoine) Mendoza 1979: 6

Etymology

“consociatum”, consociatus = united, closely associated, connected (Stearn 1973). Foslie (1905b) did not explain the origin of the epithet, but it presumably makes reference to the irregularly low fused, compact protuberances that characterises this species.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype fragments housed at TRH (Pl. 5, Figs 1 & 2). The thallus is thick, adherent and warty, producing irregularly low fused, compact protuberances. Protuberances typically measure 12 mm long X up to 6 mm in diameter. The cell surface (SEM) is of the Phymatolithon-type (Pl. 6, Fig. 2). The surface texture is matt and coarse.

No lower regions of the thallus were observed and therefore it was impossible to determine whether the thallus is monomerous or dimerous although Mendoza & Cabioch (1986) reports a dimerous thallus construction for this species. Cells of the erect filaments are square to elongate and measure 6-19 µm long X 6-11 µm in diameter. Cell fusions are abundant (Pl. 6, Fig. 5). Secondary pit connections were not seen. Trichocytes were not observed either at the surface, or buried in the thallus although Mendoza & Cabioch (1986) reported rare solitary trichocytes. Subepithallial initials are elongate (Pl. 6, Fig. 5; Pl. 8, Fig. 12), and measure 12-27 µm long X 4-9 µm in diameter. Epithallial cells (Pl. 6, Fig. 5; Pl. 8, Fig. 12) are squat to elliptical and measure 4-7 µm long X 5-9 µm in diameter, and occur in 2-4 cell layers (mostly 3-4, up to 5 when shedding).

Reproduction

Type fragments lacked gametangial material

Tetrasporangial conceptacles are flush to slightly sunken below the thallus surface, measuring 160-425 µm in external diameter (Pl. 7, Figs 6-8; Pl. 8, Fig. 13). Their chambers are elliptical to bean-shaped (Pl. 7, Figs 7, 8 & 10; Pl. 8, Fig. 13), and measure 200-315 µm in diameter X 85-125 µm high, with the roof 50-90 µm (5-9 cells; incl. epithallial cell) thick. The conceptacle floor is located 14-20 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from peripheral roof filaments (Pl. 8, Fig. 14). These cells protrude into the pore canal as papillae, and are oriented more-or-less parallel to the roof surface (Pl. 7, Fig. 11; Pl. 8, Fig. 15). There is a central columella present (giving the conceptacle chamber its bean-shape) (Pl. 7, Fig. 8), and the zonately divided tetrasporangia are located peripheral to it (Pl. 7, Fig. 9). Sporangia measure 50-69 µm long X 19-25 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus

(Pl. 7, Fig. 7), and often contain apparently viable sporangia. Both infilled and open conceptacles have not been observed.

Distribution

Argentina & its territories (Falkland Islands, Patagonia, Tierra del Fuego, Staten Island, Islas Crozet, Islas Orcadas del Sur, Arctic Peninsula) (Foslie 1900b, 1906; Lemoine 1913, 1920a; Mendoza 1979; Mendoza & Cabioch 1984, 1986; Chamberlain 1994b; Mendoza et al. 1996), Australia (Macquarie Island) (Ricker 1987; Chamberlain 1994b), Kerguelen (Foslie 1905b; Chamberlain 1994b), Namibia (Chamberlain 1994b), South Africa (Chamberlain 1994b).

Key features

Lithophyllum consociatum is characterised by the following **combination** of characters: 1) thallus thick, adherent and warty, producing irregularly low fused protuberances; 2) thallus dimerous; 3) has a single basal layer of non palisade cells; 4) tetrasporangial conceptacles that are flush to slightly sunken below the rest of the thallus surface; 5) trichocytes absent or rare? ; 6) the base of tetrasporangial conceptacle pore canals not lined by a ring of conspicuous, enlarged, domed cells; 7) the tetrasporangial conceptacle roof is formed from filaments peripheral to the conceptacle chamber; 8) the tetrasporangial pore canal is lined by narrow filaments that tilt into the pore canal, are orientated more-or-less parallel to the roof surface, and create the appearance of papillae, 9) the tetrasporangial conceptacle roof is commonly 5-9 cells thick; 10) the sporangial conceptacle floor is commonly 14 - 20 cells below the surrounding thallus surface.

Remarks

From the description of the type of Lithophyllum consociatum, it is evident that this taxon does not belong within the genus Hydrolithon. This species lacks all the characters diagnostic of Hydrolithon. Instead, from the orientation of the tetrasporangial conceptacle roof filaments, it appears that this species belongs within the genus Spongites Kützing (1841: 30). Recent work by Y.M. Chamberlain (1994b: 148) has suggested that Lithophyllum consociatum is conspecific with Spongites discoideus (Foslie) D. Penrose & Woelkerling (1988: 173)(as "discoidea"). Lithophyllum consociatum does, however, not have the typical discoid appearance of Spongites discoideus. Chamberlain (1994b) did state though that Spongites discoideus produces discoid thalli through secondary growth that finally matures into crested protuberant plants. Lithophyllum consociatum may be such a mature plant. Mendoza & Cabioch (1986) did, however, find specimens of Hydrolithon consociatum that bore the discoid thalli representative of Spongites discoideus.

In their investigations, Mendoza & Cabioch (1986) recognised distinct patterns of roof formation of the sporangial conceptacles from various genera. What Mendoza & Cabioch (1986: 171) had classified as roof formation types Porolithon and Hydrolithon are now generally accepted to be that distinctive of the genus Spongites (development of the sporangial conceptacle roof from peripheral roof filaments) and Pneophyllum (development of the sporangial conceptacle roof from interspersed cavity cells and filaments surrounding the sporangial initials) respectively. Also, from Mendoza and Cabioch's (1986: 170, Fig A) description of Lithophyllum consociatum, the development of the sporangial conceptacle roof is clearly from interspersed cavity cells and filaments surrounding the sporangial initials. This implies that Lithophyllum consociatum belongs within the genus Pneophyllum, and not Spongites.

This scenario now becomes complicated! On the one hand, Lithophyllum consociatum is identical in morphology and anatomy to Spongites discoideus (Chamberlain 1994b: 148). On the other hand, Lithophyllum consociatum's sporangial conceptacle roof development is from interspersed cavity cells and filaments surrounding the sporangial initials, making it a Pneophyllum. As the use of reproductive anatomy is now widely considered a principal feature, it must be concluded that Lithophyllum consociatum belongs within the genus Pneophyllum and should be referred to as Pneophyllym consociatum (Foslie) Maneveldt & Keats comb. nov. despite its close (morphological) affinity to Spongites discoideus.

Basionym

Lithophyllum craspedium Foslie 1900a: 26

Current Placement/Name

Hydrolithon craspedium (Foslie) P. Silva in Silva et al. 1996: 235

Refer to Paper 1 [*A revision and characterization of the species of nongeniculate coralline algae previously ascribed to the now defunct genus Porolithon (Corallinales, Rhodophyta)*] for the description of Hydrolithon craspedium.

Basionym

Lithophyllum decipiens forma caribaeum Foslie 1906: 18 (‘caribaea’)

Pl. 9-11, Figs 1-11.

Current Placement/Name

Neogoniolithon caribaeum (Foslie) Adey 1970: 8 (see also Silva et al. 1996: 263)

Lectotype

TRH. The harbour, St. Thomas Island, US Virgin Islands; unnumbered. Previous references to typification were by Adey & Lebednik 1967: 14 (as Lithophyllum), Masaki 1968: 31 (as Lithophyllum), Adey 1970: 8 (as Neogoniolithon), Woelkerling 1993: 48 (as Lithophyllum).

Synonyms

Homotypic synonyms:

Lithophyllum caribaeum (Foslie) Foslie 1907a: 22 (see also Foslie 1909: 11; Printz 1929: Pl. 53; Adey & Lebednik 1967: 4; Woelkerling 1993: 48)

Heteroderma caribaeum (Foslie) Segonzac 1984: 101

Etymology

‘decipiens’ means deceiving (used of a species closely resembling another) (Stearn 1973); ‘caribaea’, Foslie (1906) did not explain the origin of the epithet, but it presumably makes reference to the Caribbean Sea from where this specimen was collected.

Description of Type

Habit and Vegetative Structure

The following description is based on the lectotype material housed at TRH (Pl. 9, Fig. 1). The type fragments are thin and adherent, measuring only 74-240 µm thick. Thalli are flat and smooth, lacking protuberances, and have adherent margins that are entire to lobed, but lack orbital ridges. The cell surface (SEM) is mostly of the <u>Phymatolithon</u>-type (Pl. 10, Fig. 2).

The thallus is monomerous and dorsiventrally organised (Pl. 10, Fig. 3; Pl. 11, Fig. 9). The medullary filaments comprise 12-50% of the thallus thickness and consist of a central plumose (non-coaxial) core with cells that are square to rectangular and measure 3-16 µm long X 2-8 µm in diameter. Cell fusions are abundant. Secondary pit connections have not been seen.

The cortical filaments comprise 50-88% of the thallus thickness (Pl. 10, Fig. 3) with cells that are small and bead-like, and measure 3-7 µm long X 3-7 µm in diameter. Cell fusions are abundant (Pl. 10, Fig. 4). Secondary pit connections were not seen. Buried trichocytes have not been seen. Subepithallial initials are square to rectangular (Pl. 10, Fig. 4; Pl. 11, Fig. 8), and measure 4-11 µm long X 4-6 µm in diameter. Epithallial cells (Pl. 10, Fig. 4; Pl. 11, Fig. 8) are squat to elliptical and measure 2-6 µm long X 3-7 µm in diameter, and occur singly (up to 2 when shedding). Squarish to elongate trichocytes occur singly (rarely paired) at the thallus surface (Pl. 10, Fig. 4; Pl. 11, Fig. 8). Trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes measure 8-27 µm long X 5-10 µm in diameter. No buried trichocytes have been observed.

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are flush to only slightly raised above the rest of the thallus surface (Pl. 10, Figs 5 & 6; Pl. 11, Fig. 10), measuring 73-155 µm in external diameter. Their chambers are elliptical to spherical (Pl. 10, Fig. 6; Pl. 11, Fig. 10), and measure 61-85 µm in diameter X 37-66 µm high, with the roof 10-17 µm (2-4 cells; mostly 3 cells incl. epithallial cell) thick, always comprising a single squat to elliptical to spherical epithallial cell, a single elongate meristematic cell, and 1-2 small inner cells (Pl. 10, Fig. 7; Pl. 11, Fig. 11). The elongate meristematic cell is typically 2.5-5X the length of the epithallial cell. The conceptacle floor is located 12-17 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 10, Fig. 7; Pl. 11, Figs 10 & 11). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. A central columella has not been observed for this specimen although sporangia are located peripherally in the conceptacle chamber. Zonately divided tetrasporangia measure 25-50 µm long X 6-34 µm in diameter. Bisporangial plants were not seen. Buried tetrasporangial conceptacles are rare and contain apparently viable sporangia; infilling has not been observed.

Distribution

Antilles (Lemoine 1964; Krishnamurthy & Jayagopal 1985), Bahamas (Lemoine 1964; Krishnamurthy & Jayagopal 1985), Canary Islands (Tenerife) (Lemoine 1964; Afonso-Carrillo et al. 1984; Haroun et al. 2002), Comores (Segonzac 1984; Silva et al. 1996), India (Tuticorin) (Krishnamurthy & Jayagopal 1985; Silva et al. 1996), Japan (Moheji) (Masaki 1968; Krishnamurthy & Jayagopal 1985), Mauritius (Segonzac 1984; Silva et al. 1996), Puerto Rico (Krishnamurthy & Jayagopal 1985), Réunion (Segonzac 1984; Silva et al. 1996), Seychelles

(Segonzac 1984), Sri Lanka (Segonzac 1984; Silva et al. 1996), US Virgin Islands (Foslie 1906; Krishnamurthy & Jayagopal 1985).

Key features

Lithophyllum caribaeum is characterised by the following **combination** of characters: 1) thallus thin, adherent, flat, lacking protuberances; 2) thallus monomerous; 3) medullary filaments plumose; 4) cells of cortical filaments are small and bead-like; 5) tetrasporangial conceptacles that are only slightly raised or flush with the thallus surface; 6) trichocytes occurring predominantly singly; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 9) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae; 10) the tetrasporangial conceptacle roof is usually only 3 cells thick, comprising a single squat to elliptical to spherical epithallial cell, a single elongate meristematic cell that is 2.5-5X the length of the epithallial cell, and a small inner cells; 11) the conceptacle floor is located 12-17 cells below the surrounding thallus surface.

Remarks

Lithophyllum caribaeum was transferred to the genus Neogoniolithon by Adey (1970: 8) because he considered Neogonioithon to be characterised by, among other features, the presence of a monomerous ("multilayered hypothallium") thallus as opposed to the dimerous ("single-layered hypothallium") thallus of Hydrolithon (sensu Adey 1970: 11). Since Adey's (1970) descriptions, both genera have undergone substantial revision and characterization based on this feature no longer holds. Lithophyllum caribaeum has undergone a single modern taxonomic revision since Adey's (1970) characterization of this species, this by Segonzac (1984: 101) who placed Lithophyllum caribaeum within the genus Heteroderma. We now know Herteroderma to be a heterotypic synonym for Hydrolithon.

From the description above, Lithophyllum caribaeum is clearly a Hydrolithon. The apparent development of the sporangial conceptacle roof and the presence of the enlarged cells lining the pore canal are all characters diagnostic of the genus Hydrolithon (sensu Penrose and Woelkerling 1992: 87). Lithophyllum caribaeum is therefore transferred to Hydrolithon and should be referred to as Hydrolithon caribaeum (Foslie) Maneveldt & Keats comb. nov. This species, however, has cortical filaments with very small, bead-like cells, substantially smaller than any Hydrolithon discussed thus far, a feature that may be of taxonomic significance at species level.

Masaki (1968: 31-32) also described a new form of Lithophyllum caribaeum that he called Lithophyllum caribaeum Foslie f. boreale Masaki f. nov. From Masaki's descriptions and diagrams, however, this species is not Lithophyllum caribaeum, but is in fact a Spongites closely related to S. yendoi (Foslie) Y. Chamberlain (1993: 102) and S. decipiens (Foslie) Y. Chamberlain (1993: 113). Lithophyllum caribaeum f. boreale may even be one or the other, but this analysis goes beyond the scope of the immediate research.

Basionym

Lithophyllum decipiens forma *subantarcticum* Foslie 1906: 18 (‘*subantarctica*’)

Pl. 12-15, Figs 1-14.

Current Placement/Name

Spongites discoideus (Foslie) D. Penrose & Woelkerling (1988: 173) (as “*discoidea*”) (see also Chamberlain 1994b: 148)

Lectotype

TRH. Mouth of Rio Grande, Tierra del Fuego, Argentina; unnumbered (designated by Adey in Adey & Lebednik 1967: 17). Previous references to typification were by Adey & Lebednik 1967:17 (as *Lithophyllum subantarcticum*), Adey 1970: 14 (as *Pseudolithophyllum subantarcticum*), Mendoza & Cabioch 1985: 258 (as *Hydrolithon subantarcticum*), Woelkerling 1993: 209 (as *Lithophyllum*).

Synonyms

Homotypic synonyms:

Lithophyllum subantarcticum (Foslie) Foslie 1907a: 23 (see also Adey & Lebednik 1967: 17; Printz 1929: Pl. 53)

Pseudolithophyllum subantarcticum (Foslie) Adey 1970: 14

Hydrolithon subantarcticum (Foslie) Mendoza & Cabioch 1985: 258 (see also Mendoza & Cabioch 1986: 180; Mendoza et al. 1996: 30)

Heterotypic synonyms:

Lithophyllum consociatum Foslie 1905b: 15 (see also Adey & Lebednik 1967: 24)

Lithophyllum consociatum forma connata Foslie 1907b: 28 (see also Printz 1929: Pl. 59);

Pseudolithophyllum consociatum (Foslie) Lemoine 1913: 48 (see also Adey 1970: 12; Ricker 1987: 178)

Hydrolithon consociatum (Foslie) Mendoza 1979: 8 (see also Mendoza & Cabioch 1986: 178; Mendoza et al. 1996: 28)

Lithophyllum discodeum Foslie 1900b: 73

Pseudolithophyllum discoideum (Foslie) Lemoine 1913: 46

Hydrolithon discoideum (Foslie) Mendoza & Cabioch 1984: 148 (see also Mendoza & Cabioch 1986: 173)

Lithothamnion mangini Lemoine 1913: 18

Lithophyllum atalayense Lemoine 1920a: 13

Hydrolithon atalayense (Lemoine) Mendoza 1979: 6

Etymology

'decipiens' means deceiving (used of a species closely resembling another) (Stearn 1973); 'subantarctica', because the specimen was obtained from the western part of the sub Antarctic region near Fuegia (Foslie 1906).

Description of Type

Habit and Vegetative Structure

The following description is based on the lectotype fragments housed at TRH (Pl. 12, Fig. 1 & 2). The type fragment is thin and adherent, measuring only 50-275 µm thick. Thalli are flat and smooth, lacking protuberances, and have adherent margins that are entire to lobed, but lack orbital ridges. The cell surface (SEM) is predominantly of the Leptophytum-types (Pl. 13, Fig. 3).

The thallus is dimerous (Pl. 13, Figs 4 & 6). The single basal layer of non-palisade cells are squarish, and measure 6-14 µm long X 9-14 µm in diameter. Cell fusions are abundant (Pl. 13, Figs 5 & 6). Secondary pit connections have not been seen.

The erect filaments form the bulk of the thallus (Pl. 13, Fig. 4). Cells of the erect filament are typically squat to square, and measure 4-11 µm long X 5-10 µm in diameter. Cell fusions are abundant (Pl. 13, Fig. 5). Secondary pit connections were not seen. Subepithallial initials are elongate (Pl. 13, Figs 4 & 5; Pl. 15, Fig. 12), and measure 11-16 µm long X 4-7 µm in diameter. Epithallial cells (Pl. 13, Figs 4 & 5; Pl. 15, Fig. 12) are squat to elliptical and measure 4-7 µm long X 5-7 µm in diameter, and occur in 2-4 cell layers (up to 5 when shedding). Trichocytes have not been seen although Mendoza & Cabioch (1986) report solitary trichocytes occurring very rarely.

Reproduction

Gametangial plants appear dioecious. Spermatangial conceptacles are small, measuring 130-260 µm in external diameter (Pl. 14, Fig. 9; Pl. 15, Fig. 13). Spermatangial conceptacle roofs are usually more-or-less flush to only slightly raised above the rest of the thallus. The conceptacle chamber is often wide and shallow to elliptical (Pl. 14, Fig. 9; Pl. 15, Figs 13 & 14), measuring 74-93 µm in diameter X 19-22 µm high, with the roof 20-25 µm thick. Spermatangial conceptacles are often seen buried in the thallus. Simple spermatangial systems are borne only on the floor of the conceptacle chamber (Pl. 15, Figs 13 & 14).

Carpogonial conceptacles have not been observed.

Carposporangial conceptacles have not been observed.

Tetrasporangial conceptacles have not been observed.

Distribution

Argentina & its territories (Falkland Islands, Patagonia, Tierra del Fuego, Staten Island, Islas Crozet, Islas Orcadas del Sur, Arctic Peninsula) (Foslie 1900b, 1906, Lemoine 1913, 1920a; Mendoza 1979; Mendoza & Cabioch 1984, 1986; Chamberlain 1994b; Mendoza et al. 1996), Australia (Macquarie Island) (Ricker 1987; Chamberlain 1994b), Kerguelen (Foslie 1905b; Chamberlain 1994b), Namibia (Chamberlain 1994b), South Africa (Chamberlain 1994b).

Key features

Lithophyllum subantarcticum is characterised by the following **combination** of characters: 1) thallus thin, adherent and smooth, lacking protuberances; 2) thallus dimerous; 3) has a single basal layer of non palisade cells; 4) spermatangial conceptacles that are flush to only slightly raised above the thallus surface; 5) trichocytes absent to rare?; 6) Spermatangial conceptacles bearing simple spermatangia restricted to the conceptacle floor.

Remarks

The type material of Lithophyllum subantarcticum simply does not have enough material (particularly tetrasporangial) to come to any form of conclusion. In their descriptions of plants of Hydrolithon subantarcticum collected from subantarctic and Antarctic zone Argentina, Mendoza & Cabioch (1986: 180) came to the conclusion that H. consociatum, H. decipiens, H. discoideum, H. falklandicum and H. subantarcticum were all distinct entities. Mendoza & Cabioch had apparently placed these taxa in *Hydrolithon* based on the earlier descriptions of the genus by Adey (1970). Since then, the genus *Hydrolithon* has undergone substantial revision and it is apparent from Mendoza & Cabioch's (1986) descriptions, that none of these taxa belong within the genus *Hydrolithon* (*sensu stricto* Penrose & Woelkerling 1992). In their conclusion, Mendoza & Cabioch state that the construction of the tetrasporangial conceptacle roofs in these taxa appear to be different from what had been described for other taxa belonging to, for example, *Porolithon*.

Furthermore, in Mendoza & Cabioch's (1986: Pl. 3, Fig. 3) depiction of *H. discoideum* and *H. subantarcticum*, both species occur side by side on a single pebble. The scenario looks remarkably similar to that of *Spongites discoideus* (Foslie) D. Penrose & Woelkerling (1988: 173) as described by Chamberlain (1994b: 148). Chamberlain (1994b: Fig. 26) depicted *S. discoideus* on a boulder in its two typical forms: one thin, smooth, immature form; and one thick, discoid, more mature protuberant form. Mendoza & Cabioch's (1986: Pl. 3, Fig.3) depiction is possibly the thin, smooth, immature form (as *H. subantarcticum*) and the thick, discoid, more mature protuberant form (as *H. discoideum*) of *Spongites discoideus* side by side. In her list of synonyms, Chamberlain (1994b) included *Lithophyllum subantarcticum* and *Lithophyllum consociatum* (and their derivatives) as taxonomic synonyms for *Spongites discoideus*. With this in mind, it is now possible to see why Chamberlain (1994b: 148) considered *Lithophyllum subantarcticum* synonymous with *Spongites discoideus*.

However, in their investigations, Mendoza & Cabioch (1986) recognised distinct patterns of roof formation of the sporangial conceptacles from various genera. What Mendoza & Cabioch (1986: 171) had classified as roof formation types *Porolithon* and *Hydrolithon* are now generally accepted to be that distinctive of the genus *Spongites* (development of the sporangial conceptacle roof from peripheral roof filaments) and *Pneophyllum* (development of the sporangial conceptacle roof from interspersed cavity cells and filaments surrounding the sporangial initials) respectively. Furthermore, from Mendoza and Cabioch's (1986: 170, Fig. A) description of Lithophyllum consociatum, the development of the sporangial conceptacle roof is from interspersed cavity cells and filaments surrounding the sporangial initials. This implies that Lithophyllum consociatum, and possibly also Lithophyllum subantarcticum, belongs within the genus Pneophyllum, and not Spongites (see Lithophyllum consociatum above).

Based on the descriptions of their vegetative anatomy, L. consociatum and L. subantarcticum appear to be conspecific. There is a remarkable similarity in the epithallial and subepithallial layers. Both taxa have 2-4 (up to 5 when shedding) distinctly squarish epithallial cell layers subtended by very elongate subepithallial initials. No taxa described thus far bear this striking combination of similarities. Besides these similarities, a number of others exist (see descriptions above) which has led me to conclude that these two taxa are conspecific. Lithophyllum consociatum Foslie (1904), having been described first, receives priority and L. subantarcticum (Foslie) Foslie (1907a) is therefore a heterotypic synonym of Pneophyllum consociatum (Foslie) Maneveldt & Keats comb. nov.

Basionym

Lithophyllum erosum Foslie 1906: 20 (see also Adey & Lebednik 1967: 16)

Pl. 16-18, Figs 1-14.

Current Placement/Name

Neogoniolithon erosum (Foslie) Adey 1970: 8

Holotype

TRH. Magenbay, St Thomas Island, US Virgin Islands; unnumbered. Previous references to typification were by Adey & Lebednik 1967: 16 (as Lithophyllum), Adey 1970: 8 (as Neogoniolithon), Woelkerling 1993: 85 (as Lithophyllum).

Synonyms

None!

Etymology

'erosum', erosus = erose, having an irregularly toothed or apparently gnawed margin (Stearn 1973). Foslie (1906) did not explain the origin of the epithet, but it presumably makes reference to the highly irregular nature of the margins.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype material housed at TRH (Pl. 16, Fig. 1). The type fragment is thin and adherent, measuring only 50-300 µm thick. Thalli are flat and smooth, lacking protuberances, and have adherent, highly irregular margins that are entire to lobed, but lack orbital ridges. The cell surface (SEM) is predominantly of the Phymatolithon-type (Pl. 17, Fig. 2).

The thallus is monomerous and dorsiventrally organised (Pl. 17, Figs 3 & 4; Pl. 18, Figs 8 & 10). The medullary filaments comprise 25-42% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 17, Fig. 4; Pl. 18, Fig. 10), with cells that are square to elongate and measure 7-31 µm long X 4-7 µm in diameter. Cell fusions are abundant (Pl. 17, Fig. 4; Pl. 18, Fig. 10). Secondary pit connections have not been seen.

The cortical filaments comprise 58-75% of the thallus thickness (Pl. 17, Fig. 3; Pl. 18, Fig. 8) with cells that are squat to rectangular and measure 5-11 µm long X 4-7 µm in diameter. Cell fusions are abundant (Pl. 17, Fig. 3; Pl. 18, Fig. 9). Secondary pit connections were not seen. Buried trichocytes have not been seen. Subepithallial initials are square to rectangular (Pl. 17, Fig. 3; Pl. 18, Fig. 9), and measure 3.7-12.4 µm long X 5-6 µm in diameter. Epithallial cells (Pl. 17, Fig. 3; Pl. 18, Fig. 9) are squat to elliptical and measure 4-6 µm long X 5-9 µm in diameter, and occur singly (up to 2 when shedding). Rectangular to elongate trichocytes occur singly at the thallus surface (Pl. 17, Fig. 3). Trichocyte chains typically comprise only 2 cells; a megacell, and a support cell. Individual trichocytes measure 19-27 µm long X 6-12 µm in diameter. No buried trichocytes have been observed.

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are flush to only slightly raised above the rest of the thallus surface (Pl. 17, Fig. 6; Pl. 18, Fig. 11), measuring 105-275 (340) µm in external diameter. Their chambers are elliptical to spherical (Pl. 17, Fig. 6; Pl. 18, Fig. 11) and measure 79-188 (202) µm in diameter X 49-78 (98) µm high, with the roof 19-37 µm thick; the roof is 2-4 (mostly 3) cells thick, always comprising a single squat to elliptical to spherical epithallial cell, a single elongate meristematic cell, and 1-2 small inner cells (Pl. 17, Fig. 7; Pl. 18, Figs 13 & 14). The elongate meristematic cell is typically 2.5-5X the length of the epithallial cell. The conceptacle floor is located 8-15 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 17, Fig. 7, Pl. 18, Fig. 14). The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. A central columella has not been observed for this specimen. Zonately divided tetrasporangia were, however, found to occur peripherally in the conceptacle chamber (Pl. 18, Fig. 12), measuring 34-62 µm long X 15-37 µm in diameter. Bisporangial plants were not seen. Buried tetrasporangial conceptacles have not been seen.

Distribution

US Virgin Islands (Foslie 1906).

Key features

Lithophyllum erosum is characterised by the following **combination** of characters: 1) thallus thin, adherent, flat, lacking protuberances; 2) thallus monomerous; 3) medullary filaments plumose; 4) tetrasporangial conceptacles that are only slightly raised or flush with the thallus surface; 5) trichocytes occurring singly only at the thallus surface; 6) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 7) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 8) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 9) the tetrasporangial conceptacle roof is usually only 3 cells thick, comprising a single squat to elliptical to spherical epithallial cell, a single elongate meristematic cell that is 2.5-5X the length of the epithallial cell, and a small inner cells; 10) the sporangial conceptacle floor is commonly 8-15 cells below the surrounding thallus surface.

Remarks

Lithophyllum erosum was transferred to the genus Neogoniolithon by Adey (1970: 8) because he considered Neogonioithon to be characterised by, among other features, the presence of a monomerous ("multilayered hypothallium") thallus as opposed to the dimerous ("single-layered hypothallium") thallus of Hydrolithon (sensu Adey 1970: 11). Since Adey's (1970) descriptions, both genera have undergone substantial revision and characterization based on this feature no longer holds. Lithophyllum erosum has never undergone any taxonomic revision since Adey's (1970) characterization of this species.

From the description above, Lithophyllum erosum is clearly a Hydrolithon. The apparent development of the sporangial conceptacle roof and the presence of the enlarged cells lining the pore canal are all characters diagnostic of the genus Hydrolithon (sensu Penrose and Woelkerling 1992: 87). The tetrasporangial conceptacle roof structure of Lithophyllum erosum is, however, identical to that of Lithophyllum caribaeum and based on this feature, I have come to the conclusion that Lithophyllum caribaeum and Lithophyllum erosum are heterotypic synonyms. Since Lithophyllum erosum (Foslie 1906: 20) was the first of the two taxa described at the species level, Lithophyllum erosum has priority and Lithophyllum caribaeum (Foslie 1907a: 22) is thus considered a heterotypic synonym of Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov.

The type of Lithophyllum erosum, however, has much larger cell dimensions than the type of Lithophyllum caribaeum. Also, the tetrasporangial conceptacle internal and external dimensions differ with very little overlap. Although this may not seem significant, it does pose the question as to the importance of complete reporting of all anatomical characters. Foslie (1906: 20), for example, although stating very clearly that these two taxa are closely related, still separated them solely on the dimensions of the cells (as perithallial cells) of their cortical filaments. According to Foslie (1906) L. erosum has predominantly vertically elongated cortical cells, while L. caribaeum has predominantly horizontally elongated cortical cells. It is now widely accepted that such differences used as sole characters are no longer valid (Woelkerling & Irvine 1986; Woelkerling & Campbell 1992; Woelkerling et al. 1993).

Basionym

Lithophyllum gardineri Foslie 1907a: 30-31 ("forma typica") (see also Foslie 1907c: 106-107, 1907d: 190-191; Gardiner 1907: fig 30; Foslie 1909: 44-45; Printz 1929: 34; Adey & Lebednik 1967: 48; Woelkerling 1993: 102-103)

Current Placement/Name

Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine 1993: 451 (forma gardineri) (see also Verheij 1993: 46-47, 1994: 106-107).

Refer to Paper 1 [*A revision and characterization of the species of nongeniculate coralline algae previously ascribed to the now defunct genus* Porolithon *(Corallinales, Rhodophyta)*] for the description of Hydrolithon gardineri.

Basionym

Lithophyllum marlothii forma falklandicum Foslie 1905b: 17 (‘falklandica’)

Pl. 19-22, Figs 1-13.

Current Placement/Name

Hydrolithon falklandicum (Foslie) Mendoza 1979: 10 (see also Mendoza & Cabioch 1986: 175; Mendoza et al. 1996: 32)

Lectotype

TRH. Port Louis, Falkland Islands; unnumbered (designated by Adey in Adey & Lebednik 1967). Previous references to typification were by Adey & Lebednik 1967: 17 (as Lithophyllum falklandicum), Adey 1970: 12 (as Pseudolithophyllum falklandicum), Mendoza 1979: 10, and Medoza & Cabioch 1986: 175 (as Hydrolithon falklandicum).

Synonyms

Homotypic synonyms:

Lithophyllum falklandicum (Foslie) Foslie 1906: 24 (see also Adey & Lebednik 1967: 17; Printz 1929: Pl. 54)

Pseudolithophyllum falklandicum (Foslie) Adey 1970: 12

Etymology

‘falklandica’ from the type locality in the Falkland Island group.

Description of Type

Habit and Vegetative Structure

The following description is based on the lectotype material housed at TRH (Pl. 19, Fig. 1). The type fragments are adherent, measuring up to at least 1000 µm thick. Thalli are warty to lumpy bearing numerous individual to closely packed, short terete protuberances. Protuberances typically measure 4 mm in length X 5 mm in diameter. The margins are adherent, entire to lobed, but lack orbital ridges. The cell surface (SEM) is predominantly of the Leptophyum-type (Pl. 20, Fig. 2). The surface texture is matt.

The thallus is primarily dimerous and secondarily monomerous (and dorsiventrally organised) (Pl. 21, Figs 5 & 6). In dimerous thalli, the basal cells are typically square to rectangular and measure 12-25 µm long X 9-21 µm in diameter. In monomerous thalli, the medullary filaments comprise 10-30 % of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 21, Figs 6 & 10), with cells that are square to rectangular and measure 7-25 µm long X 5-16 µm in diameter. Cell fusions are abundant (Pl. 21, Figs 9 & 10). Secondary pit connections have not been seen.

In monomerous thallis, the cortical filaments comprise the larger portion of the thallus thickness (Pl. 21, Fig. 6). Cells of cortical and erect filaments are squarish and measure 6-14 µm long X 6-12 µm in diameter. Cell fusions are abundant (Pl. 21, Fig. 8). Secondary pit connections were not seen. Subepithallial initials are square to rectangular, and measure 10-17 µm long X 6-14 µm in diameter. Epithallialcells (Pl. 21, Fig. 8) are squat to elliptical and measure 4-7 µm long X 5-12 µm in diameter, and occur in 1-3 cell layers (mostly 2-3 but up to 4 when shedding). Rectangular to elongate trichocytes are rare and occur at the thallus surface singly or in pairs (Pl. 21, Fig. 7). Trichocyte chains typically comprise only 2 cells; a megacell, and a support cell. Individual trichocytes measure 14-21 µm long X 7-12 µm in diameter. Buried trichocytes have not been observed.

Reproduction

Intact conceptacles were found, but whether these are sporangial or gametangial is unknown. The conceptacles are flush to only slightly raised above the rest of the thallus surface, measuring 300-500 µm in external diameter (Pl. 20, Fig. 4). Their chambers (Pl. 22, Figs 11 & 12) are elliptical and measure 170-305 µm in diameter X 75-110 µm high, with the roof 25-37 µm (4-5 cells; incl. epithallial cell) thick. The conceptacle floor is located 0-9 cells below the surrounding thallus surface. Hardly any intact conceptacles remain (all appear to have been shed – Pl. 20, Fig. 3) and it is difficult to speculate as to how the conceptacle roof was formed. Only two buried conceptacles were found (Pl. 22, Figs 11 & 12) and from the orientation of the roof filaments, it appears that the roof was formed from peripheral roof filaments (Pl. 22, Fig. 13). A central columella or sporangia have not been observed and it is questionable whether this material is sporangial. Conceptacles are both shed and buried in the thallus; infilled conceptacles have not been observed (Pl. 20, Fig. 3; Pl. 22, Figs 11 & 12).

Distribution

Argentina (Falkland Islands, Tierra del Fuego, Staten Island) (Foslie 1905b; Lemoine 1915, 1920a; Mendoza 1979; Mendoza & Cabioch 1986; Mendoza et al. 1996).

Key features

Lithophyllum falklandicum is characterised by the following **combination** of characters: 1) thallus thick, adherent, warty to lumpy, bearing numerous individual to closely packed, short terete protuberances; 2) thallus primarily dimerous and only secondarily monomerous; 3) in monomerous thallis, medullary filaments plumose; 4) tetrasporangial? conceptacles that are only slightly raised or flush with the thallus surface; 5) trichocytes rare, occurring singly or paired at the thallus surface; 6) trichocytes are separated by the cells of normal cortical filaments; 7) the base of tetrasporangial? conceptacle pore canals not lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial? conceptacle roof is formed from peripheral roof filaments and not from filaments interspersed among the sporangia; 9) the tetrasporangial? conceptacle roof is commonly 4-5 cells thick.

Remarks

In their studies of the corallines from Subantarctic and Antarctic Argentina, Mendoza & Cabioch (1986) came to the conclusion that five well-represented taxa namely, Lithophyllum consociatum Foslie, Lithophyllum discoideum Foslie, Lithophyllum falklandicum Foslie, Lithophyllum subantarcticum Foslie, and Hydrolithon decipiens (Foslie) Adey, were indeed all members of the genus Hydrolithon (sensu Adey 1970). They based these findings on morphological, anatomical and reproductive characters. Of particular note is that these authors had recognised distinct patterns of roof formation of the sporangial conceptacles from various genera. What Mendoza & Cabioch (1986: 171) had classified as roof formation types Porolithon and Hydrolithon are now generally accepted to be that distinctive of the genus Spongites (development of the sporangial conceptacle roof from peripheral roof filaments) and Pneophyllum (development of the sporangial conceptacle roof from interspersed cavity cells and filaments surrounding the sporangial initials) respectively.

Presently, beside *Lithophyllum falklandicum*, all the above taxa have been transferred to the genus *Spongites* Kützing (*sensu stricto*, Penrose & Woelkerling 1992) (see Chamberlain 1993, 1994b). Two of these taxa (*L. consociatum* and *L. subantarcticum*) have, however, been shown to possess a character diagnotic of *Pneophyllum* and not *Spongites*.

From the description of *Lithophyllum falklandicum* above, it cannot be said with a great degree of certainty that the conceptacles are those from sporangial material. However, Mendoza & Cabioch (1986) did show that the sporangial conceptacles were larger than either the Spermatangial or the female conceptacles; the conceptacles analysed in this study, are large. Therefore, if the conceptacles reported on above are sporangial, it suggests that *Lithophyllum falklandicum*, like the other four taxa reported on by Mendoza & Cabioch (1986), is in all likelihood not a member of the genus *Hydrolithon*. A modern and more thorough investigation into this group of taxa is thus required with reference to additional material from the type localities.

Basionym

Lithophyllum munitum Foslie & Howe 1906: 132 (see also Adey & Lebednik 1967: 20; Printz 1929: Pl. 56)

Pl. 23-25, Figs 1-9.

Current Placement/Name

Hydrolithon munitum (Foslie & Howe) Penrose in Womersley 1996: 263

Pl. 26-30, Figs 1-17.

Holotype

NY. Cave Cays, Exuma Chain, Bahamas; no. 4023 (designated by Adey in Adey & Lebednik 1967: 20). Previous references to typification were by Adey and Lebednik 1967: 20 (as *Lithophyllum*), Adey 1970: 9 (as *Neogoniolithon*). Isotype material also exists in TRH (Howe 4023), BM and US.

Synonyms

Homotypic synonyms:

Neogoniolithon munitum (Foslie & Howe) Adey 1970: 9

Etymology

'*munitum*', *munitus* = provided with, fortified, protected (Stearn 1973). Foslie & Howe (1906) did not explain the origin of the epithet. How this applies to *H. munitum* is unclear.

Description of Type

Habit and Vegetative Structure

The following description is based on the isotype material housed at TRH (Pl. 23, Fig. 1). The type fragments are generally thin and adherent, measuring up to only 125 µm thick. Thalli are warty to lumpy with numerous nodular protuberances. The cell surface (SEM) is neither Phymatolithon- nor Leptophytum-type (Pl. 24, Figs 2 & 3). The surface texture is matt.

The thallus is monomerous and dorsiventrally organised (Pl. 25, Fig. 5). The medullary filaments comprise 29-37% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 25, Figs 5 & 6), with cells that are squat to rectangular and measure 7-31 µm long X 4-12 µm in diameter. Cell fusions are abundant (Pl. 25, Fig. 6). Secondary pit connections have not been seen.

The cortical filaments comprise up to 71% of the thallus thickness (Pl. 25, Fig. 5) with cells that are square to rectangular and measure 5-10 µm long X 6-11 µm in diameter. Cell fusions are abundant. Secondary pit connections were not seen. Subepithallial initials are square to rectangular, and measure 12 µm long X 6-10 µm in diameter. Epithallial cells are squat to elliptical and measure 5-6 µm long X 7-12 µm in diameter, and occur singly. Trichocytes are rare and occur singly at the thallus surface (Pl. 24, Fig. 3). Trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes measure 25 µm long X 5-10 µm in diameter. Buried trichocytes have not been seen.

Reproduction

Type fragments lacked gametangial material.

Tetrasporangial conceptacles are flush to only slightly raised above the thallus surface, measuring 400-500 µm in external diameter (Pl. 24, Fig. 4). Their chambers are elliptical (Pl. 25, Fig. 7) and measure 110-275 µm in diameter X 90-115 µm high, with the roof 31-53 µm (5-8 cells; incl. epithallial cell) thick. The conceptacle floor is located c. 9-12 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal. The pore-canal filaments are oriented more-or-less vertically, and do not project into the pore. No central columella has been observed although zonately divided tetrasporangia are seen to be located peripherally in the conceptacle chamber (Pl. 25, Fig. 8). Sporangia measure 62-87 µm long X 19-37 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 25, Fig. 7), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Description of representative specimens

Representative specimens examined

Bahamas: US Foslie (iso)type F.T.-25; Lithophyllum munitum Foslie and Howe 1906: 132; Printz 1929: Pl. 56, Figs 16 &17; Cave Keys, Exuma Island, Bahamas (W Adey, 14444).

Fiji: Fish Patch, Suva Barrier Reef (D Keats, 28.ix.1994, UWC: 94/1223); Belcher Rocks, off Lucala Bay (D Keats, 27.xi.1994, UWC: 94/1348).

Tanzania: Chwaka Point, Chwaka Bay, Zanzibar Island (D Keats, GW Maneveldt & J Kangwe, 3.vii.1999, UWC: 99/122).

Habitat

Hydrolithon munitum has been recorded to occur epiphytically (coralline rubble), epizoically (including on corals) and epilithically throughout the intertidal to depths of 15 m. This species appears to have a tropical to subtropical affinity. Additional information on this species has been provided by Penrose (1990).

Distribution

Australia (Penrose 1996), Bahamas (Foslie & Howe 1906; Penrose 1996; This study), Fiji (This study), Jamaica (Penrose 1996), Tanzania (Chwaka Bay, Zanzibar Island) (This study).

Habit and Vegetative Structure

Plants are generally adherent, measuring up to at least 1150 µm thick. Thalli are generally smooth to warty to lumpy (with numerous nodular protuberances) and may also occur as rhodoliths (Pl. 26, Fig. 1). The cell surface (SEM) is neither Phymatolithon- nor Leptophytum-type. The surface texture is matt.

The thallus is monomerous and dorsiventrally organised (Pl. 27, Fig. 5). The medullary filaments comprise 9-50% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 27, Fig. 5), with cells that are squat to elongate and measure 7-35 µm long X 4-12 µm in diameter. Cell fusions are abundant. Secondary pit connections have not been seen.

The cortical filaments comprise up to 91% of the thallus thickness (Pl. 30, Fig. 14) with cells that are square to rectangular and measure 5-10 µm long X 5-12 µm in diameter. Cell fusions are abundant. Secondary pit connections were not seen. Subepithallial initials are square to elongate (Pl. 27, Figs 3 & 4), and measure 9-19 µm long X 5-10 µm in diameter. Epithallial cells (Pl. 27, Figs 3 & 4) are predominantly elliptical but also squat, and measure 5-10 µm long X 6-12 µm in diameter, and occur singly. Trichocytes are common at the surface and may occur singly, in small horizontal groups (up to 6 cells have been recorded) (Pl. 27, Figs 2-4), and in vertical rows. Within horizontal groups, individual trichocytes are not separated by the cells of normal cortical filaments. Trichocyte chains typically comprise only 2 cells; a megacell, and a support cell. Individual trichocytes measure 12-32 µm long X 5-14 µm in diameter. Buried trichocytes have not been seen.

Reproduction

Gametangial plants may be monoecious (with spermatangia and carposporangia occurring in separate conceptacles) (Pl. 30, Fig. 14) or dioecious. Spermatangial conceptacles are relatively small, measuring about 193-296 µm in external diameter. Spermatangial conceptacle roofs are usually more-or-less flush with the surrounding thallus surface to only slightly raised above the thallus surface (Pl. 29, Fig. 12; Pl. 30, Fig. 14). The conceptacle chamber is wide and shallow to elliptical (Pl. 29, Fig. 12) measuring 109-140 µm in diameter X 31 µm high, with the roof 31-43 µm thick. Buried spermatangial conceptacles have not been seen. Simple spermatangial systems are borne only on the floor of the conceptacle chamber (Pl. 29, Figs 12 & 13).

Carpogonial conceptacles have not been seen.

Carposporangial conceptacles are relatively large, measuring 300-400 µm in external diameter (Pl. 30, Fig. 15). Chambers of carposporangial conceptacles are elliptical (Pl. 30, Fig. 15) and measure 225-250 µm in diameter X 60-100 µm high with the roof 31-37 µm thick. The pore canal is lined with small filaments. The central fusion cell is broad and both thin and thick and is continuous, with gonimoblast filaments borne peripherally (Pl. 30, Figs 15 & 16). Gonimoblast filaments are 5-6 cells long including a terminal carpospore that measures 25-56 µm long X 25-31 µm in diameter. Buried carposporic conceptacles have been observed (Pl. 30, Fig. 14).

Tetrasporangial conceptacles are more-or-less flush with the thallus surface, to slightly raised above it and measure 390-515 µm in external diameter (Pl. 28, Figs 6, 8 & 9). Their chambers are elliptical (Pl. 28, Figs 6, 8 & 9) and measure 110-275 µm in diameter X 78-164 µm high, with the roof 31-53 µm (4-8 cells) thick (Pl. 28, Fig. 11). The conceptacle floor is located 7-12 cells below the surrounding thallus surface. The roof is formed from filaments interspersed among the sporangia (Pl. 28, Fig. 6) and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 28, Figs 10 & 11). The pore-canal filaments are usually oriented more-or-less vertically, and do not tilt into the pore. There is a central columella present (Pl. 28, Fig. 10), and zonately divided tetrasporangia are located peripheral to it. Tetrasporangia measure 31-87 µm long X 9-66 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 28, Fig. 8), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Key features

Hydrolithon munitum is characterised by the following **combination** of characters: 1) thalli smooth to warty to lumpy (with numerous nodular protuberances), also occurring as rhodoliths; 2) thallus monomerous; 3) medullary filaments plumose; 4) tetrasporangial conceptacles that are only slightly raised or flush with the thallus surface; 5) trichocytes present, but only recorded at the surface, occurring singly as well as in small horizontal rows; 6) trichocytes within rows are *not* separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and *not* peripheral to them; 9) the tetrasporangial pore canal *not* usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is commonly 4-8 cells thick; 11) the sporangial conceptacle floor is commonly 7-12 cells below the surrounding thallus surface; 12) tetrasporangial conceptacles usually possessing a central columella with peripherally located sporangia.

Remarks

Hydrolithon munitum has been well documented from tropical Western Australia (Penrose 1996). Penrose (1996) characterised this species on its entire reproductive anatomy (not having cited any specific reproductive character) and concluded that H. munitum was closely related to H. onkodes and that they differed only in that the former lacked buried horizontal rows of trichocytes. Trichocyte arrangement and anatomy have consistently been argued to be less reliable as taxonomic characters (see Lemoine 1917; Cabioch 1972; Mendoza & Cabioch 1986; Penrose & Woelkerling 1988). Mendoza & Cabioch (1986) even showed that a number of distinct species occurring at two geographically distinct localities bore different trichocyte arrangements. The question thus arises as to just how different H. munitum and H. onkodes really are based on Penrose's (1996) conclusion. Upon examination of the representative material, this research supports Penrose's (1996) distinction of H. munitum from H. onkodes, but proposes that a combination of characters separates these taxa (see Table 3).

It has been suggested that H. munitum may be conspecific with H. boergensenii (Walter Adey, pers. comm.). An examination of these two taxa does indeed reveal a remarkable resemblance, and similarly so with H. rupestris (Table 4). Hydrolithon munitum and H. rupestris have been separated based on the presence and absence of a central columella, and the distribution of the sporangia within the sporangial conceptacles (Penrose 1996). Although a central columella has never been observed for the type of H. boergensenii by either this research or any previous research (see Foslie 1901a; Steentoft 1967; Masaki 1968), no sporangia have been seen either. It cannot therefore be said with any degree of certainty whether indeed H. boergensenii possesses or lacks a central columella. Examination of representative material from the type locality is therefore necessary to fully evaluate to existence of this character as it has been suggested to be important in distinguishing taxa (Verheij 1993; Penrose 1996). Also, H. boergensenii possesses a dimerous thallus while both H. munitum and H. rupestris possess a monomerous thallus. These two thallus constructions are based on completely different developmental strategies and while primarily dimerous plants may become secondarily monomerous with age, particularly when overgrowing other crusts or during wound repair (Cabioch 1972; Chamberlain & Norris 1994), these appear to be stable characters in germinating spores and young thalli (see Woelkerling & Irvine 1988; Irvine et al. 1994). Unless shown otherwise, for all intents and purposes, H. boergesenii and H. munitum are separate entities.

Basionym

Lithophyllum rupestre Foslie 1907a: 26 (see also Adey & Lebednik 1967: 18; Printz 1929: Pl. 54; Woelkerling & Campbell 1992: 100)

Pl. 41-44, Figs 1-15.

Current Placement/Name

Hydrolithon rupestris (Foslie) Penrose in Womersley 1996: 265

Pl. 45-47, Figs 1-13.

Holotype

TRH. Ocean Beach, Phillip Island, Victoria, Australia; unnumbered. Previous references to typification were by Adey & Lebednik 1967: 18 (as Lithophyllum) and Adey 1970: 26 (as Mesophyllum).

Synonyms

Homotypic synonyms:

Mesophyllum rupestre (Foslei) Adey 1970: 26

Etymology

'rupestre', rupestris = rocky, rock dwelling. Foslie (1907a) did not explain the origin of the epithet. How this applies to H. rupestris is unclear. Foslie (1907a) may simply just have been describing the epilithic nature of this species on pebbles and little boulders.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype material housed at TRH (Pl. 41, Fig. 1). The type fragments are generally thin to moderately thick and adherent, measuring up to 800 µm thick. The type fragments are smooth and featureless. The cell surface (SEM) is of the Phymatolithon-type (Pl. 42, Fig. 2). The surface texture is matt.

The thallus is monomerous and dorsiventrally organised (Pl. 43, Fig. 5). The medullary filaments comprise 9-53% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 43, Fig. 7), with cells that are square to rectangular and measure 6-19 µm long X 5-11 µm in diameter. Cell fusions are abundant (Pl. 43, Fig. 7). Secondary pit connections have not been seen.

The cortical filaments comprise 47-91% of the thallus thickness (Pl. 43, Fig. 5) with cells that are squat to rectangular and measure 3-10 µm long X 5-11 µm in diameter. Cell fusions are abundant (Pl. 43, Fig. 6). Secondary pit connections were not seen. Subepithallial initials are squat to square (Pl. 43, Fig. 6), and measure 4-7 µm long X 5-10 µm in diameter. Epithallial cells are squat to elliptical (Pl. 43, Fig. 6) and measure 4-6 µm long X 5-10 µm in diameter, and occur singly (2-3 cells recorded only when shedding). Trichocytes have not been recorded either at the surface or buried in the thallus.

Reproduction

Gametangial plants are monoecious (Pl. 44, Figs 10 & 12). Spermatangial conceptacles are rare and very small (Pl. 44, Figs 10 & 11). Only two buried spermatangial conceptacles have been observed. The conceptacle chamber is shallow to elliptical (Pl. 44, Figs 10 & 11) measuring 56 µm in diameter X 16-21 µm high. Simple spermatangial systems are borne only on the floor of the conceptacle chamber (Pl. 44, Fig. 11).

Carpogonial conceptacles are also very small and inconspicuous (Pl. 44, Figs 12 & 13). Only buried carpogonial conceptacles have been observed. Their chambers are elliptical to flask-shaped (Pl. 44, Figs 12 & 13), and measure 31-74 µm in diameter X 12-37 µm high. Carpogonial branches are 2-3 celled and occur centrally on the chamber floor (Pl. 44, Fig. 13). Carposporangia develop in carpogonial conceptacles after presumed karyogamy.

Compared with spermatangial and carpogonial conceptacles, carposporangial conceptacles are relatively large, measuring 120-240 µm in external diameter (Pl. 42, Figs 3 & 4; Pl. 44, Figs 9, 10 & 12). Chambers of carposporangial conceptacles are elliptical to spherical (Pl. 44, Figs 9, 10, 12 & 15), and measure 85-150 µm in diameter X 50-85 µm high with the roof 25-31 µm thick. The pore canal is lined with small filaments. The fusion cell is centrally placed and continuous, with gonimoblast filaments borne peripherally (Pl. 44, Figs 14 & 15). Gonimoblast filaments are 2+ cells long (entire gonimoblast filaments have not been observed) including a terminal carpospore that measures 19-22 µm long X 25-27 µm in diameter.

The type fragments lacked sporangial material!

Description of representative specimens

Representative specimens examined

Australia: US Foslie (holo)type fragment F.T.-37; *Lithophyllum rupestre* Foslie 1907a: 26-27; Printz 1929: Pl. 54, Fig 1: Gabriel, Philip Is, Ocean Beach, Victoria, Australia (*W Adey* 1456826). **Fiji**: East of Usborne Passage, Great Astrolabe Reef (*D Keats*, 9.vi.1994, UWC: 94/1057); Herald Passage, Great Astrolabe Reef (*D Keats*, 10.vi.1994, UWC: 94/1077, UWC: 94/1081, UWC:

94/1083); Fish Patch, Suva Barrier Reef (D Keats, 9.xi.1994, UWC: 94/1268; D Keats, 23.xi.1994, UWC: 94/1341).

South Africa: Mbibi, Sodwana Bay, Kwazulu-Natal (D Keats, 6.xi.1991, UWC: 91/163).

Taiwan: Hou Wan Bay, southern Taiwan (D Keats, GW Maneveldt, J Lewis & Jacson, 18.ix. 1998, UWC: 98/362.

Habitat

Hydrolithon rupestris has been recorded to occur epizoically and epilithically throughout the intertidal to depths of 15 m. In southern Australia this species commonly occurs on intertidal rock platforms (Penrose 1996). Hydrolithon rupestris appears to have a tropical to subtropical affinity. Additional information on this species has been provided by Penrose (1990).

Distribution

Australia (Foslie 1907a; Penrose 1996; This study), Fiji (This study), French Polynesia (Payri et al. 2000), Mexico (Pacific) (Fragoso & Rodríguez 2002), South Africa (Kwazulu-Natal) (This study), Taiwan (southern) (This study).

Habit and Vegetative Structure

Plants are generally adherent, measuring up to at least 1000 µm thick. Thalli are generally smooth to warty (Pl. 45, Fig. 1). The cell surface (SEM) is of the Leptophytum-type. The surface texture is matt.

The thallus is monomerous and dorsiventrally organised (Pl. 46, Fig. 2). The medullary filaments comprise 5-53% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 46, Figs 2 & 7), with cells that are squat to elongate and measure 6-25 µm long X 4-16 µm in diameter. Cell fusions are abundant. Secondary pit connections have not been seen.

The cortical filaments comprise up to 95% of the thallus thickness (Pl. 46, Fig. 2) with cells that are squat to rectangular and measure 3-12 µm long X 5-11 µm in diameter. Cell fusions are abundant (Pl. 46, Figs 4 & 6). Secondary pit connections were not seen. Subepithallial initials are squat to square (Pl. 46, Figs 3 & 4), and measure 4-11 µm long X 5-10 µm in diameter. Epithallial cells are squat to elliptical (Pl. 46, Figs 3 & 4) and measure 4-6 µm long X 4-10 µm in diameter, and occur singly (2-3 cells recorded only when shedding). Trichocytes are rare at the thallus surface and occur singly, but also in vertical rows (Pl. 46, Fig. 4). Trichocytes are separated from one another by the cells of one or generally more, normal erect filaments and trichocyte chains typically comprise 2-6 cells; a single megacell, and up to 5 support cells. Individual trichocytes measure 10-14 µm long X 9-12 µm in diameter. Individual and vertical rows of trichocytes are found buried in the thallus (Pl. 46, Fig. 5).

Reproduction

No gametangial plants have been observed from the representative specimens.

Tetrasporangial conceptacles are more-or-less flush with the thallus surface, to slightly raised above it and measure 250-400 µm in external diameter (Pl. 47, Figs 8-10). Their chambers are elliptical to spherical (Pl. 47, Figs 9 & 10) and measure 115-190 µm in diameter X 75-105 µm high, with the roof 29-43 µm (4-7 cells) thick. The conceptacle floor is located 10-14 cells below the surrounding thallus surface. The roof is formed from filaments interspersed among the sporangia (Pl. 47, Fig. 12) and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 47, Figs 12 & 13). The pore-canal filaments are usually oriented more-or-less vertically, and do not tilt into the pore. There is no central columella present, and zonately divided tetrasporangia (Pl. 47, Fig. 11) are located across the conceptacle floor (Pl. 47, Fig. 10). Tetrasporangia measure 31-68 μm long X 10-25 μm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 47, Figs 8 & 9), and often contain apparently viable sporangia; infilled conceptacles have not been observed.

Key features

Hydrolithon rupestris is characterised by the following **combination** of characters: 1) thalli smooth to warty; 2) thallus monomerous; 3) medullary filaments plumose; 4) tetrasporangial conceptacles that are only slightly raised or flush with the thallus surface; 5) trichocytes present (but rare), both at the surface and immersed in the thallus, occurring singly as well as in small vertical rows; 6) trichocytes separated by the cells of normal erect filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 9) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is commonly 4-7 cells thick; 11) the sporangial conceptacle floor is commonly 10-14 cells below the surrounding thallus surface; 12) tetrasporangial conceptacles lacking a central columella with sporangia distributed across the chamber floor.

Remarks

Hydrolithon rupestris has been well documented from Australia (Penrose 1996). Penrose (1996) characterised this species on its entire reproductive anatomy (not having cited any specific reproductive character). Hydrolithon rupestris is remarkably similar to Hydrolithon munitum and Penrose (1996) distinguishes these taxa based on the presence or absence of a central columella and the associated arrangement of the sporangia within the conceptacle chamber. This study supports this distinction between the two taxa and includes some additional characters that may be used to separate Hydrolithon rupestris from Hydrolithon munitum.

Hydrolithon rupestris possesses the following combination of diagnostic characters:

1. trichocytes are rare at the thallus surface and occur singly, but occasionally also in vertical rows;
2. trichocytes become buried in the thallus;
3. tetrasporangia arranged across the tetrasporangial conceptacle floor; and
4. a central columella is absent.

Hydrolithon munitum possesses the following combination of diagnostic characters:

1. trichocytes are common at the thallus surface and occur singly, occasionally in vertical rows, but also in small horizontal rows;
2. trichocytes do not become buried in the thallus;
3. tetrasporangia arranged peripherally in the tetrasporangial conceptacle chamber; and
4. a central columella is present.

Penrose (1996) included an additional distinction between these two taxa, citing sporangial conceptacle chamber diameter as another distinguishing feature. This study has shown that chamber diameter, although with minimal overlap, is not a reliable taxonomic character. Furthermore, Penrose's (1996) chamber dimensions for these two taxa are substantially smaller than those recorded from this study. However, collectively characters 3 and 4 may be used to distinguish between these two taxa.

Basionym

Lithophyllum samoënse Foslie 1906: 20 (see also Printz 1929: Pl. 53 Fig. 19; Masaki 1968: 37; Segonzac 1983: Table 1, 1984: 101; Krishnamurthy & Jayagopal 1985: 82; Woelkerling 1993: 182)

Pl. 48-51, Figs 1-17.

Current Placement/Name

Hydrolithon samoënse (Foslie) Keats & Chamberlain 1994: 15

Pl. 52-55, Figs 1-16.

Lectotype

TRH. Satana, Saraii Island, Western Samoa; unnumbered. Lectotype designated by Woelkerling 1993: 193. Previous references to typification were by Dawson 1960: 50 (as Lithophyllum), Adey & Lebednik 1967: 17 (as Lithophyllum), Adey 1970: 13 (as Pseudolithophyllum) and Chamberlain 1994b: 126 (as Hydrolithon).

Synonyms

Homotypic synonyms:

Pseudolithophyllum samoënse (Foslie) Adey 1970: 13;

Heterotypic synonyms:

Lithophyllum illitus Lemoine 1929: 54;

Neogoniolithon illitus (Lemoine) Afonso-Carrillo 1984: 133;

Spongites wildpretii Afonso-Carrillo 1988: 99.

Etymology

'samoënse' refers to the type locality in the Samoan island group.

Description of Type

Habit and Vegetative Structure

The following description is based on the lectotype material housed at TRH. The type fragments are thin and adherent, measuring only up to 375 µm thick. Thalli are flat and smooth, lacking protuberances, and have adherent margins that are thin and lacks orbital ridges. The cell surface (SEM) is both of the Phymatolithon- and Leptophytum-type (Pl. 48, Fig. 1). The surface texture is matt.

The thallus is monomerous and dorsiventrally organised (Pl. 48, Figs 2-4). The medullary filaments comprise 7-21% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 48, Figs 3 & 4; Pl. 49, Figs 10 & 11), with cells that are square to rectangular and measure 5-19 µm long X 4-17 µm in diameter. Cell fusions are abundant (Pl. 48, Fig. 4). Secondary pit connections have not been seen.

The cortical filaments comprise up to 93% of the thallus thickness with cells that are squat to rectangular and measure 3-15 µm long X 4-9 µm in diameter. Cell fusions are abundant. Secondary pit connections were not seen. Subepithallial initials are square to rectangular (Pl. 48, Fig. 5; Pl. 49, Fig. 9), and measure 5-12 µm long X 5-7 µm in diameter. Epithallial cells occur singly (up to 2 only when shedding), are squat to elliptical (Pl. 48, Fig. 5; Pl. 49, Fig. 9), and measure 4-6 µm long X 5-7 µm in diameter. Trichocytes commonly occur singly, paired and in small vertical rows (Pl. 48, Fig. 5; Pl. 49, Fig. 8). Trichocytes (except pairs) are separated from one another by the cells of one or generally more, normal cortical filaments and trichocyte chains typically comprise 2-5 cells; a megacell, and up to 4 support cells (Pl. 48, Fig. 5). Individual trichocytes are rectangular to elongate, and measure 16-31 µm long X 7-10 µm in diameter. They are often overgrown and buried within the thallus (Pl. 48, Fig. 5).

Reproduction

Gametangial plants appear to be monoecious. Spermatangial conceptacles are small and inconspicuous, measuring only about 75-150 µm in external diameter (Pl. 51, Fig. 16). Spermatangial conceptacle roofs are more-or-less flush with the surrounding thallus surface. The conceptacle chamber is wide and shallow to elliptical (Pl. 51, Figs 16 & 17), measuring 37-62 µm in diameter X 19-29 µm high, with the roof 10-16 µm thick. Spermatangial conceptacles are often seen buried in the thallus. Simple spermatangial systems are borne only on the floor of the conceptacle chamber (Pl. 51, Fig. 17).

Carpogonial conceptacles are also small and inconspicuous, measuring only 145-200 µm in external diameter (Pl. 50, Fig. 15). Carpogonial conceptacle roofs are slightly raised above the surrounding thallus surface and measure 11-30 µm thick. Their chambers are elliptical to spherical to flask-shaped (Pl. 50, Figs 15 & 16), and measure 56-80 µm in diameter X 25-30 µm high. 3-4 Celled carpogonial branches occur centrally on the chamber floor (Pl. 50, Figs 14 & 15). Buried carpogonial conceptacles have not been observed. Carposporangia develop in carpogonial conceptacles after presumed karyogamy.

Carposporangial conceptacles have not been observed.

Sporangial conceptacles are also small. They are more-or-less flush with the thallus surface, to slightly raised above it and measure 140-190 µm in external diameter (Pl. 48, Fig. 6; Pl 50, Fig.

12). Their chambers are elliptical to spherical (Pl. 50, Fig. 12), and measure 56-130 μm in diameter X 31-60 μm high, with the roof 15-28 μm thick. The roof is 2-4 (mostly 3) cells thick, always comprising a single squat to elliptical to spherical epithallial cell, a single elongate meristematic cell that is 2.5-5X the length of the epithallial cell, and 1-2 small inner cells (Pl. 50, Fig. 13). The conceptacle floor is located 8-16 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 50, Fig. 13). The pore-canal filaments are oriented more-or-less vertically, and do not tilt into the pore. A central columella is present. Neither tetrasporangia nor bisporangia have been observed. Both shedding and burying of sporangial conceptacles have been observed. Buried sporangial conceptacles do not become infilled. Infilling of conceptacle scars does, however, occur where conceptacles have been shed (Pl. 49, Fig. 7).

Description of representative specimens

Representative specimens examined

Fiji: Suva Point, Suva (D Keats, 3.viii.1994, UWC: 94/1146B); Suva Lagoon, Suva (D Keats, 23.xi.1995, UWC: 95/1515); Fish Patch, Suva Barrier Reef (D Keats, 26.xi.1995, UWC: 95/1523).

South Africa: Jesser Point, Sodwana Bay, Kwazulu-Natal (D Keats, 7.xi.1991, UWC: 91/179A); Holbaaipunt, Cape Hangklip (D Keats, 18.v.1992, UWC: 92/98; D Keats, 1.vi.1992, UWC: 92/146; D Keats & G Maneveldt, 21.v.1993, UWC: 93/58; D Keats & G Maneveldt, 21.vi.1993, UWC: 93/70).

Taiwan: Wanlitong Bay, southern Taiwan (D Keats, GW Maneveldt, J Lewis & Jacson, 17.ix. 1998, UWC: 98/322).

Habitat and Phenology

See Keats & Chamberlain (1994).

Distribution

British Isles (Keats & Chamberlain 1994; Chamberlain 1994b), Comores (Segonzac 1984), Canary Islands (Lemoine 1929; Afonso-Carrillo 1984, 1988; Keats & Chamberlain 1994; Chamberlain 1994b; Haroun et al. 2002), Djibouti (Segonzac 1984; Silva et al. 1996), Easter Island (Lemoine 1920b; Masaki 1968; Krishnamurthy & Jayagopal 1985), Fiji (This study), France (Atlantic) (Keats & Chamberlain 1994), French Polynesia (Payri et al. 2000), Hawaii(?) (Keats & Chamberlain 1994), India (Pudumadam) (Krishnamurthy & Jayagopal 1985; Chamberlain 1994b; Silva et al. 1996), Japan (Masaki 1968; Krishnamurthy & Jayagopal 1985; Chamberlain 1994b; Yoshida 1998), Mauritius (Segonzac 1984), Mexico (Pacific) (Dawson 1960; Masaki 1968; Mendoza-González & Mateo-Cid 1985; Chamberlain 1994b; Riosmena-Rodríguez & Woelkerling 2000; Fragoso & Rodríguez 2002), Réunion (Segonzac 1984; Silva et al. 1996), Samoa (Western) (Foslie 1906; Dawson 1960; Masaki 1968; Krishnamurthy & Jayagopal 1985; Keats & Chamberlain 1994; Chamberlain 1994b), South Africa (Keats & Chamberlain 1994; Silva et al. 1996; This study), Spain (Atlantic) (Keats & Chamberlain 1994), Sri Lanka (Segonzac 1984), Tahiti (Dawson 1960; Masaki 1968; Krishnamurthy & Jayagopal 1985; Keats & Chamberlain 1994; Chamberlain 1994b; Silva et al. 1996, see also Payri et al. 2000), Taiwan (southern) (This study), Viet Nam (Masaki 1968; Krishnamurthy & Jayagopal 1985).

Habit and Vegetative Structure

Plants are strongly adherent on coral, shells, and mixed with other corallines in rhodoliths. They measure up to at least 10 cm in diameter, and variably thin to 800 µm thick. Thalli are flat and smooth, lacking protuberances (Pl. 52, Figs 1 & 2), and have adherent margins that are thin and lacks orbital ridges. The cell surface (SEM) is both of the *Phymatolithon*- and *Leptophytum*-type. The colour is generally gleaming purplish-red, and the surface has a matt texture. The craters of old conceptacles and swirls of sloughing epithallial cells are commonly observed at the surface (Pl. 52, Figs 2 & 3). Conceptacles are crowded across the thallus surface (Pl. 52, Figs 2 & 3), appearing as tiny, white discs in fresh material.

The thallus is monomerous and dorsiventrally organised (Pl. 53, Fig. 4). The medullary filaments comprise 7-28% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 53, Figs 4 & 7), with cells that are square to elongate and measure 5-21 µm long X 4-17 µm in diameter. Cell fusions are abundant (Pl. 53, Fig. 7). Secondary pit connections have not been seen.

The cortical filaments comprise up to 93% of the thallus thickness (Pl. 53, Fig. 4). Cortical filaments comprise small, squat to squarish, bead-like cells (Pl. 53, Figs 6 & 8) that measure 3-15 µm long X 4-13 µm in diameter. Cell fusions are abundant (Pl. 53, Fig. 8). Secondary pit connections were not seen. Subepithallial initials are square to rectangular (Pl. 53, Figs 5 & 6), and measure 5-12 µm long X 5-10 µm in diameter. Epithallial cells occur singly (up to 2 only when shedding), are squat to elliptical (Pl. 53, Figs 5 & 6), and measure 3-7 µm long X 59 µm in diameter. Trichocytes commonly occur singly or in pairs (Pl. 53, Fig. 5). Trichocytes (except pairs) are separated from one another by the cells of one or generally more, normal cortical filaments and trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes are square to elongate, and measure 11-31 µm long X 7-10 µm in diameter. They are rarely overgrown and buried within the thallus.

Reproduction

Gametangial plants appear dioecious. Spermatangial conceptacles have not been seen.

Carpogonial conceptacles are small measuring only 145-200 µm in external diameter (Pl. 55, Fig. 13). Carpogonial conceptacle roofs are more-or-less flush with the surrounding thallus surface to only slightly raised above it and measure 11-30 µm thick. Their chambers are elliptical to flask-shaped (Pl. 55, Figs 13 & 14), and measure 37-84 µm in diameter X 16-30 µm high. 3-4 Celled carpogonial branches occur centrally on the chamber floor (Pl. 55, Figs 14 & 15). Buried carpogonial conceptacles have not been observed. Carposporangia develop in carpogonial conceptacles after presumed karyogamy.

Carposporangial conceptacles are only slightly larger than carpogonial conceptacles, measuring 175-234 µm in external diameter (Pl. 55, Fig. 16). Chambers of carposporangial conceptacles are elliptical to spherical, and measure 85-140 µm in diameter X 40-100 µm high with the roof 16-26 µm thick. The conceptacle roof is similar in construction to the sporangial conceptacle roofs, but the pore is lined with small papillate cells that tilt slightly into the pore canal. The continuous central fusion cell is narrow and thick with gonimoblast filaments borne peripherally (Pl. 55, Fig. 16). Gonimoblast filaments are only 4 cells long including a terminal carpospore that measures 29-43 µm long X 23-50 µm in diameter. Buried carposporangial conceptacles have not been observed.

Tetrasporangial conceptacles are slightly sunken to flush to slightly raised above the rest of the thallus surface (Pl. 54, Figs 9 & 10). Conceptacles are low domed and measure 125-200 µm in external diameter. Their chambers are elliptical to spherical, and measure 75-110 µm in diameter X 35-75 µm high, with the roof 16-22 µm thick. The roof is 2-4 (mostly 3) cells thick, always comprising a single squat to elliptical to spherical epithallial cell, a single elongate meristematic cell that is 2.5-5X the length of the epithallial cell, and 1-2 small inner cells (Pl. 54, Figs 11 & 12). The conceptacle floor is located 8-16 cells below the surrounding thallus surface. The roof is formed from filaments interspersed among the sporangia (Pl. 54, Figs 9 & 11) and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 54, Figs 9-11). The pore-canal filaments are usually oriented more-or-less vertically, and do not tilt markedly into the pore. A central columella has not been observed. In young sporangial conceptacles, zonately divided tetrasporangia are located peripherally in the conceptacle chamber but fill the chamber completely as they mature (Pl. 54, Figs 9 & 10). Tetrasporangia measure 19-31 µm long X 6-34 µm in diameter. Bisporangial plants were not seen. Old tetrasporangial conceptacles are often shed leaving craters that eventually become infilled.

Key features

<u>Hydrolithon samoënse</u> is characterised by the following **combination** of characters: 1) thallus variably thin to thick, adherent, smooth, lacking protuberances; 2) thallus monomerous; 3) medullary filaments plumose; 4) cortical filaments comprising small, squat to squarish, bead-like cells; 5) tetrasporangial conceptacles that are slightly sunken to flush to slightly raised above the thallus surface; 6) trichocytes present, both at the surface and rarely immersed in the thallus, occurring singly, paired and rarely in short vertical rows; 7) trichocytes most often separated by the

cells of normal cortical filaments; 8) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 9) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and *not* peripheral to them; 10) the tetrasporangial pore canal *not* usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 11) the tetrasporangial conceptacle roof is usually only 3 cells thick, comprising a single squat to elliptical to spherical epithallial cell, a single elongate meristematic cell that is 2.5-5X the length of the epithallial cell, and a small inner cells; 12) the sporangial conceptacle floor is commonly 8-16 cells below the surrounding thallus surface.

Remarks

The most recent review of *Lithophyllum samoënse* was by Keats & Chamberlain (1994) who transferred the species to the genus *Hydrolithon* (*sensu* Penrose & Woelkerling 1992). From their descriptions, *Hydrolithon samoënse* may be distinguished from other species of the genus *Hydrolithon* on the basis of two tetrasporangial characters. Primarily, it possesses a tetrasporangial conceptacle roof that is commonly composed of 3-cell layers (a single epithallial cell subtended by an elongate meristematic cell that in turn is subtended by a small inner cell). Secondarily, the tetrasporangial conceptacles are evident as tiny 'pinpricks' at the thallus surface that are shed individually or in small groups on senescence, leaving small scars at the thallus surface.

This diagnosis, particularly the structure of the tetrasporangial conceptacle roof, however, applies to another species namely, *Lithophyllum erosum* (Foslie 1906) which Adey (1970) had transferred and renamed *Neogoniolithon erosum*. *Lithophyllum erosum* was transferred to the genus *Neogoniolithon* by Adey (1970: 8) because he considered *Neogonioithon* to be characterised by, among other features, the presence of a monomerous ("multilayered hypothallium") thallus as opposed to the dimerous ("single-layered hypothallium") thallus of Hydrolithon (sensu Adey 1970: 11). Since Adey's (1970) descriptions, both genera have undergone substantial revision and characterization based on the thallus construction no longer holds. Based on the modern-day classification (Penrose & Woelkerling 1992), Lithophyllum erosum is clearly a Hydrolithon and should be referred to as Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov. (see description of Lithophyllum erosum earlier). The tetrasporangial conceptacle roof structure of Lithophyllum erosum is identical to that of Hydrolithon samoënse and based on this feature, I have come to the conclusion that Lithophyllum erosum (and L. caribaeum; see earlier description) and Lithophyllum samoënse are heterotypic synonyms.

From Foslie's (1906: 20) descriptions of Lithophyllum erosum and Lithophyllum samoënse there appears to be no logical reason for the separation of these taxa. Foslie's (1906: 20) descriptions of the gross morphology of the two taxa are virtually identical, both taxa forming thin crusts with irregular, crenulating margins. The only difference in Foslie's descriptions is those of the cell dimensions of the cortical filaments (perithallial cell). Lithophyllum erosum bears predominantly vertically elongated cortical cells while those of L. samoënse are roughly square. Foslie (1906: 20) also separated L. erosum from L. caribaeum based on the cell dimensions of the cortical filaments. According to Foslie (1906) L. caribaeum has predominantly horizontally elongated cortical cells. It is now widely accepted that such differences used as sole characters are no longer valid (Woelkerling & Irvine 1986; Woelkerling & Campbell 1992; Woelkerling et al. 1993). Furthermore, Foslie (1906) concludes his description of L. samoënse by stating that … "A couple of specimens from Tahiti, that I have earlier, with doubt, described as L. decipiens, belong to the same species (herb. Bornet)." Foslie (1906) was presumably referring to L. caribaeum (as L. decipiens f. caribaeum).

Foslie (1906: 20) recorded and described L. erosum and L. samoënse in the same paper, listing them alphabetically. Lithophyllum erosum therefore has nomenclatural priority and Lithophyllum samoënse, along with all its taxonomic synonyms, should thus be considered heterotypic synonyms of Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov. Hydrolithon samoënse (as Lithophyllum samoënse and Hydrolithon samoënse) was and still is, however, very widely used (e.g. Setchell 1926; Dawson 1960; Masaki 1968; Segonzac 1984; Krishnamurthy & Jayagopal 1985; Keats & Chamberlain 1994; Riosmena-Rodríguez & Woelkerling 2000; Fragoso & Rodríguez 2002). On this basis it may be argued that the epithet samoënse instead be given priority, but this suggestion requires further investigation.

Basionym

Lithothamnion onkodes Heydrich 1897: 6-7

Current Placement/Name

Hydrolithon onkodes (Heydrich) Penrose & Woelkerling 1992: 83

Refer to Paper 1 [*A revision and characterization of the species of nongeniculate coralline algae previously ascribed to the now defunct genus Porolithon (Corallinales, Rhodophyta)*] for the description of Hydrolithon onkodes.

Basionym

Hydrolithon megacystum Adey, Townsend & Boykins 1982: 32

Pl. 56, Figs 1-4.

Current Placement/Name

Hydrolithon megacystum Adey, Townsend & Boykins 1982: 32

Holotype

USNC. Waikiki, Oahu, Hawaii; 71-50-100. Paratype material exists from Hawaii (71-58-68), Maui (71-66-14), Midway (71-82-3) and Oahu (71-50-100) (see Adey, Townsend & Boykins 1982: 34).

Synonyms

None?

Etymology

"megacystum", mega = very big, very large + cyst(is) = the bladder (Stearn 1973). The epithet refers to the unusually large reproductive structures (Adey et al. 1982).

Description of Type

Habit and Vegetative Structure

The following description is based on slide material of the paratype from Hawaii. The type fragments are warty to lumpy described by Adey et al. (1982) as rugulose and nodular, becoming thick. The type fragments from the slides are thin to moderately thick and adherent, measuring only 25-600 µm thick.

The thallus is dimerous consisting of a single basal layer of non-palisade cells from which arise the erect filaments that make up most of the thallus (Pl. 56, Figs 1 & 3). Cells of the basal filaments are more or less square and measure 10-25 µm long X 9-26 µm in diameter. Cells of the erect filaments are square to rectangular and measure 10-22 µm long X 10-19 µm in diameter. Cell fusions are common (Pl. 56, Fig. 1). Secondary pit connections were not seen. Subepithallial initials are square to rectangular (Pl. 56, Figs 1 & 2), and measure 11-16 µm long X 7-16 in diameter. Epithallial cells (Pl. 56, Figs 1 & 2) are square to rectangular, occur singly, and measure 10-15 µm long X 5-7 µm in diameter. Trichocytes have not been observed at the thallus surface although enlarged cells that may be buried trichocytes have been observed occurring in horizontal rows (Pl. 56, Fig. 4). Adey et al. (1982), however, make mention of trichocytes occurring singly. Individual trichocytes measure 37-56 µm long X 16-26 µm in diameter.

Reproduction

No reproductive material was observed! See Adey et al. (1982).

Distribution

Hawaiian Archipelago (Adey et al. 1982).

Key features

Hydrolithon megacystum is characterised by the following **combination** of characters: 1) thallus moderately thick, adherent, warty to lumpy (rugulose and nodular); 2) thallus dimerous; 3) has a single basal layer of non palisade cells; 4) trichocytes present, occurring singly.

Remarks

Based on the slide observed in this study and the description of Hydrolithon megacystum from Adey et al. (1982), it cannot be said with any degree of certainty that this taxon belongs within the genus Hydrolithon, let alone that it is new to science. The description of Hydrolithon megacystum given by Adey et al. (1982) was based on the earlier concept of the genus Hydrolithon (sensu Adey 1970). Since then, the Hydrolithon (sensu Penrose & Woelkerling 1992) has undergone substantial revision and it is now generally accepted that the development of the sporangial conceptacle roof (Penrose & Woelkerling 1992; Penrose & Chamberlain 1993), is of critical importance. Adey et al. (1982) have not provided any such information, nor has this study. A thorough investigation of the USNC type as well as material from the type locality is therefore needed to fully evaluate this species.

Basionym

Hydrolithon murakoshii Iryu & Matsuda 1996: 528

Current Placement/Name

Hydrolithon murakoshii Iryu & Matsuda 1996: 528

Pl. 57-59, Figs 1-12.

Holotype

IGPS. Off Kabira, Ishigaki-jima, Ryukyu Islands, Japan; no. 102674. Paratype material also exists at IGPS (see Iryu & Matsuda 1996: 529).

Synonyms

None!

Etymology

Named "murakoshii" in honour of Dr. Masayoshi Murakoshi, deputy of the Okinawa Prefectural Fisheries Experimental Station in Okinawa, Japan.

Description of Type

Habit and Vegetative Structure

The type specimen was not available for examination during this study although Iryu & Matsuda (1996) report the thallus to be generally smooth and flat, lacking any protuberances with a thallus surface that is microscopically tessellate.

Description of representative specimens

Representative specimens examined

Fiji: Nukulau Island (D Keats, 5.xii.1994, UWC: 94/1384); Fish Patch, Suva Barrier Reef, Suva (D Keats, 8.xii.1994, UWC: 94/1390).

Habitat

See Iryu & Matsuda (1996).

Distribution

French Polynesia (Payri et al. 2000), Japan (Ryukyu Islands) (Iryu & Matsuda 1996; Yoshida 1998), Tropical Pacific (Littler & Littler 2003).

Habit and Vegetative Structure

Plants are adherent, measuring up to at least 50 mm in diameter and up to 650 µm thick. Thalli are generally smooth and flat, lacking any protuberances with a thallus surface that is microscopically tessellate. The cell surface (SEM) is neither of the Phymatolithon- nor Leptophytum-type.

The thallus is monomerous and dorsiventrally organised (Pl. 57, Fig. 1). The medullary filaments comprise 22-38% of thallus thickness and consist of a central plumose core (Pl. 57, Figs 1 & 5), with rectangular to elongate cells measuring 10-29 µm long X 4-12 µm in diameter. Cell fusions are abundant. Secondary pit connections have not been seen.

The cortical filaments comprise up to 78% of the thallus thickness (Pl. 57, Fig. 2) with cells that are square to rectangular and measure 5-12 μm long X 4-11 μm in diameter. Cell fusions are abundant (Pl. 57, Fig. 4). Secondary pit connections were not seen. Buried trichocytes have not been observed for this species, although Iryu & Matsuda (1996) have recorded some. Subepithallial initials commonly square to elongate (Pl. 57, Figs 3 & 4), and measure 10-15 μm length X 4-6 μm in diameter. Epithallial cells (Pl. 57, Figs 3 & 4) are elliptical and measure 5-7 μm long X 5-10 μm diameter, and occur singly (2 only when shedding). Trichocytes are common at the surface and occur singly, in small horizontal rows (individual trichocytes not separated by normal cortical filaments) and in long vertical chains (Pl. 57, Figs 2-4). Trichocytes chains typically comprise 2-23 cells; a megacell and up to 22 support cells. Individual trichocytes measure 12-45 μm long X 10-21 μm in diameter. Buried trichocytes have not been observed for this species, although Iryu & Matsuda (1996) have recorded some.

Reproduction

Gametangial plants have not been observed.

Tetrasporangial conceptacles are slightly sunken to flush to slightly raised above the thallus surface and measure 240-400 μm in external diameter (Pl. 58, Figs 6-9; Pl. 59, Fig. 10). Their chambers are elliptical (Pl. 59, Figs 10 & 11) and measure 130-325 μm in diameter X 55-150 μm high, with the roof 31-40 μm (4-6; mostly 4-5 cells) thick. The conceptacle floor is located 8-11 cells below the surrounding thallus surface. The roof is formed from filaments interspersed among the sporangia and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 58, Figs 6-9; Pl. 59, Fig. 12). The pore-canal filaments are usually oriented more-or-less vertically, and do not tilt markedly into the pore. There is a central columella present and the zonately divided tetrasporangia are located peripheral to it (Pl. 59, Figs 10 & 11). Tetrasporangia measure 31-62 µm long X 11-43 µm in diameter. Bisporangial plants were not seen. Tetrasporangial conceptacles often become buried in the thallus (Pl. 59, Fig. 10), and often contain apparently viable sporangia; both infilled and un-infilled conceptacles have been observed.

Key features

Hydrolithon murakoshii is characterised by the following **combination** of characters: 1) thallus thin, adherent, lacking branches, surface microscopically tessellate; 2) thallus monomerous; 3) medullary filaments plumose; 4) tetrasporangial conceptacles that are slightly sunken to flush to only slightly raised above the thallus surface; 5) trichocytes occur singly, in small horizontal groups and in long vertical chains; 6) within horizontal groups, trichocytes are not separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 9) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae; 10) the tetrasporangial conceptacle roof is commonly 4-6 cells thick; 11) the sporangial conceptacle floor is commonly 8-11 cells below the surrounding thallus surface; 12) tetrasporangial conceptacles usually possessing a central columella with peripherally located sporangia.

Remarks

Up till now, Hydrolithon murakoshii has only been recorded from Ishigaki-jima, Ryukyu Islands, southwestern Japan (Iryu & Matsuda 1996; Yoshida 1998) and Moorea (Tahiti), French Polynesia (Payri et al. 2000). From the authors descriptions (Iryu & Matsuda 1996), the species is a very notable feature of the immediate subtidal to depths of 5m bearing a characteristic microscopically tessellate surface and differs substantially from other taxa ascribed to the genus Hydrolithon (Iryu & Matsuda 1996, Table 1). A detailed analysis of this species, however, shows a very close affinity to H. munitum (Table 4). The two taxa are similar in all respects except for their general thallus form and the width of the central fusion cell.

The extent to which differences in growth form can be used to delimit taxa had for a long time remained unresolved (Woelkerling et al. 1993). While many authors have used the gross morphology largely or solely as identifying characters (eg. Foslie 1898 - 1909; Lemoine 1917; Printz 1929; Adey et al. 1982), others have shown that considerable variation within species may exist (eg. Steneck & Adey 1976; Penrose 1991; Woelkerling & Campbell 1992; Littler & Littler 2003). It is now widely considered that morphological features may be useful in the identification of species, but that these features should not be used as diagnostic characters (Woelkerling & Irvine 1986; Woelkerling & Campbell 1992; Woelkerling et al. 1993). In light of these statements, can we really say just how characteristic the tessellate surface of H. murokoshii really is? The authors (Iryu & Matsuda 1996: 529) themselves state that they are uncertain as to how the tessellate surface is formed. Certainly the width of the central fusion cell should be considered in a similar light. Also, there is no record of the two taxa occurring together in the same general locality. Therefore, in view of these suggestions, I would argue that H. murakoshii and H. munitum are conspecific and that H. munitum having been published before H. murakoshii in the same year, has nomenclatural priority. Also, the name H. munitum is much more widely used than H. murakoshii.

Basionym

Hydrolithon superficiale Keats & Chamberlain 1994: 12.

Pl. 60-64, Figs 1-23.

Current Placement/Name

Hydrolithon superficiale Keats & Chamberlain 1994: 12.

Pl. 65-67, Figs 1-9.

Holotype

L. Mbibi, Kwazulu-Natal, South Africa; D. Keats COR/302. A holotype fragment exists in the UWC herbarium; UWC: COR/302.

Synonyms

None!

Etymology

'superficiale', superficialis = occurring on the upper surface (Stearn 1973). The epithet refers to the distinct superficial layer within which the conceptacles develop.

Description of Type

Habit and Vegetative Structure

The following description is based on the holotype fragment housed at UWC (Pl. 60, Figs 1 & 2). The single holotype fragment is thin to variably thick and adherent, measuring up to 825 µm thick. Thalli are flat and smooth, lacking protuberances, and have free margins that are thin and lack orbital ridges (Pl. 61, Fig. 4). The cell surface (SEM) is both of the Phymatolithon- and Leptophytum-type (Pl. 61, Fig. 3). The surface texture is matt.

The thallus is monomerous and dorsiventrally organised (Pl. 61, Figs 4 & 5; Pl. 63, Fig. 12). The medullary filaments comprise 15-48% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 61, Figs 4-6; Pl. 63, Figs 12, 16 & 17), with cells that are squat to rectangular and measure 7-19 µm long X 6-12 µm in diameter. Cell fusions are abundant (Pl. 61, Fig. 7; Pl. 63, Figs 16 & 17). Secondary pit connections have not been seen.

The cortical filaments comprise up to 85% of the thallus thickness (Pl. 61, Fig. 5; Pl. 63, fig12). Cells of cortical filaments are squat to rectangular but occasionally also bead-like (Pl. 63, Fig. 15) and measure 3-14 µm long X 6-12 µm in diameter. Cell fusions are abundant (Pl. 61, Fig. 6). Secondary pit connections were not seen. Subepithallial initials are square to elongate (Pl. 61, Fig. 6; Pl. 63, Fig. 14), and measure 6-12 µm long X 5-10 µm in diameter. Epithallial cells occur singly (up to 2 only when shedding) (Pl. 61, Fig. 6; Pl. 63, Fig. 14), are square to elliptical, and measure 6-11 µm long X 5-12 µm in diameter. Trichocytes occur singly (Pl. 63, Fig. 13), are separated from one another by the cells of one or generally more, normal erect filaments and trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes are rectangular and measure 13-16 µm long X 8-10 µm in diameter. They are rarely seen buried within the thallus.

Reproduction

It is unclear as to whether gametangial plants are monoecious or dioecious. Spermatangial conceptacles have, however, been observed alongside tetrasporangial conceptacles on the same fragment (Pl. 64, Fig. 22). Spermatangial conceptacles are small, measuring only about 109-187 µm in external diameter (Pl. 64, Figs 22 & 23). Conceptacle roofs are more-or-less flush with the surrounding thallus surface to only slightly raised above the surface. The conceptacle chamber is triangular in shape (Pl. 64, Fig. 23), measuring 62-124 µm in diameter X 25-31 µm high, with the roof 16-19 µm thick. Spermatangial conceptacles are shed in a superficial layer and have not been seen buried in the thallus. Simple to elongate spermatangial systems are borne only on the floor of the conceptacle chamber (Pl. 64, Fig. 23).

Carpogonial conceptacles have not been observed.

Carposporangial conceptacles have not been observed.

Tetrasporangial conceptacles are also small; they are raised above the thallus surface and measure 110-200 µm in external diameter (Pl. 62, Figs 8-10; Pl. 64, Figs 18 & 19). The conceptacle pores are distinctly sunken (Pl. 62, Fig. 9) and the mature tetrasporangial conceptacles are characteristically borne in a distinct superficial layer of thin walled, lightly calcified, rectangular to elongate cells that are well differentiated from the well-calcified outer cortical filaments below (Pl. 60, Fig. 2). Their chambers are elliptical to spherical (Pl. 62, Fig. 10; Pl. 64, Figs 18 & 19), and measure 85-125 µm in diameter X 55-95 µm high, with the roof 19-25 µm thick. The roof is 2-4 (mostly 3) cells thick, comprising a single, spherical to domed to elongate epithallial cell, a single elongate meristematic cell that is roughly 1.5-2X the length of the epithallial cell, and 1-2 small inner cells that are also roughly spherical (Pl. 62, Fig. 11; Pl. 64, Figs 20 & 21). As the conceptacles are borne in a superficial layer above the surrounding thallus surface, the conceptacle floor is typically 4 cells above the surrounding thallus surface to flush with the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal and remnants of the filaments that give rise to these enlarged cells are visible well after the roof has been formed (Pl. 62, Figs 10 & 11). The pore-canal filaments are oriented more-or-less vertically, and do not tilt into the pore. A central columella has not been seen. Tetrasporangia have been observed to occur across the conceptacle chamber floor except at the very centre from were the pore canal cells have originated. Tetrasporangial conceptacles are characteristically sloughed off along with the entire superficial layer and burying of the conceptacles does thus not occur.

Description of representative specimens

Representative specimens examined

South Africa: Mbibi, Sodwana Bay, KwaZulu-Natal (D Keats, 22.i.1991, UWC: COR-139; D Keats, 18.i.1992, UWC: 92/2).

Habitat and Phenology

See Keats & Chamberlain (1994).

Distribution

South Africa (Sodwana Bay) (Keats & Chamberlain 1994).

Habit and Vegetative Structure

Thalli are flat, smooth and featureless, lacking protuberances and bearing irregularities only as a result of conforming to an irregular surface (Pl. 65, Fig. 1). The thallus is thin to variably thick measuring up to 830 µm. Intact margins have not been examined. The cell surface (SEM) is both of the Phymatolithon- and Leptophytum-type and is generally of a matt texture.

The thallus is monomerous and dorsiventrally organised (Pl. 66, Fig. 2). The medullary filaments comprise 15-48% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 66, Fig. 4), with cells that are squat to rectangular and measure 5-19 µm long X 6-14 µm in diameter. Cell fusions are abundant (Pl. 66, Fig. 4). Secondary pit connections have not been seen.

The cortical filaments comprise 52-85% of the thallus thickness with cells that are squat to rectangular and measure 3-14 µm long X 5-12 µm in diameter. Cell fusions are abundant. Secondary pit connections were not seen. Subepithallial initials are square to elongate (Pl. 66, Fig. 3), and measure 5-12 µm long X 5-10 µm in diameter. Epithallial cells occur singly (up to 2 only when shedding) (Pl. 66, Fig. 3), are square to elliptical, and measure 4-11 µm long X 5-12 µm in diameter. Trichocytes occur singly, are separated from one another by the cells of one or generally more, normal erect filaments and trichocyte chains typically comprise only 2 cells; a megacell and a support cell. Individual trichocytes are rectangular and measure 13-16 µm long X 6-10 µm in diameter. They are rarely seen buried within the thallus.

Reproduction

Representative gametangial plants have not been observed.

Tetrasporangial conceptacles are small and domed; they are raised above the thallus surface and measure 110-265 µm in external diameter (Pl. 67, Figs 5-7). The conceptacle pores are distinctly sunken and the tetrasporangial conceptacles are characteristically borne in a distinct superficial layer of thin walled, lightly calcified, rectangular to elongate cells that are well differentiated from the well-calcified outer cortical filaments below (Pl. 67, Fig. 6). Their chambers are elliptical to spherical (Pl. 67, Figs 6 & 7), and measure 58-125 µm in diameter X 31-95 µm high, with the roof 19-25 µm thick. The roof is 2-4 (mostly 3) cells thick, comprising a single, spherical to domed to elongate epithallial cell, a single elongate meristematic cell that is roughly 1.5-2X the length of the epithallial cell, and 1-2 small inner cells that are also roughly spherical (Pl. 67, Fig. 8). As the conceptacles are borne in a superficial layer above the surrounding thallus surface, the conceptacle floor is typically 4 cells above the surrounding thallus surface to flush with the surrounding thallus surface (Pl. 67, Figs 6 & 7). The conceptacle roof is formed from filaments interspersed among the sporangia (Pl. 67, Fig. 8) and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 67, Fig. 9). Remnants of the filaments that give rise to the enlarged cells are visible well after the roof has been formed (Pl. 67, Fig. 9). The pore-canal filaments are oriented more-or-less vertically, and do not tilt into the pore. A central columella has not been seen. Tetrasporangia have been observed to occur across the conceptacle chamber floor except at the very centre from were the pore canal cells have originated. Tetrasporangial conceptacles are characteristically sloughed off along with the entire superficial layer and burying of the conceptacles does thus not occur. However, crescent-shaped scars indicating infilling of areas previously occupied by sporangial conceptacles are visible at the thallus surface (Pl. 67, Fig. 5).

Key features

Hydrolithon superficiale is characterised by the following **combination** of characters: 1) thallus variably thin to thick, adherent, smooth, lacking protuberances; 2) thallus monomerous; 3) medullary filaments plumose; 4) mature tetrasporangial conceptacles that are domed and raised above the thallus surface and borne in a superficial, lightly calcified layer; 5) trichocytes present, both at the surface and rarely immersed in the thallus, occurring singly; 6) trichocytes are separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and <u>not</u> peripheral to them; 9) the tetrasporangial pore canal <u>not</u> usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is usually only 3 cells thick, comprising a single, spherical to domed epithallial cell, a single elongate meristematic cell that is roughly 1.5-2X the length of the epithallial cell, and a small inner cell that is also roughly spherical; 11) the sporangial conceptacle floor is commonly 0 (flush) to 4 cells above the surrounding thallus surface.

Remarks

<u>Hydrolithon superficiale</u> has been well documented and described. Keats & Chamberlain (1994) have shown convincingly that <u>Hydrolithon superficiale</u> is unique, differing from a host of other species belonging to the genus <u>Hydrolithon</u>. This species is, however, very similar to <u>Hydrolithon samoënse</u>, bearing a very similar tetrasporangial roof structure that has characterised the latter species. Both species have a tetrasporangial conceptacle roof that is commonly 3 cells thick; a single epithallial cell subtending an elongate meristematic cell, which in turn subtends a small inner cell. There are, however, a few subtle differences in their tetrasporangial roof anatomies.

<u>Hydrolithon samoënse</u>

The tetrasporangial conceptacle roof is usually only 3 cells thick,

1. comprising a single squat to elliptical to spherical epithallial cell,
2. a single elongate meristematic cell that is 2.5-5X the length of the epithallial cell,
3. and a small inner cells that is generally squat.

<u>Hydrolithon superficiale</u>

The tetrasporangial conceptacles roof is usually only 3 cells thick,

1. comprising a single, spherical to domed epithallial cell,
2. a single elongate meristematic cell that is 1.5-2X the length of the epithallial cell,
3. and a small inner cell that is roughly spherical.

Beside the above subtle differences, the most pronounced difference between these two species is the vegetative anatomy surrounding the tetrasporangial conceptacles, and the manner in which the tetrasporangial conceptacles are shed. In <u>Hydrolithon superficiale</u> the conceptacles are produced in a superficial layer above the thallus surface and consequently the conceptacle floor is typically 4 cells above the surrounding thallus surface to flush with the surrounding thallus surface. Upon senescence, these conceptacles are shed in unison in the superficial layer. In <u>Hydrolithon samoënse</u> the tetrasporangial conceptacles are produced in the outer thallus, with the conceptacle floor 8-16 cells below the thallus surface. Upon senescence, the conceptacles are most often shed as discrete units leaving scars that eventually become infilled.

Basionym

Neogniolithon rufum Adey, Townsend & Boykins 1982: 17

Pl. 68-71, Figs 1- 18.

Current Placement/Name

Neogniolithon rufum Adey, Townsend & Boykins 1982: 17

Holotype

USNC. Waikiki, Oahu, Hawaii; D. Child, 71-50-80. Paratypes exist from French Frigate (71-78-14), Hawaii (71-58-14), Oahu (71-81-28), Waikiki (71-50-20, 71-50-31, 71-50-72, 71-50-80) and Midway (71-82-57)) (see Adey, Townsend & Boykins 1982: 20).

Synonyms

None.

Etymology

'rufum', rufus = reddish brown (Stearn 1973). The epithet refers to the unique colour of the crusts ranging from bright pink to yellow brown.

Description of Type

Habit and Vegetative Structure

The following description is based on the micro-slides of the holotype material housed at USNC as well as the paratypes collected from all localities (see figure legend for specimen numbers). The type fragments are generally thin to moderately thick and adherent, measuring up to 1325 µm thick. The type material is generally smooth and featureless to only slightly warty (knobby) (see Adey et al. 1982).

The thallus is monomerous and dorsiventrally organised (Pl. 68, Figs 1 & 2). The medullary filaments comprise 8-56% of the thallus thickness and consist of a central, predominantly plumose (non-coaxial) core that may also be coaxial (Pl. 68, Figs 1, 2, 4 & 6), with cells that are square to elongate and measure 7-20 µm long X 5-11 µm in diameter. Cell fusions are abundant (Pl. 68, Figs. 4 & 6). Secondary pit connections have not been seen.

The cortical filaments comprise up to 92% of the thallus thickness (Pl. 68, Figs 1 & 2) with cells that are squat to rectangular and measure 4-16 µm long X 5-12 µm in diameter. Cell fusions are abundant (Pl. 68, Fig. 3). Secondary pit connections were not seen. Subepithallial initials are squat to square (Pl. 68, Fig. 3), and measure 4-8 µm long X 4-10 µm in diameter. Epithallial cells occur singly (Pl. 68, Fig. 3), are squat to elliptical, and measure 2-6 µm long X 4-10 µm in diameter. Trichocytes are rare but when they are found, they occur singly, in pairs and in small vertical rows (Pl. 68, Figs 5 & 6; Pl. 71, Fig. 16). Trichocytes (except pairs) are separated from one another by the cells of one or generally more, normal erect filaments and trichocyte chains typically comprise 2-11 cells; a megacell, and up to 10 support cells. Individual trichocytes are square to elongate, and measure 11-32 µm long X 7-11 µm in diameter. Trichocytes are overgrown and buried within the thallus (Pl. 68, Fig. 7; Pl. 71, Fig. 16).

Reproduction

Gametangial plants may be both monoecious and dioecious (Pl. 70, Fig. 11). Spermatangial conceptacles are quite large, raised, and measure 315-600 µm in external diameter (Pl. 70, Fig.

12). The conceptacle chamber is elliptical to boat-shaped (Pl. 70, Fig. 12), measuring 250-385 µm in diameter X 47-110 µm high, with the roof 62-81 µm thick. Simple spermatangial systems are borne only on the floor of the conceptacle chamber (Pl. 70, Figs 12 & 13). Spermatangial conceptacles are overgrown and become buried in the thallus (Pl. 70, Fig. 11).

Only a single large, raised, carpogonial conceptacle has been observed, measuring 350 µm in external diameter (Pl. 71, Fig. 14), with a roof 74.4 µm thick. Its chamber is wide and shallow, and more-or-less triangular in shape, measuring 125-178 µm in diameter X 31-47 µm high. 3-Celled carpogonial branches occur across the chamber floor (Pl. 71, Fig. 15). Carposporangia develop in carpogonial conceptacles after presumed karyogamy.

Carposporangial conceptacles are also large, measuring 312-530 µm in external diameter (Pl. 71, Fig. 17). Chambers of carposporangial conceptacles are elliptical to bean-shaped, and measure 203-309 µm in diameter X 47-81 µm high with the roof 87-122 µm thick. The continuous, discoid central fusion cell is wide and thick (Pl. 71, Fig. 18), with gonimoblast filaments borne peripherally and unfertilised carpogonia persisting across the centre of the fusion cell (Pl. 71, Figs 17 & 18). Gonimoblast filaments are 6-7 cells long including a terminal carpospore that measures 12-29 µm long X 19-34 µm in diameter. Buried carposporangial conceptacles have been observed (Pl. 70, Fig. 11).

Tetrasporangial conceptacles are flush to slightly raised above the rest of the thallus surface (Pl. 69, Fig. 8). Conceptacles are low domed and measure 225-325 µm in external diameter. Their chambers are elliptical to spherical (Pl. 69, Figs 8 & 9), and measure 91-156 µm in diameter X 56-94 µm high, with the roof 295-43 µm (5-7 cells) thick. The conceptacle floor is located 8-14 cells below the surrounding thallus surface. The roof is formed from filaments interspersed among the sporangia and a ring of enlarged, domed cells lines the base of the pore canal (Pl. 69, Fig. 10).

The pore-canal filaments are usually oriented more-or-less vertically, and do not tilt markedly into the pore. A central columella has not been observed and zonately divided tetrasporangia are located across the conceptacle chamber floor (Pl. 69, Fig. 9). Tetrasporangia measure 36-56 µm long X 10-16 µm in diameter. Bisporangial plants were not seen. Old tetrasporangial conceptacles are often seen buried in the thallus containing apparently viable tetrasporangia; infilling of conceptacles have not been observed (Pl. 69, Fig. 8).

Distribution

Hawaiian Archipeligo (Adey et al. 1982).

Key features

Neogoniolithon rufum is characterised by the following **combination** of characters: 1) thallus variably thin to thick, adherent, smooth to only slightly lumpy, lacking protuberances; 2) thallus monomerous; 3) medullary filaments predominantly plumose, but also occationally coaxial; 4) tetrasporangial conceptacles that are domed, and flush to slightly raised above the thallus surface; 5) trichocytes rare, both at the thallus surface and immersed in the thallus, occurring singly, paired and in vertical rows; 6) individual unpaired trichocytes are separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and *not* peripheral to them; 9) the tetrasporangial pore canal *not* lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is usually 5-7 cells thick; 11) the sporangial conceptacle floor is commonly 8-14 cells below the surrounding thallus surface; 12) tetrasporangial conceptacles lacking a central columella with sporangia distributed across the chamber floor.

Remarks

The context within which Neogoniolithon rufum was described (Adey et al. 1982) was at a time when the genus Neogoniolithon was considered to represent all Mastophoroid taxa bearing monomerous thalli that bore predominantly coaxial medullary filaments. In contrast, Hydrolithon was considered to encompass all Mastophoroid taxa bearing dimerous thalli. Of secondary importance too, were the trichocyte arrangements. This study has shown that although coaxial areas exist, Neogoniolithon rufum has predominantly plumose medullary filaments. Since the review of Penrose & Woelkerling (1992), it is now widely accepted that the thallus construction and the trichocyte arrangements cannot be used at the genus level, but that the development of the sporangial conceptacle roof is of particular importance at this taxonomic level. The development of the sporangial concepacle roof in Neogoniolithon rufum is from filaments interspersed among the sporangia and not peripheral to them. Also, the base of the sporangial pore canal is lined by a ring of conspicuous, enlarged, domed cells and **not** by narrow filaments that tilt into the pore canal creating the appearance of papillae. These features are diagnostic of the genus Hydrolithon and in light of these findings it is clear that Neogoniolithon rufum belongs within the confines of the genus Hydrolithon and not Neogoniolithon. An analysis of the taxa ascribed to the genus Hydrolithon suggests that Neogoniolithon rufum is conspecific with Hydrolithon rupestris (Table 5). With the exception of a few subtle differences (internal dimensions of gametangial conceptacles) the two taxa are alike in all respects.

Basionym

Neogoniolithon rugulosum Adey, Townsend & Boykins 1982: 17

Pl. 72-73, Figs 1- 9.

Current Placement/Name

Neogoniolithon rugulosum Adey, Townsend & Boykins 1982: 17

Holotype

USNC. Palea Point, Hanauma Bay, Oahu, Hawaii; D.Child, 71-53-2.

Paratypes also exist from: Hawaii: Hilo Bay, 71-59-1; Oahu: Hanauma Bay, 71-53-4, 71-53-22.

Synonyms

None.

Etymology

'rugulosum', rugulosus = somewhat wrinkled (Stearn 1973). The epithet refers to the rugulose, somewhat wrinkled nature of the thallus surface.

Description of Type

Habit and Vegetative Structure

The following description is based on the micro-slides of the paratypes material housed at USNC (71-53-4) collected from Hanauma bay, Oahu. The type fragments are very thin and adherent, measuring only up to 295 µm thick. The type material is generally smooth and featureless to only slightly lumpy and rugulose (see Adey et al. 1982).

The thallus is monomerous and dorsiventrally organised (Pl. 72, Fig. 1; Pl. 73, Fig. 4). The medullary filaments ccomprise 7-30% of the thallus thickness and consist of a central plumose (non-coaxial) core (Pl. 72, Figs 1 & 3; Pl. 73, Fig. 4), with cells that are square to rectangular and measure 6-17 µm long X 4-11 µm in diameter. Cell fusions are abundant (Pl. 72, Fig. 3). Secondary pit connections have not been seen.

The cortical filaments comprise 70-93% of the thallus thickness (Pl. 72, Fig. 1; Pl. 73, Fig. 4) with cells that are squat to rectangular and measure 3-10 µm long X 5-14 µm in diameter. Cell fusions are abundant (Pl. 72, Fig. 2). Secondary pit connections were not seen. Subepithallial initials are square to rectangular (Pl. 72, Fig. 2), and measure 7-15 µm long X 6-10 µm in diameter. Epithallial cells occur singly (up to 2 only when shedding) (Pl. 72, Fig. 2), are squat to elliptical, and measure 2-9 µm long X 3-10 µm in diameter. Trichocytes commonly occur singly and paired (Pl. 72, Fig. 2), and individual trichocyte chains typically comprise 2 cells; a megacell and a support cells. Individual trichocytes are rectangular to elongate, and measure 16-27 µm long X 10-15 µm in diameter. Buried trichocytes have not been observed.

Reproduction

Gametangial plants have not been observed.

Tetrasporangial conceptacles are small (Pl. 73, Figs 5-7). They are more-or-less flush with the thallus surface, to slightly raised above it and measure 136-198 µm in external diameter. Their chambers are elliptical to spherical (Pl. 73, Figs 5-7), and measure 72-104 µm in diameter X 29-50 µm high, with the roof 25-31 µm thick. The roof is 2-4 (mostly 3) cells thick, always comprising a single squat to elliptical to spherical epithallial cell, a single elongate meristematic cell that is 2.5-5X the length of the epithallial cell, and 1-2 small inner cells (Pl. 73, Fig. 9). The conceptacle floor is located 6-12 cells below the surrounding thallus surface. From the orientation of the conceptacle roof cells, it appears that the roof is formed from filaments interspersed among the sporangia. A ring of enlarged, domed cells lines the base of the pore canal (Pl. 73, Fig. 8) and the remains of the sterile filaments that gave rise to the pore canal cells are often visible (Pl. 73, Figs 6 & 8). The pore-canal filaments are oriented more-or-less vertically, and do not tilt into the pore. A central columella has not been observed and mature zonately divided tetrasporangia fill the chamber completely (Pl. 73, Fig. 6). Tetrasporangia measure 20-43 µm long X 7-27 µm in diameter. Bisporangial plants were not seen. Sporangial conceptacles are shed individually although old tetrasporangial conceptacles are often seen buried in the thallus containing apparently viable tetrasporangia; infilling of conceptacles have not been observed (Pl. 73, Fig. 5).

Distribution

Hawaii (Hawaii, Oahu) (Adey et al. 1982), Tropical Pacific (Littler & Littler 2003).

Key features

Neogoniolithon rugulosum is characterised by the following **combination** of characters: 1) thallus thin, adherent, smooth to lumpy, lacking protuberances; 2) thallus monomerous; 3) medullary filaments plumose; 4) tetrasporangial conceptacles that are flush to only slightly raised above the thallus surface; 5) trichocytes present only at the thallus surface, occurring singly and paired; 6) trichocytes (except pairs) are separated by the cells of normal cortical filaments; 7) the base of tetrasporangial conceptacle pore canals lined by a ring of conspicuous, enlarged, domed cells; 8) the tetrasporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them; 9) the tetrasporangial pore canal not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae, 10) the tetrasporangial conceptacle roof is usually only 3 cells thick, comprising a single squat to elliptical to spherical epithallial cell, a single elongate meristematic cell that is 2.5-5X the length of the epithallial cell, and a small inner cell; 11) the sporangial conceptacle floor is commonly 6-12 cells below the surrounding thallus surface.

Remarks

The context within which Neogoniolithon rugulosum was described (Adey et al. 1982) was at a time when the genus Neogoniolithon was considered to represent all Mastophoroid taxa bearing monomerous thalli that bore predominantly coaxial medullary filaments. In contrast, Hydrolithon was considered to encompass all Mastophoroid taxa bearing dimerous thalli. Of secondary importance too, were the trichocyte arrangements. This study has shown that Neogoniolithon rugulosum has plumose medullary filaments. Since the review of Penrose & Woelkerling (1992), it is now widely accepted that the thallus construction and the trichocyte arrangements cannot be used at the genus level, but that the development of the sporangial conceptacle roof is of particular importance at this taxonomic level. The development of the sporangial concepacle roof in Neogoniolithon rugulosum is from filaments interspersed among the sporangia and not peripheral to them. Also, the base of the sporangial pore canal is lined by a ring of conspicuous, enlarged, domed cells and **not** by narrow filaments that tilt into the pore canal creating the appearance of papillae. These features are diagnostic of the genus Hydrolithon and in light of these findings it is clear that Neogoniolithon rugulosum belongs within the confines of the genus Hydrolithon and not Neogoniolithon.

An analysis of the taxa ascribed to the genus Hydrolithon suggests that Neogoniolithon rugulosum is conspecific with Hydrolithon samoënse and thus also Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov. (which has nomenclatural priority - see Table 6), based on the sporangial conceptacle roof anatomy and depth of the conceptacle floor. Adey et al. (1982: 15) even make mention of Neogoniolithon caribauem as a “pair species” to Neogoniolithon rugulosum, a species this research has also shown to be conspecific with Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov. Neogoniolithon rugulosum also bears a similar sporangial conceptacle roof structure to Hydrolithon superficiale but like Hydrolithon samoënse it differs from the former with regard to the dimensions of the roof cells (see Hydrolithon superficiale earlier). Also, Neogoniolithon rugulosum buries as well as sheds its sporangial conceptacles individually upon senescence. This is in contrast to Hydrolithon superficiale that produces its conceptacles in a superficial layer above the thallus surface and then sheds the entire superficial layer in unison upon senescence.

TYPE MATERIAL NOT OBTAINED

1. Basionym (& Herbarium)

Hydrolithon arenicolum Dawson 1960: 26 ("arenicola") (AHFH – transferred to LAM, see Anderson 1991: 29)

Current Placement/Name

Hydrolithon arenicolum Dawson 1960: 26 ("arenicola")

Synonyms

None.

Herbarium policy prevented the loan and examination of this specimen.

2. Basionym (& Herbarium)

Hydrolithon iyengarii Desikachary & E. Ganesan 1967: 89 (no mention of herbarium at which type was deposited)

Current Placement/Name

Hydrolithon iyengarii Desikachary & E. Ganesan 1967: 89 (see also Krishnamurthy & Jayagopal 1987: 89)

Synonyms

None.

The above authors were unable to supply material from the type locality.

3. Basionym (& Herbarium)

Hydrolithon krusadiense V. Krishnamurthy & Jayagopal 1987: 89 (no mention of herbarium at which type was deposited)

Current Placement/Name

Hydrolithon krusadiense V. Krishnamurthy & Jayagopal 1987: 89

Synonyms

None.

The above authors were unable to supply material from the type locality.

Krishnamurthy & Jayagopal (1987: 90) described this new species without any reference to sporangial material. Since Sporangial material is critical for the designation of taxa to the genus Hydrolithon, it remains questionable as to whether indeed this species is a distinct species, or whether it even belongs within the genus Hydrolithon.

4. Basionym (& Herbarium)

Hydrolithon verrucosum V. Krishnamurthy & Jayagopal 1987: 91 (no mention of herbarium at which type was deposited)

Current Placement/Name

Hydrolithon verrucosum V. Krishnamurthy & Jayagopal 1987: 91

Synonyms

None.

The above authors were unable to supply material from the type locality.

Not enough characters (particularly sporangial) are supplied to determine the generic delimitation of this taxon within a modern context. Generic considerations, particularly between the genera Pneophyllum and Hydrolithon, are simply outdated and cannot be used to adequately evaluate this taxon. A revision within a modern context is suggested.

DISCUSSION

From the descriptions above it is evident that a number of taxa are conspecific (Tables 7 & 8). Although vegetative characters and characters pertaining to tetra/bisporangial conceptacles have been widely used to delimit species of Hydrolithon (see Table 9), it appears that within the group, the gross morphology is quite often a useful character in delineating those taxa ascribed to Hydrolithon. We should, however, bear in mind that this very character (gross morphology) has been the reason for much of the varied names by which these taxa have been referred. It has only been through ecological studies (e.g. Bosence 1976; Littler et al. 1995; Littler & Littler 2000, 2003) that morphology in response to environmental factors has shown the variable nature of the morphology of many coralline algae. None-the-less, these ecological studies have shown that we can use the gross morphology (once we have identified the environmental factor that the spcies is responding to) to delineate taxa at least to a degree of accuracy.

According to Chamberlain (1991) it was a widely accepted practice to describe taxa largely or even solely on differences in growth forms. Foslie, for example, described a large number of taxa in this manner, quite often using specific morphological and vegetative features to delineate taxa, and basing his descriptions on single specimens or collections (see Woelkerling 1984, 1993). With many researchers following suit (eg. Lemoine) this lead to a substantial increase in the number of described taxa, many of which were poorly delimited (Woelkerling 1984; Chamberlain 1991). This problem was confounded by the fact that even characters used to delineate genera where no longer reliable (Woelkerling 1985; Penrose & Woelkerling 1988).

It was only recently that the generic delimitation of Hydrolithon was resolved (Penrose 1991, 1992; Penrose & Woelkerling 1991, 1992; Penrose & Chamberlain 1993). The primary character used to delineate Hydrolithon from other Mastophoroid genera concerns those cells lining the base of the tetrasporangial pore canal. In Hydrolithon, the pore canals of the tetrasporangial conceptacles are lined by a ring of conspicuous, enlarged cells that arise from filaments interspersed among the sporangial initials. These cells do not protrude into the pore canal and are oriented more-or-less perpendicularly to the roof surface.

Key to the genus Hydrolithon (excluding species of which material has not been obtained)

1. Thallus dimerous; trichocytes most often occurring singly, occasionally in pairs and/or small horizontal rows ..………………………………………………………….... **2**

   Thallus monomerous; trichocytes occurring in large horizontal pustulate fields without any vegetative filaments between the individual trichocytes …..… ………………….…. **4**

2. Plants commonly composed of applanate branches that overgrow one another; sporangial conceptacle pores not sunken ……..………..…………….... **H. improcerum**

   Plants rarely with applanate branches that overgrow one another; sporangial conceptacle pores sunken ……………………………………..……………………..…...……..... **3**

3. Cells of erect filaments strongly horizontally arranged ………..……….….. **H. reinboldii**

   Cells of erect filaments not strongly horizontally arranged …………..… **H. boergesenii**

4. Plants forming massive mountain-like upgrowths when mature or are fruticose ……... **5**

   Plants smooth, warty, lumpy or lobed …………...………...………….……………..… **6**

5. Plants forming massive mountain-like upgrowths when mature …..…..... **H. craspedium**

   Plants fruticose, producing narrow, terete, somewhat dichotomously branched and generally unfused protuberances ………………..…………….…..…..… **H. gardineri**

6. Plants commonly comprised of only one layer of epithallial cells ...…..……..………… **7**

   Plants commonly with up to 5 layers of epithallial cells ……..……..……..… **H. onkodes**

7. Tetrasporangial conceptacle roofs typically 3 cells thick, comprising a single epithallial cell, a single elongate meristematic cell, and a single small inner cell ………….....…… **8**

Tetrasporangial conceptacle roofs usually more than 3 cells thick ……..…...…….…....... **9**

8. 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 1.5-2X the length of the epithallial cell ....……..…....……… **H. superficiale**

Mature conceptacles not occurring in a superficial layer, conceptacles shed individually or in small groups upon senescence; conceptacle roofs comprising an elongate meristematic cell that is 2.5-5X the length of the epithallial cell ……........…. **H. erosum**

9. Tetrasporangial conceptacles usually possessing a central columella with peripherally located sporangia ……………………...……...………………….....……… **H. munitum**

Tetrasporangial conceptacles lacking a central columella with sporangia distributed across the chamber floor ……………………………………………....…… **H. rupestris**

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Table 1. Taxa examined that have been ascribed to the genus Hydrolithon Foslie 1909.

Original Foslie species (Type species in bold)

1. Hydrolithon boergesenii (Foslie) Foslie 1909: 56.
   Goniolithon boergesenii Foslie 1901a: 19.
2. Hydrolithon. breviclavium (Foslie) Foslie 1909: 56.
   Goniolithon breviclavium Foslie 1907a: 20.
3. Hydrolithon improcerum (Foslie & Howe) Foslie 1909: 55.
   Goniolithon improcerum Foslie & Howe in Foslie 1907b: 24.
4. **Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie 1909: 55.**
   Lithophyllum reinboldii Weber van Bosse & Foslie in Foslie 1901b: 5.

Additional taxa

5. Hydrolithon craspedium (Foslie) P. Silva in Silva et al, 1996: 235.
   Lithophyllum craspedium Foslie 1900a: 26.
6. Hydrolithon gardineri (Foslie) Verheij & Prud'homme van Reine 1993: 451.
   Lithophyllum gardineri Foslie 1907a: 30.
7. Hydrolithon falklandicum (Foslie) Mendoza 1979: 10.
   Lithophyllum marlothii forma falklandica Foslie 1905b: 17
8. Hydrolithon munitum (Foslie & Howe) Penrose in Womersley 1996: 263.
   Lithophyllum munitum Foslie & Howe 1906: 132.
9. Hydrolithon ruprestris (Foslie) Penrose in Womersley 1996: 265.
   Lithophyllum rupestre Foslie 1907a: 26.
10. Hydrolithon samoënse (Foslie) Keats & Chamberlain 1994: 15.
    Lithophyllum samoënse Foslie 1906: 20.
11. Hydrolithon onkodes (Heydrich) Penrose & Woelkerling 1992: 83
    Lithothamnion onkodes Heydrich 1897: 6-7
12. Hydrolithon megacystum Adey, Townsend & Boykins 1982: 32
13. Hydrolithon murakoshii Iryu & Matsuda 1996: 528
14. Hydrolithon superficiale Keats & Chamberlain 1994: 12
15. Spongites discoideus (Foslie) D. Penrose & Woelkerling 1988: 173
    1. Lithophyllum consociatum Foslie 1905b: 15 [Hydrolithon consociatum (Foslie) Mendoza 1979: 8]
    2. Lithophyllum decipiens forma subantarctica Foslie 1906: 18 [Hydrolithon subantarcticum (Foslie) Mendoza & Cabioch 1985: 259]

Table 2. The list of Herbaria cited in Paper 2: Hydrolithon (Acronyms follow Holmgren et al. 1990).

AHFH	LOS ANGELES: Herbarium, Allan Hancock Foundation, University of Southern California, Los Angeles, California 90089-0371, U.S.A. – transferred to LAM and RSA
BM	LONDON: Herbarium, Botany Department, The Natural History Museum, Cromwell Road, London SW7 5BD, England, U.K.
C	COPENHAGEN: Herbarium, Botanical Museum, University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen K, Denmark
HAK	HAKODATE: Herbarium, Laboratory of Marine Botany, Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido 041, Japan
IGPS[1]	SENDAI: Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Aobayama, Sendai 980-77, Japan
L	LEIDEN: Rijksherbarium, Postbus 9514, 2300 RA Leiden, Netherlands
LAM	LOS ANGELES: Herbarium, Botany Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A.
NY	NEW YORK: Herbarium, New York Botanical Garden, Bronx, New York 10458-5126, U.S.A.
PC	PARIS: Herbier, Laboratoire de Cryptogamie, Muséum National d'Histoire Naturelle, 12 rue Buffon, F-75005 Paris, France
RSA	CLAREMONT: Herbarium, Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711-3157, U.S.A.
TO	TORINO: Erbario, Dipartimento di Biologia Vegetale, Università degli Studi di Torino, Viale Pier Andrea Mattioli 25, I-10125 Torino, Italy
TRH	TRONDHEIM: Herbarium, Museum of Natural History and Archaeology, Department of Botany, University of Trondheim, N-7004 Trondheim, Norway
UC	BERKELEY: University Herbarium, University of California, Berkeley, California 94720, U.S.A.
US	WASHINGTON: United States National Herbarium, Botany Department, NHB-166, Smithsonian Institute, Washington, D.C. 20560-0001, U.S.A.
USNC	WASHINGTON: Herbarium, Paleobiology Department, Smithsonian Institute, Washington, D.C. 20560-0001, U.S.A.
UWC	BELLVILLE: Herbarium, Botany Department, University of the Western Cape, Private Bag X17, Bellville 7535, Cape Province, South Africa

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[1] Not a registered herbarium.

Table 3. A comparative analysis of selective vegetative and reproductive characters of Hydrolithon onkodes (Heydrich) Penrose & Woelkerling (1992: 83) and Hydrolithon munitum Penrose (1996: 263) (all measurements are in µm).

Feature:	**Hydrolithon onkodes**	**Hydrolithon munitum**
General thallus form	Generally smooth to occasionally warty to lumpy	Smooth to warty to lumpy (with numerous nodular protuberances) and may also occur as rhodoliths
No. of epithallial cell layers	1-3 cell layers (mostly 2-3 but up to 5 when shedding)	1
Trichocyte arrangement	In large horizontal pustulate fields	Singly, occasionally in vertical rows, but also in small horizontal (non-pustulate) rows
Trichocytes buried in thallus	yes	no
No. of cells in gonimoblast filaments	9-11	5-6
No. of cells in sporangial conceptacle roof	7-11	4-8
Depth of sporangial conceptacle floor (cells)	12-19	7-12

Table 4. A comparative analysis of the vegetative and reproductive anatomy of Hydrolithon boergesenii (Foslie) Foslie (1909: 56), Hydrolithon munitum Penrose (1996: 263), Hydrolithon rupestris Penrose (1996: 265) and Hydrolithon murakoshii Iryu & Matsuda (1996: 528) (all measurements are in µm).

Feature:	**Hydrolithon boergesenii**	**Hydrolithon munitum**	**Hydrolithon rupestris**	**Hydrolithon murakoshii**
General thallus form	smooth to warty to lumpy	smooth to warty to lumpy	smooth to warty	smooth, **microscopically tessellate**
Thallus construction	**dimerous**	monomerous	monomerous	monomerous
No. of epithallial cell layers	1	1	1	1
Epithallial cell: shape	squat to elliptical	squat to elliptical	squat to elliptical	elliptical
length	4-7	5-10	4-6	5-7
diameter	7-14	6-12	4-10	5-10
Subepithallial cell: shape	square to rectangular	square to elongate	squat to square	square to elongate
length	7-15	9-19	4-11	10-15
diameter	6-15	5-10	5-10	4-6
Thickness (%) comprised of cortical filaments	N/A	63-91	47-91	62-78
Trichocyte: arrangement	singly, small horizontal groups of 2-3	singly, small horizontal groups and in vertical rows	single and in vertical rows	singly, small horizontal groups and in vertical rows
buried in thallus	yes	yes	yes	yes
Condition of medullary filaments	N/A	plumose	plumose	predominantly plumose
Sporangial conceptacle	flush to slightly raised	slightly sunken to flush to slightly raised	flush to slightly raised	slightly sunken to flush to slightly raised
external diameter	240-480	390-515	250-400	240-400
no. of roof cells	4-5	4-8	4-7	3-6

Feature (cont.):	**Hydrolithon boergesenii**	**Hydrolithon munitum**	**Hydrolithon rupestris**	**Hydrolithon murakoshii**
chamber diameter	225-255	110-275	115-190	130-325
chamber height	110-160	78-164	75-105	43-150
depth of floor (cells)	12	7-12	10-14	8-11
Sporangial distribution	**?**	**peripheral**	**across**	**peripheral**
Columella	**?**	**present**	**absent**	**present**
Gametangial plants	**-**	monoecious/**dioecious**	monoecious	monoecious
Spermatangial conceptacle	**-**	flush to slightly raised	flush to slightly raised	flush to slightly raised
chamber diameter	**-**	109-352	**49-56**	94-245
chamber height	**-**	31-140	16-49	28-46
Carposporangial conceptacle	**-**	flush to slightly raised	flush to slightly raised	flush to slightly raised
chamber diameter	**-**	164-250	77-150	135-188
chamber height	**-**	60-115	50-90	48-69
Type of fusion cell	**-**	**broad**, thin to thick & continuous	**broad**, thick & continuous	**narrow**, thick & continuous
# of cells in gonimoblast filament	**-**	5-6	2+	5*
gonimoblast distribution	**-**	peripheral	peripheral	peripheral

Data from type and representative specimens from the present research are included here.

Additional data from Penrose (1996) and Iryu & Matsuda (1996).

* Iryu & Matsuda (1996: 531) do not include the carpospore in the count of gonimoblast filament cells.

Table 5. A comparative analysis of the vegetative and sporangial anatomy of *Neogoniolithon rufum* Adey, Townsend & Boykins (1982: 17) and *Hydrolithon rupestris* Penrose (1996: 265) (all measurements are in µm).

Feature:	***Neogoniolithon rufum***	***Hydrolithon rupestris***
General thallus form	smooth to warty, lacking protuberances	smooth to warty, lacking protuberances
Thallus construction	monomerous	monomerous
No. of epithallial cell layers	1	1 (2-3 only when shedding)
Epithallial cell: shape	squat to elliptical	squat to elliptical
length	2-6	4-6
diameter	4-10	4-10
Subepithallial cell: shape	squat to square	squat to square
length	4-8	4-11
diameter	4-10	5-10
Thickness (%) of thallus comprised of cortical filaments	44-92	47-91
Cortical cell: shape	squat to rectangular	squat to rectangular
length	4-16	3-12
diameter	5-12	5-11
Trichocyte: occurrence	rare	rare
arrangement	single, paired and in vertical rows	single and in vertical rows
buried in thallus	yes	yes
No. of cells in vertical trichocyte chain	2-10	2-6
Condition of medullary filaments	plumose (mostly) and coaxial	plumose
Thickness (%) of thallus comprised of medullary filaments	8-56	9-53
Sporangial conceptacle	flush to slightly raised	flush to slightly raised
external diameter	225-325	250-400
chamber shape	elliptical to spherical	elliptical to spherical
no. of roof cells	5-7	4-7
Sporangial distribution	across floor	across floor
Columella	absent	absent

Feature (cont.):	**Neogoniolithon rufum**	**Hydrolithon rupestris**
Gametangial plants	monoecious & dioecious	monoecious
Spermatangial conceptacle	slightly raised	flush to slightly raised
chamber diameter	**250-385**	**49-56**
chamber height	**47-110**	**16-49**
Carposporangial conceptacle	flush to raised	flush to slightly raised
chamber diameter	**203-309**	**77-150**
chamber height	47-81	50-90
Type of fusion cell	broad, thick & continuous	broad, thick & continuous
# of cells in gonimoblast filament	6-7	2+
gonimoblast distribution	peripheral	peripheral

Table 6. A comparative analysis of the sporangial anatomy of Neogoniolithon erosum (Foslie) Adey (1970: 8), Hydrolithon samoënse (Foslie) Keats & Chamberlain (1994: 15), Neogoniolithon caribaeum (Foslie) Adey (1970: 8) and Neogoniolithon rugulosum Adey, Townsend & Boykins (1982: 17) (all measurements are in µm and those in brackets are extremes).

Presently valid name:	Neogoniolithon erosum (Foslie) Adey 1970: 8	Hydrolithon samoënse (Foslie) Keats & Chamberlain 1994: 15	Neogoniolithon caribaeum (Foslie) Adey 1970: 8	Neogoniolithon rugulosum Adey, Townsend & Boykins 1982: 17
Basionym:	Lithophyllum erosum Foslie 1906: 20	Lithophyllum samoënse Foslie 1906: 20	Lithophyllum decipiens f. caribaea Foslie 1906:18 - Lithophyllum caribaeum (Foslie) Foslie 1907: 22 -	Neogoniolithon rugulosum Adey, Townsend & Boykins 1982: 17
Derived name:	Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov.	Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov.	Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov.	Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov.
Tetrasporangial features				
Conceptacle orientation	flush to slightly raised	slightly sunken to flush to slightly raised	flush to slightly raised	flush to slightly raised
Shape	low domed	low domed	low domed	low domed
External diameter	105 – 275 **(330)**	125 - 200	73 - 155	136 - 198
Chamber shape	elliptical to spherical	elliptical to spherical	elliptical to spherical	elliptical to spherical
Chamber diameter	79-188 **(202)**	56 - 130	61 - 85	72 - 104
Chamber height	49-78 **(98)**	31 - 75	37 - 66	29 - 50
Depth of conceptacle floor (incl. epithallial cell)	8 - 15	8 - 16	12 - 17	6 - 12
Roof thickness	19 - 37	15 - 25	10 - 17	25 - 31

No. of roof cells (incl. epithallial cell)	2 - 4 (mostly 3)	2 - 4 (mostly 3)	2 - 4 (mostly 3)	2 - 4 (mostly 3)
Conceptacles buried	none seen buried	buried and shed	rarely buried	buried
Sporangia distribution	peripheral	across	peripheral	across
Columella	none seen	absent	none seen	absent

Table 7. The status and conspecificity of the taxa investigated that have been ascribed to the genus Hydrolithon.

Taxon	**Present Status**	**Conspecificity**
Hydrolithon boergensenii	unchanged	
Hydrolithon breviclavium	Spongites breviclavius	
Hydrolithon craspedium	unchanged	
Hydrolithon falklandicum	Pneophyllum/Spongites falklandicum ?	
Hydrolithon gardineri	unchanged	
Hydrolithon improcerum	unchanged	
Hydrolithon munitum	unchanged	
Hydrolithon murakoshii		Hydrolithon munitum
Hydrolithon onkodes	unchanged	
Hydrolithon reinboldii	unchanged	
Hydrolithon rupestris	unchanged	
Hydrolithon samöense		Hydrolithon erosum
Hydrolithon superficiale	unchanged	
Neogoniolithon caribaeum		Hydrolithon erosum
Neogoniolithon erosum	Hydrolithon erosum	
Neogoniolithon rufum		Hydrolithon rupestris
Neogoniolithon rugulosum		Hydrolithon erosum
Lithophyllum consociatum	Spongites discoideus / Pneophyllum consociatum ?	
Lithophyllum subantarcticum	Spongites discoideus	Pneophyllum consociatum ?

? – these taxa required greater investigation with analysis of additional material from the type localities.

Table 8. A comparative summary of the diagnostic characters in those taxa studied that have been ascribed to the genus Hydrolithon.

Species	**Thallus construction**	**No. of epithallial cell layers**[1]	**Trichocyte arrangement**	**Trichocyte fields pustulate (Yes/No)**	**No. of cells in sporangial concept. roof**	**Other**
Hydrolithon boergesenii	dimerous	1	Singly, but also in small groups of 2-3; at surface and buried.	No	4-5	Plants knobby, lumpy to smooth
Hydrolithon breviclavium	dimerous	1	Singly, but also in small groups of 2-3; at surface and buried.	No	8-9	Plants warty to lumpy
Hydrolithon consociatum	dimerous[2]	2-4	Singly[2], rare.	No	5-9	Plants warty
Hydrolithon craspedium	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	5-9	The thallus is massive and mountain-like, bearing broad individual to fused vertical columns.
Hydrolithon falklandicum	dimerous (secondarily monomerous)	2-3	Singly, but also paired, rare; only seen at thallus surface.	No	4-5?	Plants warty to lumpy
Hydrolithon gardineri	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	5-6	Plants fruticose, producing narrow, terete, somewhat dichotomously branched and generally unfused protuberances.
Hydrolithon improcerum	dimerous	1	Singly, but also in small horizontal rows; at surface and buried.	No	2-3	Plants smooth, flat; occur as applanate branches that overgrow one another
Hydrolithon megacystum	dimerous	1	Singly, but also in large horizontal rows?	No	-	Plants warty to lumpy[3]

Hydrolithon munitum	monomerous	1	Singly, but also in small horizontal rows, rare; only seen at thallus surface	No	5-8	Plants warty to lumpy, also as rhodoliths
Hydrolithon murakoshii	monomerous	1	Singly, but also in small horizontal rows and long vertical chains	No	4-6	Plants smooth and flat and microscopically tessellate[4]
Hydrolithon onkodes	monomerous	2-3	Large horizontal fields; at surface and buried.	Yes	7-11	Plants generally smooth and featureless but may also be upright, lobed and honey-combed in form.
Hydrolithon rupestris	monomerous	1	Singly, but also in vertical rows, rare; at surface and buried.	No	4-7	Plants smooth to warty
Hydrolithon reinboldii	dimerous	1	Singly, but also in pairs; at surface and buried.	No	4-5	Plants commonly occur as rhodoliths; cells of erect filaments strongly horizontally arranged
Hydrolithon samoënse	monomerous	1	Singly, but also paired and in vertical rows; at surface and buried.	No	2-4 (mostly 3)	Plants smooth, flat
Hydrolithon subantarcticum	dimerous	2-4	Singly[2], rare	No	-	Plants smooth, flat
Hydrolithon superficiale	monomerous	1	Singly; at the surface and buried	No	2-4 (mostly 3)	Plants smooth, flat

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[1] This excludes cell layers that are in the process of being shed.

[2] See Mendoza & Cabioch (1986).

[3] See Adey et al. (1982).

[4] See Iryu & Matsuda (1996).

Table 9. Characters that have been used previously in delimiting species of Hydrolithon (Data based on information in species keys and accounts from selected publications).

A. Vegetative characters

1. Thallus dimerous or monomerous (Chamberlain 1994a)
2. Thallus bistratose or multistratose (Chamberlain 1994a)
3. Plants epiphytic or epilithic (Chamberlain 1994a)
4. Plants branched or not branched (Verheij 1993)
5. Thalli forming imbricating layers or not forming imbricating layers (Chamberlain 1994a)
6. Number of cells surrounding germination disc (4, 8, 12) (Chamberlain 1994a)
7. Trichocytes (absent, present, individual or grouped into fields) (Keats & Chamberlain 1994)
8. Shape of cells of cortical filaments (Keats & Chamberlain 1994)

B. Characters pertaining to tetra/bisporangial conceptacles

1. Columella present or absent (Verheij 1993)
2. Height of conceptacles (Verheij 1993)
3. Depth of conceptacle floor (Verheij 1993)
4. Diameter of pore (Verheij 1993)
5. Conceptacles produced in a superficial layer of weakly calcified filaments or not (Keats & Chamberlain 1994)
6. Conceptacles buried or shed on senescence (Keats & Chamberlain 1994)
7. Tetrasporangial roof structure (Keats & Chamberlain 1994)

FIGURE CAPTIONS

Pl. 1

Goniolithon breviclavium Foslie

Fig. 1. The habit of the type of Goniolithon breviclavium Foslie.

Pl. 2

Goniolithon breviclavium Foslie

Figs 2-6. Vegetative anatomy of the type of Goniolithon breviclavium Foslie.

Fig. 2. The thallus surface showing relatively thin walled epithallial cells (arrowheads) with broad centrally located depressions bearing intact primary pit connections (arrow) (scale bar = 15 µm).

Fig 3. The thallus surface showing relatively thick walled epithallial cells (arrowheads) with narrow centrally located deep to shallow depressions. Some primary pit connections (arrow) are still visible (scale bar = 15 µm).

Fig. 4. A vertical fracture of the dimerous thallus showing a single basal layer (arrowhead), the erect filaments (C) and the epithallial cell layer (arrow) (scale bar = 100 µm).

Fig. 5. A vertical fracture of the outer thallus showing the epithallial cells (arrows), subepithallial initials (i), fusions between adjacent subepithallial initial (arrowheads) and cell fusions between adjacent erect filaments (f) (scale bar = 30 µm).

Fig. 6. A vertical fracture of the basal region showing the basal layer of non-palisade cells (arrows) and cell fusions (f) between adjacent erect filaments (scale bar = 30 µm).

Pl. 3

Goniolithon breviclavium Foslie

Figs 7-10. The tetrasporangial conceptacle anatomy of the type of Goniolithon breviclavium Foslie.

Fig. 7. A view of a single protuberance showing apically placed conical tetrasporangial conceptacles (arrows) (scale bar = 500 µm).

Fig. 8. A vertical fracture through a single apical tetrasporangial conceptacle showing the pore canal (P) and the conceptacle chamber (K) (scale bar = 250 µm).

Fig. 9. A vertical fracture through the pore canal of a tetrasporangial conceptacle showing the papillate cells (arrows) that line and project into the pore canal (scale bar = 60 µm)

Fig. 10. A fracture through the side of a tetrasporangial conceptacle chamber showing peripherally placed tetrasporangia (t) (scale bar = 50 µm).

Pl. 4

Goniolithon breviclavium Foslie

Figs 11-16. The vegetative and sporangial anatomy of the type of Goniolithon breviclavium Foslie.

Fig. 11. A vertical section of the dimerous thallus showing the single basal layer of non-palisade cells (arrow), the erect filaments (C) and the single epithallial layer (arrowhead) (scale bar = 60 µm).

Fig. 12. A vertical section of the outer thallus showing the single epithallial layer (e), the subepithallial initial (i) fused (f) with an adjoining subepithallial initial, the first erect filament cell (c) and a solitary bottle-shaped trichocyte (T) (scale bar = 15 µm).

Fig. 13. A vertical section of the basal layer (B) showing non-palisade basal cells giving rise to erect filaments that are often fused (c) together (scale bar = 15 µm).

Fig. 14. A section through the apex of a protuberance showing terminal tetrasporangial conceptacles (K) with their exposed pores (arrows) and tetrasporangial conceptacles (k) buried in the protuberance. Note the superimposed layers of thalli (scale bar = 300 µm).

Fig. 15. A vertical section through a single raised tetrasporangial conceptacle showing the pore canal (P), the central columella (arrow) and peripheral tetrasporangia (arrowheads) (scale bar = 150 µm).

Fig. 16. A section through the periphery of a tetrasporangial conceptacle roof showing a peripheral tetrasporangium (t) and the orientation of the roof filaments (arrows) and their origin from the peripheral roof filaments (scale bar = 30 µm).

Pl. 5

Lithophyllum consociatum Foslie

Figs 1-2. The habit of the type of Lithophyllum consociatum Foslie.

Fig. 1. The gross morphology of the type of Lithophyllum consociatum Foslie (scale bar = 20 mm).

Fig. 2. A magnified view of the habit of the type of Lithophyllum consociatum Foslie (scale bar = 2 mm).

Pl. 6

Lithophyllum consociatum Foslie

Figs 3-5. The vegetative anatomy of the type of Lithophyllum consociatum Foslie.

Fig. 3. The thallus surface showing thick walled epithallial cells with narrow, centrally located, deep depressions (scale bar = 15 µm).

Fig. 4. The thallus surface showing a single large pustulate trichocyte field (scale bar = 30 µm).

Fig. 5. A vertical fracture of the outer thallus showing a multi-layered epithallus (e), elongated subepithallial initials (i), an elongate first erect filament cell (c), and cell fusions between adjacent erect filaments (f) (scale bar = 15 µm).

Pl. 7

Lithophyllum consociatum Foslie

Figs 6-11. Tetrasporangial anatomy of the type of Lithophyllum consociatum Foslie.

Fig. 6. The thallus surface showing flush tetrasporangial conceptacles (arrows) (scale bar = 120 µm).

Fig. 7. A vertical fracture of the thallus showing tetrasporangial conceptacles (K) both at the surface (with exposed pore canal [arrow]) and buried in the thallus (scale bar = 120 µm).

Fig. 8. A vertical fracture through a slightly sunken tetrasporangial conceptacle (K) showing a central columella (arrow) (scale bar = 100 µm).

Fig. 9. A fracture through the chamber of a tetrasporangial conceptacle showing peripheral tetrasporangia (t) (scale bar = 30 µm).

Fig. 10. A magnified view of a fracture through the chamber (K) and pore canal (P) of a tetrasporangial conceptacle (scale bar = 60 µm).

Fig. 11. A vertical fracture through the pore canal of a tetrasporangial conceptacle showing small cells lining the base of the pore canal (arrowheads) and papillate cells (arrows) lining and projecting into the pore canal (scale bar = 30 µm).

Pl. 8

Lithophyllum consociatum Foslie

Figs 12-15. Vegetative and tetrasporangial anatomy of the type of Lithophyllum consociatum Foslie.

Fig. 12. A vertical section of the outer thallus showing a multiple epithallial cell layer (e), an elongate subepithallial initial (i) and a first erect filament cell (c) (scale bar = 15 µm).

Fig. 13. A vertical section through the chamber (K) and pore canal (P) of a slightly sunken tetrasporangial conceptacle (scale bar = 60 µm).

Fig. 14. A vertical section of the pore canal (P) and roof of a tetrasporangial conceptacle showing the orientation of the roof filaments (arrows) and their origin from the peripheral roof filaments (scale bar = 30 µm).

Fig. 15. A vertical section of the pore canal (P) of a tetrasporangial conceptacle showing papillate cells (arrowheads) lining and projecting into the pore canal (scale bar = 30 µm).

Pl. 9

Lithophyllum decipiens forma *caribaeum* Foslie

Fig. 1. The habit (A) and microslide section (B) of the type of *Lithophyllum decipiens* forma *caribaeum* Foslie (scale bars = 20 mm).

Pl. 10

Lithophyllum decipiens forma *caribaeum* Foslie

Figs 2-7. Vegetative and sporangial anatomy of the type of *Lithophyllum decipiens* forma caribaeum Foslie.

Fig. 2. The thallus surface showing relatively thick walled epithallial cells (arrowheads) with narrow, centrally located, deep to shallow depressions bearing intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. A vertical fracture through the crust showing a monomerous thallus with outer epithallial layer (e), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 30 µm).

Fig. 4. A vertical fracture of the outer thallus showing the epithallial cells (arrowheads), subepithallial initials (i), the first cortical cell (c), a solitary trichocyte (T) and extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 5. The thallus surface showing flush and raised tetrasporangial conceptacles (arrows) (scale bar = 100 µm).

Fig. 6. A vertical fracture of the crust showing a monomerous thallus (arrowhead) and a tetrasporangial conceptacle through its chamber (K) and pore canal (scale bar = 60 µm).

Fig. 7. A vertical fracture of the pore canal (P) of a typical tetrasporangial conceptacle showing the remnants of the large cells (arrowheads) lining the base of the pore canal (scale bar = 15 µm).

Pl. 11

Lithophyllum decipiens forma caribaeum Foslie

Figs 8-11. The vegetative and sporangial anatomy of the type of Lithophyllum decipiens forma caribaeum Foslie.

Fig. 8. A vertical section of the outer thallus showing a single epithallial cell layer (arrowhead), square to elongate subepithallial initials (i), the first cortical cells (c) and a pair of bottle-shaped trichocytes (T) (scale bar = 15 µm).

Fig. 9. A vertical section of the lower portion of a monomerous thallus showing plumose medullary filaments (scale bar = 15 µm).

Fig. 10. A vertical section through a tetrasporangial conceptacle showing the conceptacle chamber (K), pore canal (P) and enlarged cells (E) lining the base of the pore canal (scale bar = 30 µm).

Fig. 11. A section through the pore canal (P) of a tetrasporangial conceptacle showing the enlarged cells (E) lining the base of the pore canal and the roof that is typically comprised of 3 cells (1-3) (scale bar = 15 µm).

Pl. 12

Lithophyllum decipiens forma subantarctica Foslie

Figs 1-2. The habit of the type of Lithophyllum decipiens forma subantarctica Foslie.

Fig. 1. The habit of the type of Lithophyllum decipiens forma subantarctica Foslie (scale bar = 20 mm).

Fig. 2. A magnified view of the habit of the type of Lithophyllum decipiens forma subantarctica Foslie (scale bar = 2 mm).

Pl. 13

Lithophyllum decipiens forma subantarctica Foslie

Figs 3-6. Vegetative anatomy of the type of Lithophyllum decipiens forma subantarctica Foslie.

Fig. 3. The thallus surface showing thin to thick walled epithallial cells (arrowheads) with narrow to broad, centrally located, shallow depressions bearing intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 4. A vertical fracture of the dimerous thallus showing a multiple epithallial cell layer (arrowheads), elongate subepithallial initials (i), first erect filament cells (c) and a single basal layer of non-palisade cells (B) (scale bar = 30 µm).

Fig. 5. A vertical fracture of the outer thallus showing a multiple epithallial cell layer (arrowheads), elongated subepithallial initials (i), first erect filament cells (c), and cell fusions between adjacent erect filaments (f) (scale bar = 15 µm).

Fig. 6. A vertical fracture of the lower region of the thallus showing a single basal layer of non-palisade cells (B) and cell fusions (f) between the cells of adjacent erect filaments (scale bar = 15 μm).

Pl. 14

Lithophyllum decipiens forma subantarctica Foslie

Figs 7-10. Spermatangial conceptacle anatomy of the type of Lithophyllum decipiens forma subantarctica Foslie.

Fig. 7. The thallus surface showing numerous flush to only slightly raised spermatangial conceptacles (arrows) (scale bar = 860 μm).

Fig. 8. The thallus surface showing a close-up of a flush (arrow) and a slightly raised (arrowhead) spermatangial conceptacle (scale bar = 120 μm).

Fig. 9. A vertical fracture through a spermatangial conceptacle showing the pore canal (arrow) and the orientation of the roof filaments with their origin from the peripheral roof filaments (arrowheads) (scale bar = 30 μm).

Fig. 10. A vertical fracture through the pore canal (P) of a spermatangial conceptacle (scale bar = 15 μm).

Pl. 15

Lithophyllum decipiens forma subantarctica Foslie

Figs 11-14. Vegetative and spermatangial anatomy of the type of Lithophyllum decipiens forma subantarctica Foslie.

Fig. 11. A vertical section of the dimerous thallus (scale bar = 100 μm).

Fig. 12. A vertical section of the outer thallus showing a multiple epithallial cell layer (arrowheads), an elongate subepithallial initial (i) and a first erect filament cell (c) (scale bar = 15 µm).

Fig. 13. A vertical section of the thallus through the chamber of a spermatangial conceptacle (scale bar = 30 µm).

Fig. 14. A section through the chamber of a spermatangial conceptacle showing simple spermatangia restricted to the conceptacle floor (arrowheads) (scale bar = 15 µm).

Pl. 16

Lithophyllum erosum Foslie

Fig. 1. The habit of the type of Lithophyllum erosum Foslie.

Pl. 17

Lithophyllum erosum Foslie

Figs 2-7. Vegetative and tetrasporangial conceptacle anatomy of the type of Lithophyllum erosum Foslie.

Fig. 2. The thallus surface showing thick walled epithallial cells with narrow, deeply concave, central depressions (scale bar = 15 µm).

Fig. 3. A vertical fracture of the monomerous thallus showing a single epithallial cell layer (arrowhead), somewhat elongate subepithallial initials (i), first cortical cell (c), cell fusions between adjacent filaments (f), solitary bottle-shaped trichocytes (T), and plumose medullary filaments (M) (scale bar = 30 µm).

Fig. 4. A vertical fracture of the lower portion of the monomerous thallus showing plumose medullary filaments with abundant cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Fig. 5. The thallus surface showing slightly raised tetrasporangial conceptacles (arrows) (scale bar = 120 µm).

Fig. 6. A vertical fracture through a tetrasporangial conceptacle showing the conceptacle chamber (K) and the pore canal (arrow) (scale bar = 60 µm).

Fig. 7. A fracture through the pore canal (arrow) of a tetrasporangial conceptacle showing the remnants of the enlarged cells (arrowheads) that typically line the base and length of the pore canal (scale bar = 30 µm).

Pl. 18

Lithophyllum erosum Foslie

Figs 8-14. The vegetative and tetrasporangial anatomy of the type of Lithophyllum erosum Foslie.

Fig. 8. A vertical section of the monomerous thallus showing the epithallial cell layer (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 30 µm).

Fig. 9. A vertical section of the outer thallus showing a single epithallial cell layer (arrowhead), square to rectangular subepithallial initials (i), the first cortical cell (c) and cell fusions (f) between adjacent cortical filaments (scale bar = 15 µm).

Fig. 10. A section of the plumose medullary filaments showing cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 11. A vertical section through a tetrasporangial conceptacle (K) showing the pore canal (arrow) (scale bar = 60 µm).

Fig. 12. A section through the chamber of a tetrasporangial conceptacle showing peripherally located tetrasporangia (t) (scale bar = 30 µm).

Fig. 13. A section through the roof of a tetrasporangial conceptacle showing the typical number of cells (1-3) making up the roof structure (scale bar = 15 µm).

Fig. 14. A section through the pore canal (P) of a tetrasporangial conceptacle showing an enlarged cell (E) lining the base and length of the pore canal (scale bar = 15 µm).

Pl. 19

Lithophyllum marlothii forma falklandica Foslie

Fig. 1. The habit of the type of Lithophyllum marlothii forma falklandica Foslie (scale bar = 20 mm).

Pl. 20

Lithophyllum marlothii forma falklandica Foslie

Figs 2-4. The vegetative and reproductive anatomy of the type of Lithophyllum marlothii forma falklandica Foslie.

Fig. 2. The thallus surface showing badly fractured epithallial cells with thin cell walls and broad central, shallow concavities with intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing numerous circular concavities indicative of shed conceptacles (scale bar = 600 µm).

Fig. 4. A magnified view of the thallus showing two poorly defined conceptacles visible only by their pores (arrows) (scale bar = 120 µm).

Pl. 21

Lithophyllum marlothii forma falklandica Foslie

Figs 5-10. The vegetative anatomy of the type of Lithophyllum marlothii forma falklandica Foslie.

Fig. 5. A vertical section of a primary dimerous margin showing a single epithallial cell layer (e), a subepithallial initial (i), first erect filament cell (c), and the single basal layer of rectangular, yet non-palisade cells (B). Note the primary marginal initial (arrow) (scale bar = 15 µm).

Fig. 6. A vertical section of a mature monomerous margin showing the epithallial cell layer (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 60 µm).

Fig. 7. A vertical section of the outer thallus showing a solitary elongate trichocyte (T) (scale bar = 15 µm).

Fig. 8. A vertical section of the outer thallus showing a multiple epithallial cell layer (e), square to rectangular subepithallial initials (i), a first cortical cell (c) and a cell fusion (f) between two adjacent cortical filaments (scale bar = 15 µm).

Fig. 9. A section of the plumose medullary filaments showing cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 10. A section of the lower portion of the thallus showing a plumose medullar with extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Pl. 22

Lithophyllum marlothii forma falklandica Foslie

Figs 11-13. The reproductive anatomy of the type of Lithophyllum marlothii forma falklandica Foslie.

Fig. 11. A section of the thallus showing buried conceptacles (arrows) (scale bar = 300 µm).

Fig. 12. A magnified section through the chambers (K) of two conceptacles showing an intact roof (arrow) (scale bar = 150 µm).

Fig. 13. A vertical section through the pore canal (P) and roof of a conceptacle showing a papillate cell (arrow) lining the base of the pore canal, and from the orientation of the roof

filaments (arrowhead), it appears that the roof of this conceptacle may have been formed from filaments to the periphery of the conceptacle chamber (scale bar = 15 µm).

Pl. 23

Lithophyllum munitum Foslie & Howe

Fig. 1. The habit of the type of Lithophyllum munitum Foslie & Howe (scale bar = 20 mm).

Pl. 24

Lithophyllum munitum Foslie & Howe

Figs 2-4. The surface and sporangial anatomy of the type of Lithophyllum munitum Foslie & Howe.

Fig. 2. The thallus surface showing relatively thin to thick walled epithallial cells (arrowheads) with broad, very shallow, central concave depressions (scale bar = 15 µm).

Fig. 3. The thallus surface showing a number of solitary trichocytes (T) (scale bar = 15 µm).

Fig. 4. The thallus surface showing three poorly defined sporangial conceptacles visible only by their pores (arrows) (scale bar = 120 µm).

Pl. 25

Lithophyllum munitum Foslie & Howe

Figs 5-9. The vegetative and sporangial anatomy of the type of Lithophyllum munitum Foslie & Howe.

Fig. 5. A vertical section of a monomerous thallus showing the epithallial cell layer (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 60 µm).

Fig. 6. A vertical section of the monomerous thallus showing the plumose medullary filaments with a number of cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 7. A vertical section of the thallus showing a large number of buried tetrasporangial conceptacles (K) with one sectioned through the pore canal (arrow) (scale bar = 150 µm).

Fig. 8. A horizontal section through a single tetrasporangial conceptacle showing the peripherally located tetrasporangia (arrows) (scale bar = 60 µm).

Pl. 26

Hydrolithon munitum (Foslie & Howe) Penrose

Fig. 1. A rhodolith form of Hydrolithon munitum (Foslie & Howe) Penrose (scale bar = 20 mm) (UWC: 99/122).

Pl. 27

Hydrolithon munitum (Foslie & Howe) Penrose

Figs 2-5. The vegetative anatomy of Hydrolithon munitum (Foslie & Howe) Penrose (W Adey 14444).

Fig. 2. A vertical section of the outer thallus showing trichocytes (T) occurring singly as well as in small and large horizontal rows (scale bar = 30 µm).

Fig. 3. A vertical section of the outer thallus showing a single epithallial cell layer (e), bottle-shaped subepithallial initials (i), the first cortical cell (c), cell fusions (f) between adjacent cortical filaments, and a solitary bottle-shaped trichocyte (T) (scale bar = 15 µm).

Fig. 4. A vertical section of the outer thallus showing a single epithallial cell layer (e), elongate subepithallial initials (i), the first cortical cell (c), and solitary bottle-shaped trichocytes (T) (scale bar = 15 µm).

Fig. 5. A vertical section of the lower portion of the thallus showing the plumose medullary filaments (scale bar = 15 µm).

Pl. 28

Hydrolithon munitum (Foslie & Howe) Penrose

Figs 6-11. The tetrasporangial anatomy of Hydrolithon munitum (Foslie & Howe) Penrose (all W Adey 14444, except Figs 6 & 7).

Fig. 6. A vertical section through the chamber and pore canal (P) of an immature tetrasporangial conceptacle showing the development of the conceptacle roof from sterile filaments (arrowheads) interspersed among central (arrow) and peripheral (s) sporangial initials (scale bar = 30 µm) (UWC: 94/12230).

Fig. 7. A magnified view of an immature tetrasporangial conceptacle showing the development of the conceptacle roof from sterile filaments (arrowheads) interspersed among central (arrows) and peripheral sporangial initials (scale bar = 15 µm) (UWC: 94/1223).

Fig. 8. A vertical section of the thallus showing tetrasporangial conceptacles both at the surface (arrow) and buried in the thallus (k). Mature tetrasporangia (arrowheads) often fill the entire conceptacle chamber (scale bar = 120 µm).

Fig. 9. A section through a raised tetrasporangial conceptacle showing mature tetrasporangia (t) filling the entire conceptacle chamber (scale bar = 60 µm).

Fig. 10. A section through a tetrasporangial conceptacle showing mature tetrasporangia (t) located peripherally to a large central columella (arrow) and the base of the pore canal (p) lined by a ring of enlarged cells (arrowheads) (scale bar = 30 µm).

Fig. 11. A section through the roof and pore canal (P) of a tetrasporangial conceptacle showing enlarged cells (E) located at the base and along the length of the pore canal (scale bar = 15 µm).

Pl. 29

Hydrolithon munitum (Foslie & Howe) Penrose

Figs 12-13. The spermatangial anatomy of Hydrolithon munitum (Foslie & Howe) Penrose (UWC: 94/1348).

Fig. 12. A vertical section through the chamber and pore canal (P) of a spermatangial conceptacle showing simple spermatangial restricted to the conceptacle floor (scale bar = 30 µm).

Fig. 13. A magnified view of a spermatangial conceptacle chamber showing simple spermatangia (arrowheads) restricted to the conceptacle floor (scale bar = 15 µm).

Pl. 30

Hydrolithon munitum (Foslie & Howe) Penrose

Figs 14-17. The carposporangial anatomy of Hydrolithon munitum (Foslie & Howe) Penrose (all UWC: 94/1348 except Fig. 14).

Fig. 14. A section of the thallus showing an immature tetrasporangial conceptacle (S) located at the surface and a carposporangial conceptacle (Cs) buried in the thallus (scale bar = 120 µm) (UWC: 94/1223).

Fig. 15. A section through a carposporangial conceptacle showing gonimoblast filaments located peripherally around a central, discoid fusion cell (arrow) (scale bar = 60 µm).

Fig. 16. A section through the chamber of a carposporangial conceptacle showing gonimoblast filaments bearing terminal carpospores (c) located peripherally around a thin central, discoid fusion cell (arrow) (scale bar = 30 µm).

Fig. 17. A magnified view of a single gonimoblast filament comprised of 5 cells and terminating in a carpospore (scale bar = 15 µm).

Pl. 31

Lithophyllum reinboldii Weber van Bosse & Foslie

Fig. 1. The typical habit of the type of Lithophyllum reinboldii Weber van Bosse & Foslie.

Pl. 32

Lithophyllum reinboldii Weber van Bosse & Foslie

Figs 2-5. The vegetative anatomy of the type of Lithophyllum reinboldii Weber van Bosse & Foslie.

Fig. 2. The thallus surface showing large convex epithallial cells bearing intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. A vertical fracture of the outer thallus showing shedding of an old epithallial cell layer (arrow), an intact single epithallial cell layer (arrowhead), subepithallial initial (i), first cortical cell (c) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 4. A fracture of the outer thallus showing a single epithallial cell layer (arrowhead), subepithallial initial (i), first cortical cell (c) and solitary trichocytes (T). Note the cell fusions (arrow) between adjacent subepithallial initials (scale bar = 30 µm).

Fig. 5. A vertical fracture of the inner thallus showing a single basal layer (B) of non-palisade cells giving rise to erect filaments nearing extensive cell fusions (f) (scale bar = 30 µm).

Pl. 33

Lithophyllum reinboldii Weber van Bosse & Foslie

Figs 6-10. The tetrasporangial anatomy of the type of Lithophyllum reinboldii Weber van Bosse & Foslie.

Fig. 6. A vertical fracture of the thallus showing tetrasporangial conceptacles both at the surface (arrowheads) and buried in the thallus (arrows) (scale bar = 860 µm).

Fig. 7. The thallus surface showing numerous raised tetrasporangial conceptacles (arrows) (scale bar = 860 µm).

Fig. 8. A single raised tetrasporangial conceptacle (arrow) (scale bar = 150 µm).

Fig. 9. A vertical fracture through a tetrasporangial conceptacle showing an exposed, slightly sunken pore canal (arrow) and an open, un-infilled chamber (K) (scale bar = 100 µm).

Fig. 10. A fracture through the slightly sunken tetrasporangial conceptacle pore canal showing remnants of a ring of enlarged cells (arrowheads) lining the base of the pore canal (scale bar = 30 µm).

Pl. 34

Lithophyllum reinboldii Weber van Bosse & Foslie

Figs 11-17. The vegetative anatomy of the type of Lithophyllum reinboldii Weber van Bosse & Foslie.

Fig. 11. A section of the outer thallus showing solitary and paired trichocytes (T) (scale bar = 30 µm).

Fig. 12. A section of the outer thallus showing a single epithallial cell layer (e), subepithallial initial (i), first cortical cell (c) and a cell fusion (f) between two adjacent cortical filaments (scale bar = 15 µm).

Fig. 13. A section of the thallus showing a strong horizontal arrangement of large (arrows) and small (arrowheads) cells. The large cells are in fact extensive connections of the erect filaments by broad cell fusions (scale bar = 60 µm).

Fig. 14. A section of the inner portion of a dimerous thallus along a single basal filament (B) showing primary pit connections (arrowheads) (scale bar = 30 µm).

Fig. 15. A section of the inner portion of a dimerous thallus across a series of basal filaments (B) showing a cell fusion between two adjacent basal filaments (arrow), primary pit

connections (arrowheads) and cell fusions between adjacent erect filaments (f) (scale bar = 30 µm).

Fig. 16. A close-up of the dimerous thallus along a single basal filament (B) showing the locations of primary pit connections (arrows) (scale bar = 15 µm).

Fig. 17. A close-up of the dimerous thallus across a series of basal filaments (B) showing a cell fusion (f) between two adjacent basal filaments (scale bar = 15 µm).

Pl. 35

Lithophyllum reinboldii Weber van Bosse & Foslie

Figs 18-21. The tetrasporangial anatomy of the type of Lithophyllum reinboldii Weber van Bosse & Foslie.

Fig. 18. A section of the horizontally zoned thallus showing a single raised tetrasporangial conceptacle (K) at the thallus surface, and numerous buried conceptacles (k) (scale bar = 300 µm).

Fig. Insert. A single tetrasporangium (t) (scale bar = 30 µm).

Fig. 19. A section through a raised tetrasporangial conceptacle (K) showing an exposed pore canal (arrow) (scale bar = 150 µm).

Fig. 20. A section through the pore canal and roof of a tetrasporangial conceptacle showing the slightly sunken pore (arrow), pore canal (P) and enlarged cells (arrowheads) lining the base of the pore canal (scale bar = 30 µm).

Fig. 21. A section through the sunken pore canal (P) of a tetrasporangial conceptacle showing the enlarged cells (E) located at the base of the pore canal. Note the faint ring of enlarged cells (arrowheads) in the background (scale bar = 15 µm).

Pl. 36

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie

Fig. 1. The typical habit forms of Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie. A. An encrusting form (UWC: 94/1244). B. The typical rhodoliths form (UWC: 94/1264). (scale bars = 20 mm)

Pl. 37

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie

Figs 2-7. The vegetative anatomy of Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie (UWC: 94/1150).

Fig. 2. The thallus surface showing relatively thin walled epithallial cells (arrowheads) bearing broad, shallow concave centers (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing large convex epithallial cells some of which still bear intact primary pit connections (scale bar = 15 µm).

Fig. 4. The thallus surface showing numerous solitary trichocytes (arrows) (scale bar = 30 µm).

Fig. 5. A vertical fracture of the thallus showing the epithallial cell layer (arrow) and single basal layer (arrowhead) of non-palisade cells. Note the large inflated cells near the thallus surface that have resulted from extensive cell fusions between adjacent erect filaments (scale bar = 60 µm).

Fig. 6. A fracture of the outer thallus surface showing a single epithallial cell layer (arrowhead), subepithallial initial (i), first cortical cell (c) and solitary bottle-shaped trichocytes (T) (scale bar = 30 µm).

Fig. 7. A fracture of the inner portion of the thallus showing the single basal layer (B) of non-palisade cells giving rise to erect filaments with extensive cell fusions (f) between them and large quantities of starch grains (arrowheads) in their empty cytoplasms (scale bar = 30 µm).

Pl. 38

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie

Figs 8-11. The sporangial anatomy of Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie (UWC: 94/1150).

Fig. 8. The thallus surface showing large numbers of raised sporangial conceptacles (between arrowheads) (scale bar = 860 µm).

Fig. 9. A close-up of the thallus surface showing the variable range in sizes of the sporangial conceptacles (arrows) (scale bar = 150 µm).

Fig. 10. A vertical fracture of the outer thallus showing raised sporangial conceptacles at the surface (K) and some buried within the thallus (k) (scale bar = 150 µm).

Fig. 11. A fracture through the sunken pore (arrow) and pore canal (P) of a sporangial conceptacle showing a ring of enlarged cells (arrowheads) lining the base of the pore canal (scale bar = 30 µm).

Pl. 39

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie

Figs 12-17. The vegetative anatomy of Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie (UWC: 94/1150).

Fig. 12. A vertical section of the dimerous thallus showing a single basal layer (B) of non-palisade cells, a single epithallial cell layer (arrowhead) and subepithallial initial (i) with a cell fusion between two adjacent subepithallial initial (arrow) (scale bar = 30 µm).

Fig. 13. A section of the thallus showing a strong horizontal arrangement of large (arrows) and small (arrowheads) cells. The large cells are in fact extensive connections of the erect filaments by broad cell fusions (scale bar = 60 µm).

Fig. 14. A section of the outer thallus showing a solitary bottle-shaped trichocyte, a single epithallial cell layer (e), subepithallial initial (i) and a cell fusion between two, first cortical cells (cf) (scale bar = 15 µm).

Fig. 15. A close-up of the thallus showing the strong horizontal arrangement of large (arrows) and small (arrowheads) cells. The large cells are in fact extensive connections of the erect filaments by broad cell fusions (scale bar = 30 µm).

Fig. 16. A section through the inner thallus along a single basal filament (B) showing the location of primary pit connections (arrows) (scale bar = 15 µm).

Fig. 17. A section through the inner thallus across a series of basal filaments (B) showing cell fusions (f) between adjacent basal filaments (scale bar = 15 µm).

Pl. 40

Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie

Figs 18-21. The sporangial anatomy of Hydrolithon reinboldii (Weber van Bosse & Foslie in Foslie) Foslie.

Fig. 18. A section of the thallus showing the surface (arrow), erect filaments (C) and buried sporangial conceptacles (k) (scale bar = 300 µm). (UWC: 94/1150)

Fig. 19. A section through a raised sporangial conceptacle (K) (scale bar = 60 µm). (UWC: 94/1382)

Fig. Insert. A single bisporangium (b) (scale bar = 30 µm). (UWC: 94/1382)

Fig. 20. A section through a tetrasporangial conceptacle showing its sunken pore (arrow) and a single large tetrasporangium (t) completely filling the conceptacle chamber (scale bar = 60 µm). (UWC: 94/1041)

Fig. 21. A section through the sunken pore (arrow) and pore canal (P) of a sporangial conceptacle showing a single enlarged cell (E) located at the base of the pore canal (scale bar = 15 µm). (UWC: 94/1041)

Pl. 41

Lithophyllum rupestre Foslie

Fig. 1. The habit of the type of Lithophyllum rupestre Foslie (scale bar = 20 mm).

Pl. 42

Lithophyllum rupestre Foslie

Figs 2-4. The surface and gametangial anatomy of the type of Lithophyllum rupestre Foslie.

Fig. 2. The thallus surface showing thin to thick walled epithallial cells (arrowheads) with broad, shallow concave centers bearing intact primary pit connections (arrows) (scale bar = 15 µm).

Fig. 3. The thallus surface showing a mixture of both carposporangial and spermatangial conceptacles (arrows) (scale bar = 600 µm).

Fig. 4. A magnified view of the thallus surface showing a carposporangial (larger conceptacle) and a spermatangial conceptacle (smaller conceptacle) side by side (scale bar = 120 µm).

Pl. 43

Lithophyllum rupestre Foslie

Figs 5-8. The vegetative anatomy of the type of Lithophyllum rupestre Foslie.

Fig. 5. A vertical section of the monomerous thallus showing the epithallial cell layer (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 30 µm).

Fig. 6. A vertical section of the outer thallus showing a single epithallial cell layer (arrowhead), the subepithallial initial (i), the first cortical cell (c) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 15 µm).

Fig. 7. A magnified view of the plumose medullary filaments showing extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 8. A vertical section of the lower portion of the thallus showing medullary filaments terminating in inner dome-shaped epithallial cells (arrowheads) (scale bar = 15 µm).

Pl. 44

Lithophyllum rupestre Foslie

Figs 9-15. The gametangial anatomy of the monoecious type of Lithophyllum rupestre Foslie.

Fig. 9. A vertical section of the thallus showing gametangial conceptacles both at the surface and buried in the thallus (scale bar = 300 µm).

Fig. 10. A magnified section of the thallus showing a spermatangial (S) and a carposporangial (Cs) conceptacle buried side by side (scale bar = 30 µm).

Fig. 11. A section of the thallus through a buried spermatangial conceptacle showing simple spermatangia restricted to the conceptacle floor (arrowheads) (scale bar = 15 µm).

Fig. 12. A magnified section of the thallus showing a carpogonial (Cg) and a carposporangial (Cs) conceptacle buried side by side (scale bar = 30 µm).

Fig. 13. A section of the thallus through a buried carpogonial conceptacle showing carpogonial branches across the conceptacle floor bearing carpogonia (arrow) subtended by extended trichogynes (arrowhead) (scale bar = 15 µm).

Fig. 14. A magnified section through the chamber of a carposporangial conceptacle showing a centrally located thick and narrow, lightly staining, discoid fusion cell (arrowhead) bearing

peripheral gonimoblast filaments with terminal carpospores (C) and unfertilized carpognial branches across its centre (arrow) (scale bar = 15 µm).

Fig. 15. A section of the thallus through a buried carposporangial conceptacle showing a central fusion cells bearing peripheral gonimoblast filaments (arrowheads) and unfertilized carpogonial branches across its centre (arrow) (scale bar = 30 µm).

Pl. 45

Hydrolithon rupestris (Foslie) Penrose

Fig. 1. The typical habit of Hydrolithon rupestris (Foslie) Penrose (scale bar = 20 mm) (UWC: 94/1341).

Pl. 46

Hydrolithon rupestris (Foslie) Penrose

Figs 2-7. The vegetative anatomy of Hydrolithon rupestris (Foslie) Penrose.

Fig. 2. A vertical section of the monomerous thallus showing the epithallial cell layer (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 30 µm) (UWC: 94/1341).

Fig. 3. A vertical section of the outer thallus showing a single epithallial cell layer (e), the subepithallial initial (i), the first cortical cell (c) and a cell fusion (arrowhead) between two adjacent cortical filaments (scale bar = 15 µm) (UWC: 94/1341).

Fig. 4. A section of the outer thallus showing a single epithallial cell layer (arrowhead), the subepithallial initial (i), the first cortical cell (c), cell fusions (f) between adjacent cortical filaments and solitary trichocytes (T) one of which still has an intact hair (arrow) (scale bar = 15 µm) (W Adey 1456826).

Fig. 5. A magnified section of the thallus showing a pair of buried trichocytes occurring in short vertical rows (T) (scale bar = 15 µm) (UWC: 94/1341).

Fig. 6. The cortical filaments often comprise small, squat to squarish, bead-like cells with cell fusions (arrowheads) being very common (scale bar = 15 µm) (W Adey 1456826).

Fig. 7. A vertical section of the lower portion of the thallus showing the plumose medullary filaments (scale bar = 15 µm) (UWC: 94/1341).

Pl. 47

Hydrolithon rupestris (Foslie) Penrose

Figs 8-13. The sporangial anatomy of *Hydrolithon rupestris* (Foslie) Penrose (all W Adey 1456826 except Fig. 9).

Fig. 8. A vertical section of the thallus showing numerous empty sporangial conceptacles both at the surface and buried in the thallus (scale bar = 300 µm).

Fig. 9. A magnified section of the thallus showing sporangial conceptacles both at the surface (K) and buried (k) in the thallus (scale bar = 120 µm) (UWC: 91/163).

Fig. 10. A section of the thallus through a sporangial conceptacle showing immature sporangia (arrows) distributed across the conceptacle floor (scale bar = 30 µm).

Fig. 11. A mature tetrasporangium (t) (scale bar = 10 µm).

Fig. 12. A section through a sporangial conceptacle showing immature sporangia (t), the ring of enlarged cells (arrowheads) that typically line the base and length of the pore canal, and the sterile filaments (arrows) that had given rise to the enlarged cells (scale bar = 15 µm).

Fig. 13. A section through the pore canal (arrow) of a sporangial conceptacle showing the enlarged cells (arrowheads) that line the base and length of the pore canal (scale bar = 15 µm).

Pl. 48

Lithophyllum samoënse Foslie

Figs. 1-6. The vegetative and sporangial anatomy of the type of Lithophyllum samoënse Foslie.

Fig. 1. The thallus surface showing relatively thin walled epithallial cell (arrowheads) with broad, shallow to deep, central concave depressions bearing intact primary pit connections (arrows). A solitary trichocyte (T) is also visible (scale bar = 15 µm).

Fig. 2. A vertical fracture of a monomerous margin showing the epithallial cell layer (arrow), cortical filaments (c) and plumose medullary filaments (M) (scale bar = 60 µm).

Fig. 3. A vertical fracture of a monomerous thallus showing the epithallial cell layer (arrow), cortical filaments (c) and plumose medullary filaments (M) (scale bar = 60 µm).

Fig. 4. A vertical fracture of the lower portion of the thallus showing the plumose medullary filaments with extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Fig. 5. A fracture of the outer thallus showing numerous solitary trichocytes in short vertical rows (T) both at the surface and buried in the thallus (scale bar = 30 µm).

Fig. 6. The thallus surface showing a single flush sporangial conceptacle (arrow) (scale bar = 100 µm).

Pl. 49

Lithophyllum samoënse Foslie

Figs 7-11. The vegetative anatomy of the type of Lithophyllum samoënse Foslie.

Fig. 7. A vertical section of the thallus showing a series of infilling (I) where conceptacles had been shed (scale bar = 60 µm).

Fig. 8. A section of the outer thallus showing a pair of bottle-shaped trichocytes (T) (scale bar = 15 µm).

Fig. 9. A vertical section of the outer thallus showing a single epithallial cell layer (arrowhead), a subepithallial initial (i), a first cortical cell (c) and cell fusions (f) between adjacent cortical filaments (scale bar = 15 µm).

Fig. 10. A vertical section of the lower portion of the crust showing an extremely thin monomerous thallus appearing very much like a dimerous one (scale bar = 15 µm).

Fig. 11. A vertical section of the lower portion of a monomerous thallus showing the plumose medullary filaments (scale bar = 15 µm).

Pl. 50

Lithophyllum samoënse Foslie

Figs 12-15. The sporangial and carpogonial anatomy of the type of Lithophyllum samoënse Foslie.

Fig. 12. A vertical section of a thallus lacking the basal region and showing a buried sporangial conceptacle (K) with the remains of the enlarged cells (arrowhead) lining the pore canal (scale bar = 30 µm).

Fig. 13. A vertical section through the pore canal of a buried sporangial conceptacle showing the ring of enlarged cells (arrowheads) that line the base and length of the pore canal, and the number of cells (1-3) that comprise the conceptacle roof (scale bar = 15 µm).

Fig. 14. A magnified section through the chamber of a carpogonial conceptacle showing carpogonial branches (arrow) distributed across the chamber floor (scale bar = 15 µm).

Fig. 15. A vertical section through a raised carpogonial conceptacle showing carpogonial branches (arrow) distributed across the chamber floor (scale bar = 30 µm).

Pl. 51

Lithophyllum samoënse Foslie

Figs 16-17. The spermatangial anatomy of the type of Lithophyllum samoënse Foslie.

Fig. 16. A section of the outer thallus through a spermatangial conceptacle showing simple spermatangia restricted to the conceptacle floor (arrowheads) (scale bar = 30 µm).

Fig. 17. A section of the thallus through a buried spermatangial conceptacle showing simple spermatangia restricted to the conceptacle floor (arrowheads) (scale bar = 15 µm).

Pl. 52

Hydrolithon samoënse (Foslie) Keats & Chamberlain

Figs 1-3. The gross physiognomy of Hydrolithon samoënse (Foslie) Keats & Chamberlain .

Fig. 1. The typical habit of Hydrolithon samoënse (Foslie) Keats & Chamberlain (scale bar = 20 mm) (UWC: 93/70).

Fig. 2. The craters of old conceptacles are commonly observed at the surface giving the surface a pock-marked appearance (scale bar = 1 mm) (UWC: 93/58).

Fig. 3. Conceptacles are crowded across the thallus surface, appearing as tiny, white discs in fresh material (scale bar = 500 µm) (UWC: 93/58).

Pl. 53

Hydrolithon samoënse (Foslie) Keats & Chamberlain

Figs 4-8. The vegetative anatomy of Hydrolithon samoënse (Foslie) Keats & Chamberlain (all UWC: 92/146 except Fig. 5).

Fig. 4. A vertical section of the thallus showing the epithallial cell layer (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 60 µm).

Fig. 5. A section of the outer thallus showing a single epithallial cell layer (arrowhead), a subepithallial initial (i), a first cortical cell (c) and solitary trichocytes (T) (scale bar = 15 µm) (UWC: 95/1515).

Fig. 6. A vertical section of the outer thallus showing a single epithallial cell layer (arrowhead) below a recently shed epithallial layer (arrow), a subepithallial initial (i) and a first cortical cell (c) (scale bar = 15 µm).

Fig. 7. A magnified section of the plumose medullary filaments showing extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 8. The cortical filaments often comprise small, squat to squarish, bead-like cells with abundant cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Pl. 54

Hydrolithon samoënse (Foslie) Keats & Chamberlain

Figs 9-12. The tetrasporangial anatomy of Hydrolithon samoënse (Foslie) Keats & Chamberlain.

Fig. 9. A vertical section through a tetrasporangial conceptacle chamber and pore canal (p) showing the enlarged cells (arrowheads) that typically line the base and length of the pore canal, the sterile filaments (arrows) that had given rise to the enlarged cells, and undifferentiated tetrasporangia (t) (scale bar = 30 µm) (UWC: 98/322).

Fig. 10. A vertical section through a tetrasporangial conceptacle chamber and pore canal (arrow) showing the enlarged cells (arrowheads) that typically line the base and length of the pore canal, and differentiated tetrasporangia (t) (scale bar = 30 µm) (UWC: 92/146).

Fig. 11. A magnified section of the pore canal (P) and roof of a tetrasporangial conceptacle showing the enlarged cells (arrowheads) that typically line the base and length of the pore canal and the sterile filaments (arrows) that had given rise to them (scale bar = 15 µm) (UWC: 98/322).

Fig. 12. A magnified section of the roof of a tetrasporangial conceptacle showing the typical construction of the conceptacle roof. The apex of a tetrasporangium (t) is also visible (scale bar = 15 µm) (UWC: 92/146).

Pl. 55

Hydrolithon samoënse (Foslie) Keats & Chamberlain

Figs 13-16. The female anatomy of Hydrolithon samoënse (Foslie) Keats & Chamberlain (all UWC: 95/1515 except Fig. 16).

Fig. 13. A section of the thallus through a carpogonial conceptacle (arrow) (scale bar = 30 µm).

Fig. 14. A vertical section through a carpogonial conceptacle showing carpogonial branches bearing trichogynes (arrowheads) and carpogonia (c), distributed across the conceptacle floor (scale bar = 15 µm).

Fig. 15. A magnified section through the chamber of a carpogonial conceptacle showing carpogonial branches comprised of a carpogonium (C) terminating in a trichogyne, a support cell (S) and a sterile cell (arrow) (scale bar = 10 µm).

Fig. 16. A vertical section through the chamber and pore canal (p) of a carposporangial conceptacle showing a thick and narrow, discoid, central fusion cell (arrow) bearing peripheral gonimoblast filaments terminating in carpospores (c) (scale bar = 30 µm) (UWC: 91/179).

Pl. 56

Hydrolithon megacystum Adey, Townsend & Boykins

Figs 1-4. The vegetative anatomy of the type of Hydrolithon megacystum Adey, Townsend & Boykins.

Fig. 1. A vertical section of the dimerous thallus showing a single epithallial cell layer (arrow), the subepithallial initial (i), the first erect filament cell (c), a cell fusion (f) between two adjacent erect filaments, and a single basal layer (arrowheads) of non-palisade cells (scale bar = 30 µm).

Fig. 2. A magnified section of the outer portion of the thallus showing a single epithallial cell layer (e), the subepithallial initials (i) and the first erect filament cells (c) (scale bar = 15 µm).

Fig. 3. A magnified section of the lower portion of the dimerous thallus showing the single basal layer (B) of non-palisade cells (scale bar = 15 µm).

Fig. 4. A section of the thallus showing enlarged cells that may be buried trichocytes (T) in a large horizontal row (scale bar = 60 µm).

Pl. 57

Hydrolithon murakoshii Iryu & Matsuda

Figs 1-5. The vegetative anatomy of Hydrolithon murakoshii Iryu & Matsuda (UWC: 94/1390).

Fig. 1. A vertical section of the thallus showing plumose medullary filaments (M), outer cortical filaments (C) and tetrasporangial conceptacles both at the surface (K) and buried in the thallus (k). Buried sporangial conceptacles may also become infilled (arrow) (scale bar = 150 µm).

Fig. 2. A vertical section of the outer thallus showing a large horizontal field of trichocytes (T) and a vertical trichocyte chain (arrow) (scale bar = 30 µm).

Fig. 3. A magnified view of the outer thallus showing a solitary long vertical (arrow) trichocyte (T) chain (scale bar = 15 µm).

Fig. 4. A magnified view of the outer thallus showing a single epithallial layer (arrowheads), subepithallial initial (i), first cortical cell (c), solitary trichocytes (T) and a cell fusion (f) between two cortical filaments (scale bar = 15 μm).

Fig. 5. A magnified view of the thallus showing plumose medullary filaments (scale bar = 15 μm).

Pl. 58

Hydrolithon murakoshii Iryu & Matsuda

Figs 6-9. Stages in tetrasporangial conceptacle development of Hydrolithon murakoshii Iryu & Matsuda (UWC: 94/1390).

Fig. 6. Initial stage of development showing conceptacle initials and shedding of the epithallial layer (scale bar = 50 μm).

Fig. 7. An early stage of development showing early development of the conceptacle roof from filaments (arrowheads) interspersed among the sporangial initials (scale bar = 50 μm).

Fig. 8. A later stage of development showing advanced conceptacle roof formation in which the central sterile cells that had given rise to the roof, is still in tact (scale bar = 50 μm).

Fig. 9. A later stage of development showing advanced conceptacle roof formation with sporangial initials (arrows) located across the conceptacle floor (scale bar = 50 μm).

Pl. 59

Hydrolithon murakoshii Iryu & Matsuda

Figs 10-12. Tetrasporangial anatomy of Hydrolithon murakoshii Iryu & Matsuda (UWC: 94/1390).

Fig. 10. A vertical section of the outer thallus showing a tetrasporangial conceptacle at the surface (arrow) bearing a central columella (arrowhead) as well as a second un-infilled, buried (k) conceptacle (scale bar = 60 µm).

Fig. 11. A vertical section through the chamber and pore (arrow) of a tetrasporangial conceptacle showing a central columella (arrowhead) and peripherally located tetrasporangia (t) (scale bar = 30 µm).

Fig. 12. A magnified section of the roof and pore (p) of a tetrasporangial conceptacle showing enlarged cells (E) lining the base of the conceptacle pore and the remains of sterile filaments (arrows) that had given rise to the conceptacle roof. Although located to the periphery of the conceptacle chamber, these filaments still had their origin between the sporangial initials and have been pushed to the periphery by the growing tetrasporangia (scale bar = 15 µm).

Pl. 60

Hydrolithon superficiale Keats & Chamberlain

Figs 1-2. The habit and gross morphology of the type of Hydrolithon superficiale Keats & Chamberlain (UWC: COR/302).

Fig. 1. The habit of the type of Hydrolithon superficiale Keats & Chamberlain (scale bar = 20 mm).

Fig. 2. The thallus surface showing the distinct superficial layer (arrows) within which conceptacles develop (scale bar = 200 µm)

Pl. 61

Hydrolithon superficiale Keats & Chamberlain

Figs 3-7. The vegetative anatomy of the type of Hydrolithon superficiale Keats & Chamberlain (UWC: COR/302).

Fig. 3. The thallus surface showing thin walled epithallial cells with broad, shallow concave depression bearing intact primary pit connections (arrows). Solitary trichocytes (T) are commonly found at the surface (scale bar = 15 µm).

Fig. 4. A vertical fracture of the monomerous margin showing the epithallial cell layer (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 60 µm).

Fig. 5. A vertical fracture of the monomerous thallus showing the epithallial cell layer (arrowhead), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 60 µm).

Fig. 6. A vertical fracture of the outer thallus showing the single epithallial cell layer (arrow), the subepithallial initial (i) and extensive cell fusions (f) between adjacent cortical filaments (scale bar = 30 µm).

Fig. 7. A vertical fracture of the lower portion of the thallus showing plumose medullary filaments with extensive cell fusions (f) between adjacent filaments (scale bar = 30 µm).

Pl. 62

Hydrolithon superficiale Keats & Chamberlain

Figs 8-11. The sporangial anatomy of the type of Hydrolithon superficiale Keats & Chamberlain (UWC: COR/302).

Fig. 8. The thallus surface showing the distribution of sporangial conceptacles (arrows) along the bases of shallow protuberances (scale bar = 860 µm).

Fig. 9. The thallus surface showing the raised sporangial conceptacles with their distinctly sunken pores all located within a superficial layer at the surface (scale bar = 120 µm).

Fig. 10. A vertical fracture through a sporangial conceptacle chamber (K) showing sterile filaments (arrowhead) borne from the centre of the conceptacle floor giving rise to the ring of enlarged cells that line the base and length of the pore canal (scale bar = 60 µm).

Fig. 11. A fracture through the pore canal (Pc) and roof of a sporangial conceptacle showing the roof construction (1-3), the remnants of the ring of enlarged cells (arrowheads) that line the base and length of the pore canal, and the sterile filaments (arrows) that had given rise to the enlarged cells (scale bar = 15 µm).

Pl. 63

Hydrolithon superficiale Keats & Chamberlain

Figs 12-17. The vegetative anatomy of the type of Hydrolithon superficiale Keats & Chamberlain (UWC: COR/302).

Fig. 12. A vertical section of the monomerous thallus showing the epithallial cell layer (arrow), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 150 µm).

Fig. 13. A section of the outer thalus showing solitary trichocytes (T) (scale bar = 15 µm).

Fig. 14. A section of the outer thallus showing a recently shed epithallial cell layer (arrow) above an intact epithallial cell layer (e), a subepithallial initial (i) and a first cortical cell (c) (scale bar = 15 µm).

Fig. 15. The cortical filaments often comprise small, squat to rectangular, often bead-like cells (scale bar = 15 µm).

Fig. 16. A magnified section of the plumose medullary filaments showing extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Fig. 17. A section of the lower portion of the thallus showing plumose medullary filaments with a number of cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Pl. 64

Hydrolithon superficiale Keats & Chamberlain

Figs 18-23. The sporangial and spermatangial anatomy of the type of Hydrolithon superficiale Keats & Chamberlain (UWC: COR/302).

Fig. 18. A vertical section of the thallus showing raised sporangial conceptacles at the surface (scale bar = 300 µm).

Fig. Insert. A mature tetrasporangium (t) (scale bar = 15 µm).

Fig. 19. A vertical section through the chamber (K) and pore canal (p) of a sporangial conceptacle showing the enlarged cells (arrowheads) located at the base and along the length of the pore canal (scale bar = 30 µm).

Fig. 20. A vertical section through the pore canal (P) of a sporangial conceptacle showing the enlarged cells (E) lining the base and length of the pore canal (scale bar = 15 µm).

Fig. 21. A vertical section through the roof of a sporangial conceptacle showing the construction of the conceptacle roof (scale bar = 15 µm).

Fig. 22. A vertical section of the thallus showing a tetrasporangial (T) and a spermatangial (S) conceptacle side by side (scale bar = 60 µm).

Fig. 23. A magnified section through the chamber of a spermatangial conceptacle showing simple spermatangia (arrow) restricted to the conceptacle floor (scale bar = 15 µm).

Pl. 65

Hydrolithon superficiale Keats & Chamberlain

Fig. 1. The typical habit of Hydrolithon superficiale Keats & Chamberlain (scale bar = 20 mm) (UWC: COR/139).

Pl. 66

Hydrolithon superficiale Keats & Chamberlain

Figs 2-4. The vegetative anatomy of Hydrolithon superficiale Keats & Chamberlain (UWC: COR/139).

Fig. 2. A vertical section through a newly formed monomerous margin showing darkly staining primary marginal initials (arrow) (scale bar = 30 µm).

Fig. 3. A vertical section of the outer thallus showing a single epithallial cell layer (e), a subepithallial initial (i) and the first cortical cell (C) (scale bar = 15 µm).

Fig. 4. A vertical section of the plumose medullary filaments showing a number of cell fusions (f) between adjacent filaments (scale bar = 15 µm).

Pl. 67

Hydrolithon superficiale Keats & Chamberlain

Figs 5-9. The sporangial anatomy of Hydrolithon superficiale Keats & Chamberlain (UWC: COR/139).

Fig. 5. A vertical section of the thallus showing raised sporangial conceptacles (arrows) at the surface and crescent-shaped scars (arrowheads) indicating infilling of areas previously occupied by sporangial conceptacles (scale bar = 300 µm).

Fig. 6. A vertical section of the thallus showing a sporangial conceptacle (K) located within a superficial layer (arrow) above the surface (arrowheads) (scale bar = 60 µm).

Fig. 7. A vertical section through a sporangial conceptacle showing the pore canal (arrow) and the sterile filaments (arrowheads) that give rise to the ring of enlarged cells that line the base of the pore canal (scale bar = 30 µm).

Fig. 8. A vertical section through the roof of a developing sporangial conceptacle showing the construction of the 3-celled roof (1-3) from sterile filaments (arrowheads) located between the sporangial initials (t) (scale bar = 15 µm).

Fig. 9. A section through a more mature sporangial conceptacle roof and pore canal (P) showing the enlarged cells (E) that typically line the base and length of the pore canal, the sterile filaments (arrows) that give rise to the enlarged cells, and the sporangial initials (arrowheads) (scale bar = 15 µm).

Pl. 68

Neogniolithon rufum Adey, Townsend & Boykins

Figs 1-7. The vegetative anatomy of the type of Neogniolithon rufum Adey, Townsend & Boykins.

Fig. 1. A vertical section of a monomerous thallus showing the epithallial cell layer (arrowhead), cortical filaments (C) and plumose medullary filaments (M) (scale bar = 30 µm) (71-50-80).

Fig. 2. A vertical section of a monomerous thallus showing cortical filaments (C) and coaxial medullary filaments (M) (scale bar = 30 µm) (71-81-28).

Fig. 3. A vertical section of the outer thallus showing a single epithallial cell layer (arrowhead), a subepithallial initial (i), a first cortical cell (c) and a number of cell fusions (f) between adjacent cortical filaments (scale bar = 15 µm) (71-50-80).

Fig. 4. A section through the plumose medullary filaments showing extensive cell fusions (f) between adjacent filaments (scale bar = 15 µm) (71-50-31).

Fig. 5. A vertical section of the outer thallus showing solitary and paired trichocytes (T) (scale bar = 15 µm) (71-50-80).

Fig. 6. A vertical section of the inner portion of the thallus showing a plumose medullary filaments with a number of cell fusions (f) between adjacent filaments. Medullary filaments end in inner somewhat domed epithallial cells (arrowheads) (scale bar = 15 µm) (71-50-20).

Fig. 7. A vertical section through the cortical filaments showing two solitary trichocyte chains occurring in vertical rows (T) (scale bar = 15 µm) (71-50-20).

Pl. 69

Neogniolithon rufum Adey, Townsend & Boykins

Figs 8-10. The tetrasporangial anatomy of the type of Neogniolithon rufum Adey, Townsend & Boykins.

Fig. 8. A vertical section of the thallus showing numerous tetrasporangial conceptacles both at the surface and buried in the thallus (scale bar = 300 µm) (71-50-80).

Fig. 9. A vertical section through a raised tetrasporangial conceptacle chamber and pore canal (arrow) showing a number of apparently viable tetrasporangia (t) (scale bar = 30 µm) (71-50-20).

Fig. 10. A vertical section through the roof and pore canal (arrow) of a tetrasporangial conceptacle showing a single enlarged cell (E) lining the base of one side of the pore canal, the sterile filament (arrowhead) that had given rise to the enlarged cell, and the apex of a tetrasporangium (t) (scale bar = 15 µm) (71-50-80).

Pl. 70

Neogniolithon rufum Adey, Townsend & Boykins

Figs 11-13. The gametangial anatomy of the type of Neogniolithon rufum Adey, Townsend & Boykins.

Fig. 11. A vertical section of a monoecious thallus bearing buried carposporangial (K) and spermatangial (arrows) conceptacles (scale bar = 300 µm) (71-81-28).

Fig. 12. A vertical section through a spermatangial conceptacle showing simple spermatangia restricted to the conceptacle floor (arrows) (scale bar = 60 µm) (71-78-14).

Fig. 13. A magnified section of the spermatangial conceptacle showing the simple spermatangia restricted to the conceptacle floor (arrows) (scale bar = 15 µm) (71-78-14).

Pl. 71

Neogniolithon rufum Adey, Townsend & Boykins

Figs 14-18. The female anatomy of the type of Neogniolithon rufum Adey, Townsend & Boykins.

Fig. 14. A vertical section through a carpogonial conceptacle showing carpogonial branches (arrow) distributed across the conceptacle floor (scale bar = 60 µm) (71-50-31).

Fig. 15. A section through the chamber of a carpogonial conceptacle showing carpogonial branches distributed across the conceptacle floor bearing twisted trichogynes (arrows) subtended by carpogonia (arrowheads) that in turn are subtended by support cells (s) (scale bar = 15 µm) (71-50-31).

Fig. 16. A vertical section of the carpogonial thallus showing long vertical trichocyte chains (arrows) buried in the thallus (scale bar = 15 µm) (71-82-57).

Fig. 17. A vertical section through a carposporangial conceptacle showing a broad, thick discoid fusion cell bearing unfertilised carpogonial branches across its centre (arrow) and gonimoblast filaments at its periphery (arrowheads) (scale bar = 60 µm) (71-82-57).

Fig. 18. A magnified section of the carposporangial conceptacle showing the thick, broad, discoid central fusion cell (arrowheads) bearing unfertilised carpogonial branches across its centre (arrow) and peripheral gonimoblast filaments terminated by lightly staining carpospores (C) (scale bar = 30 µm) (71-82-57).

Pl. 72

Neogoniolithon rugulosum Adey, Townsend & Boykins

Figs 1-3. The vegetative anatomy of the type of Neogoniolithon rugulosum Adey, Townsend & Boykins (71-53-4).

Fig. 1. A vertical section of the monomerous thallus showing cortical filaments (C) bearing a number of solitary trichocytes at the surface (arrows) and plumose medullary filaments (M) (scale bar = 60 µm).

Fig. 2. A vertical section of the outer thallus showing a single epithallial cell layer (arrowhead), a subepithallial initials (i), the first cortical cell (c), a cell fusion (f) between two adjacent cortical filaments, and a solitary and paired trichocytes (T) (scale bar = 15 µm).

Fig. 3. A vertical section of the lower portion of the thallus showing plumose medullary filaments with a cell fusion (f) between two adjacent filaments (scale bar = 15 µm).

Pl. 73

Neogoniolithon rugulosum Adey, Townsend & Boykins

Figs 4-9. The sporangial anatomy of the type of Neogoniolithon rugulosum Adey, Townsend & Boykins (71-53-4).

Fig. 4. A vertical section of a monomerous thallus showing a recently sloughed layer of epithallial cells (arrow) above a series of darkly staining sporangial initials (arrowheads) (scale bar = 30 µm).

Fig. 5. A vertical section of the thallus showing sporangial conceptacles (K) both at the surface and buried in the thallus (scale bar = 60 µm).

Fig. 6. A vertical section through a tetrasporangial conceptacle showing mature tetrasporangia (t) and the remains of a sterile filament (arrowhead) that gave rise to the conceptacle roof (scale bar = 30 µm).

Fig. 7. A vertical section through the chamber of a tetrasporangial conceptacle showing a well-differentiated tetrasporangium (t) (scale bar = 30 µm).

Fig. 8. A vertical section through the roof and pore canal of a tetrasporangial conceptacle showing a ring of enlarged cells (arrowheads) lining the base and length of the pore canal and the remains of the sterile filaments (arrows) that had given rise to the roof filaments (scale bar = 15 µm).

Fig. 9. A vertical section through the roof of a tetrasporangial conceptacle showing the characteristic 3-celled filaments (1-3) that make up the conceptacle roof (scale bar = 15 µm).

Plate 1


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1368 og 1432 (skråsn.) af dette ekspl.
1426 af mindste ekspl.
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Eugenia Exp. (?)
Goniolithon (Hydrolithon)
[redacted]
breviclavium
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Lith. Monogr. pl. 52
fig. 14-15
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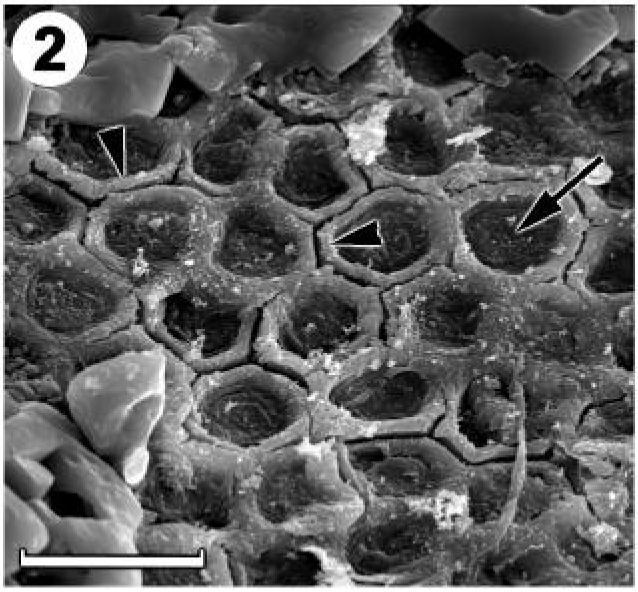
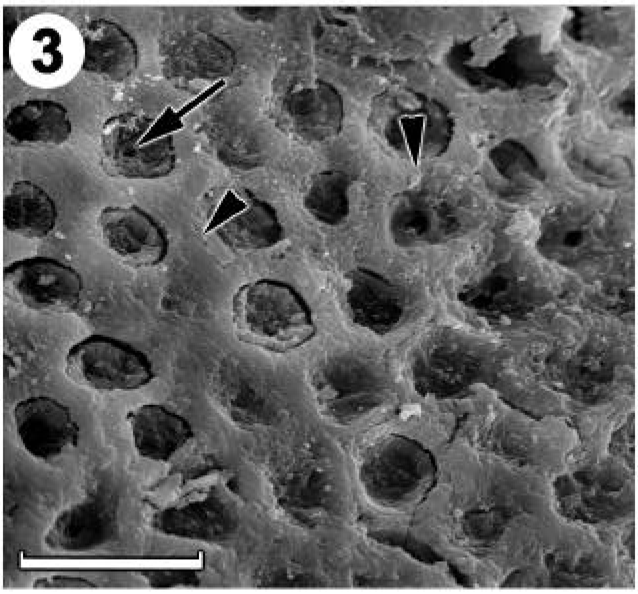
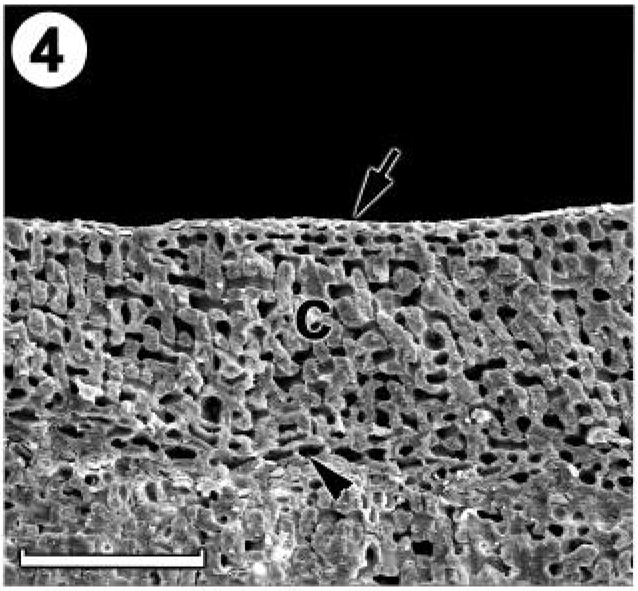
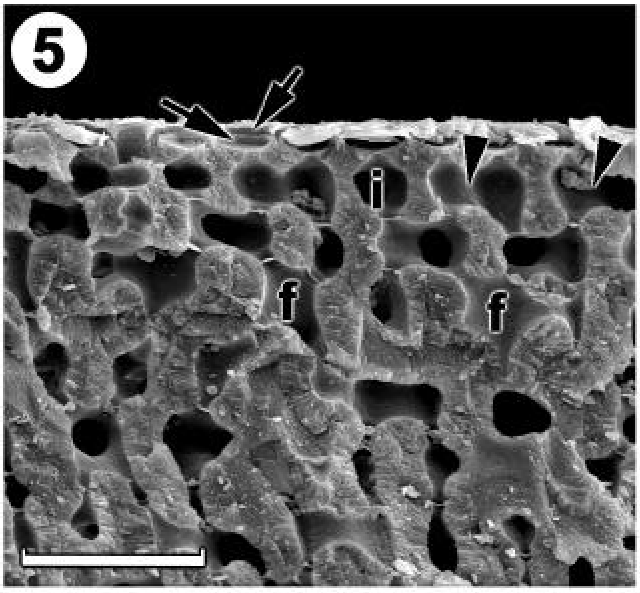
Plate 2









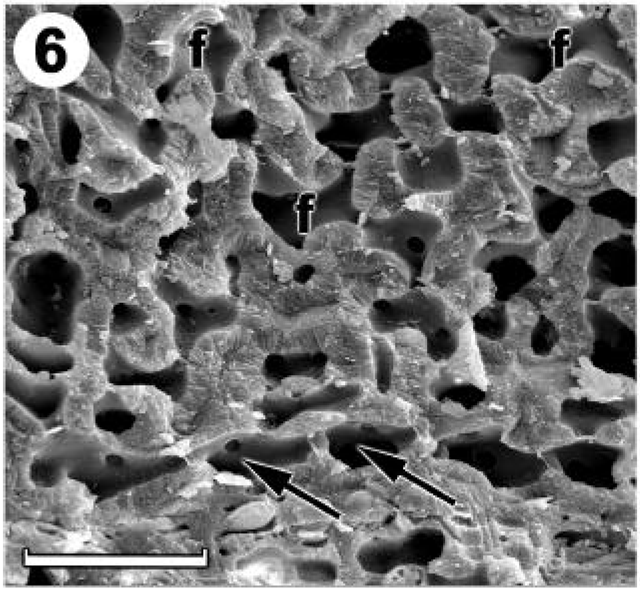
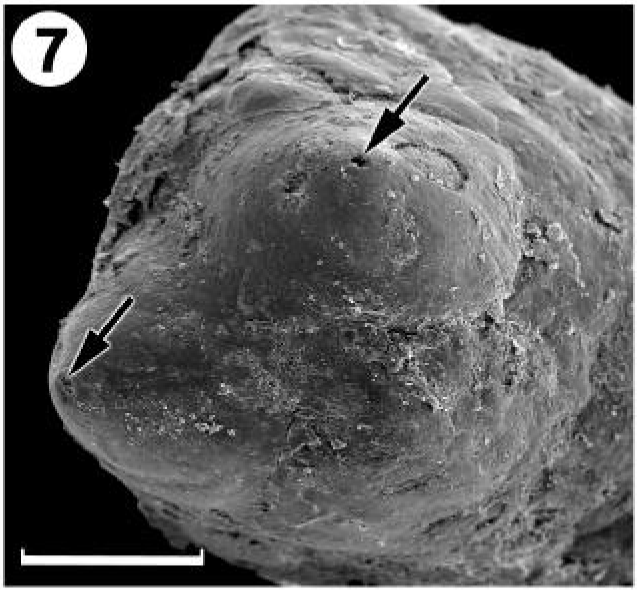
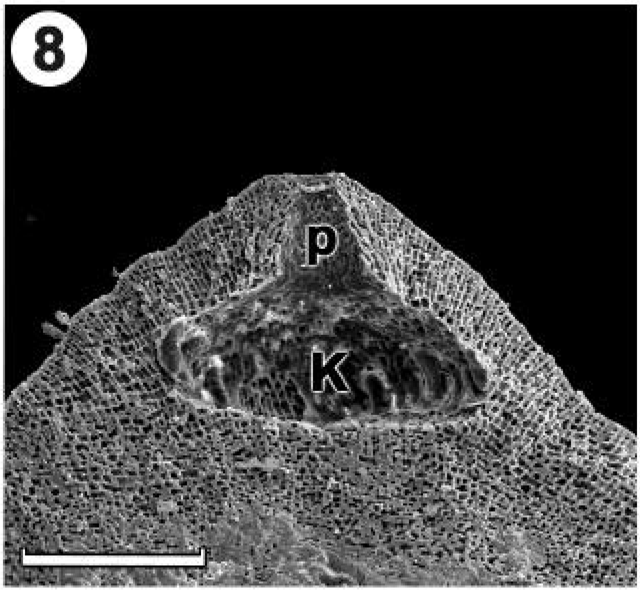
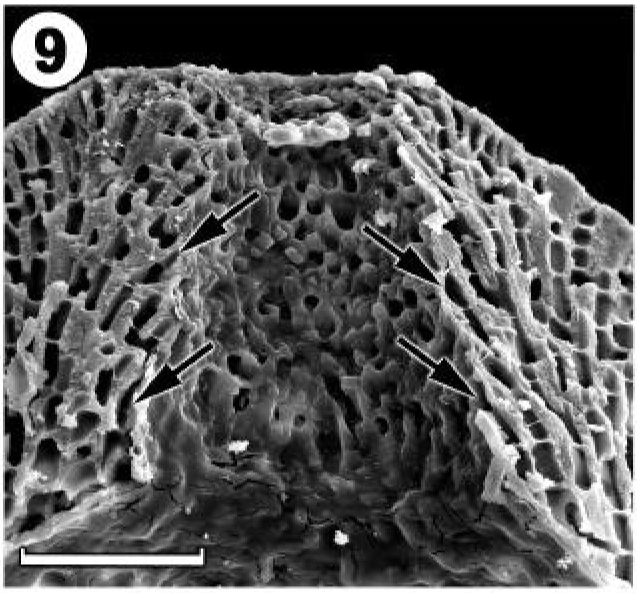


Plate 3







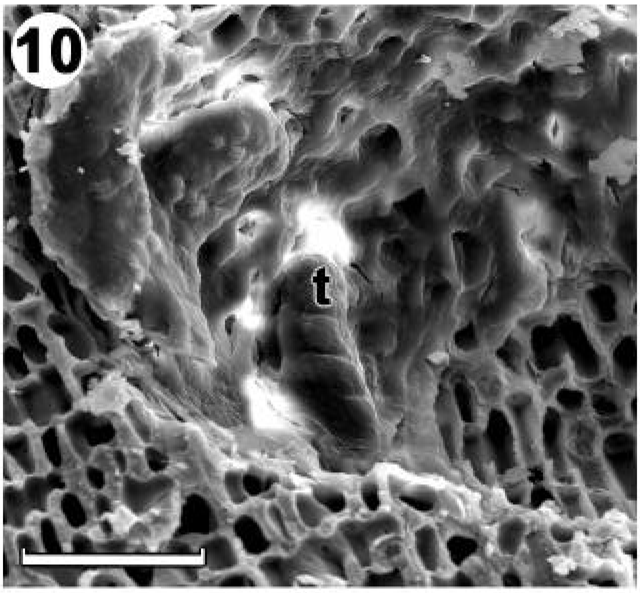


Plate 4

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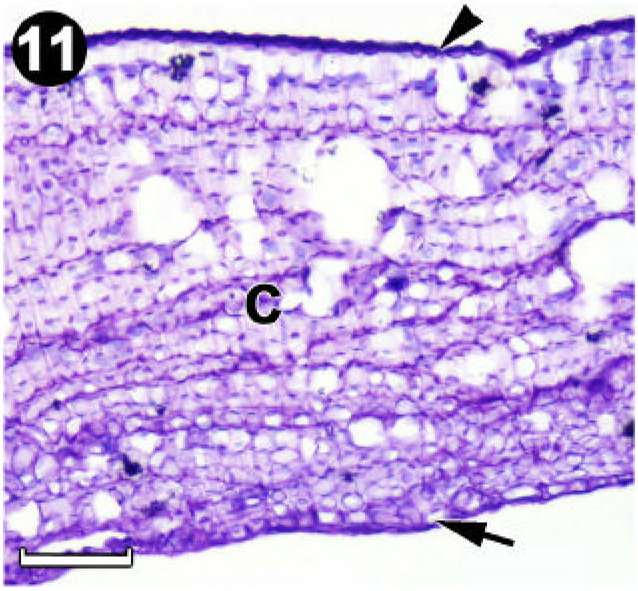

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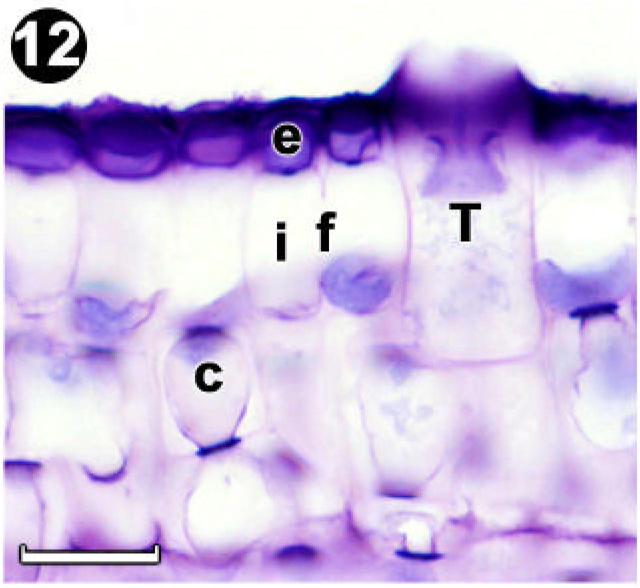

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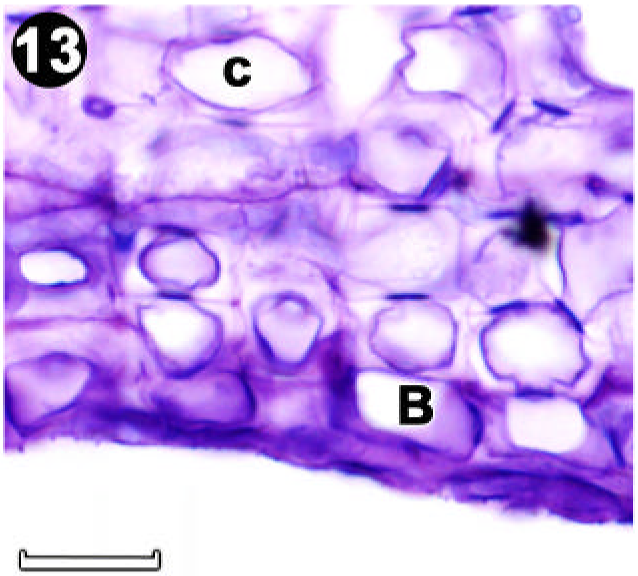

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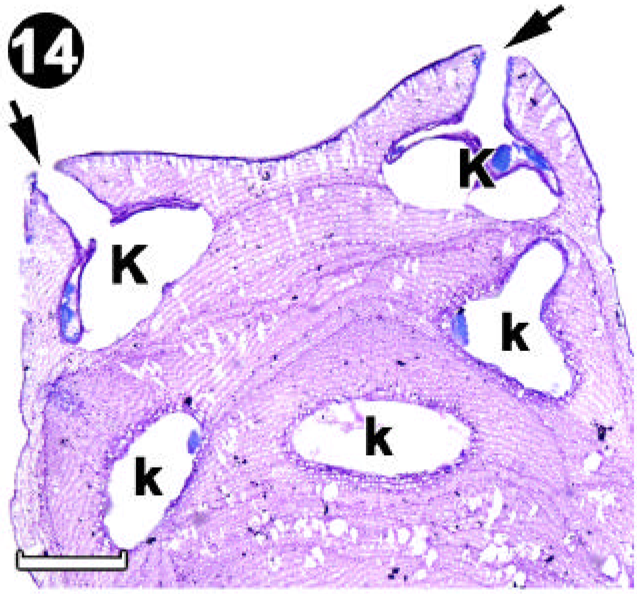

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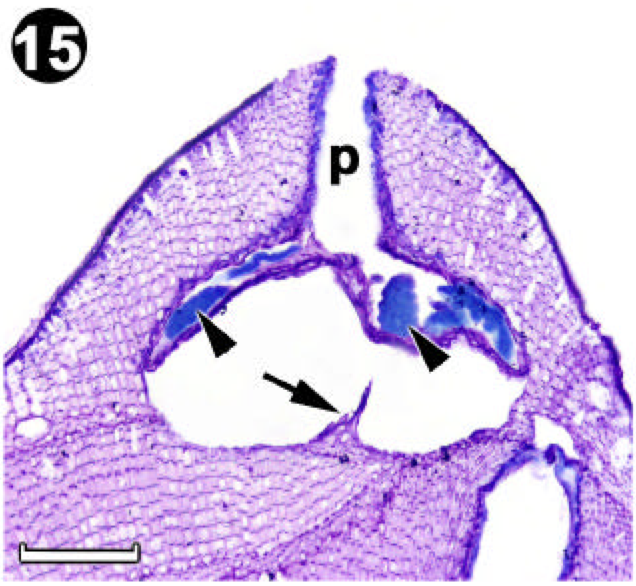

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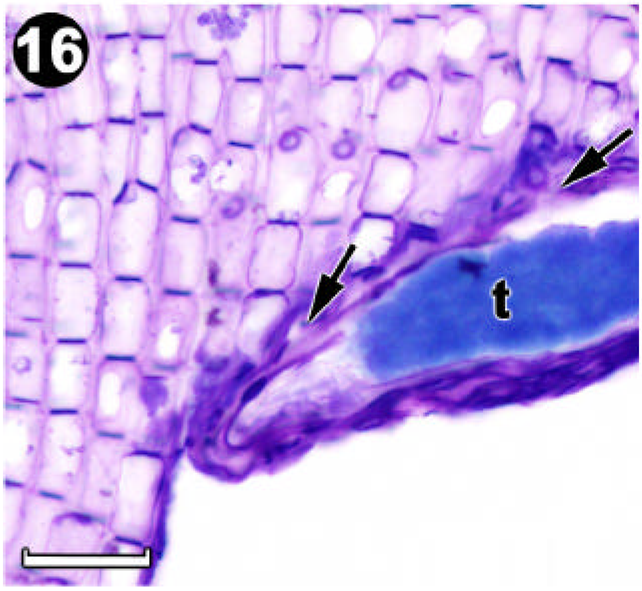

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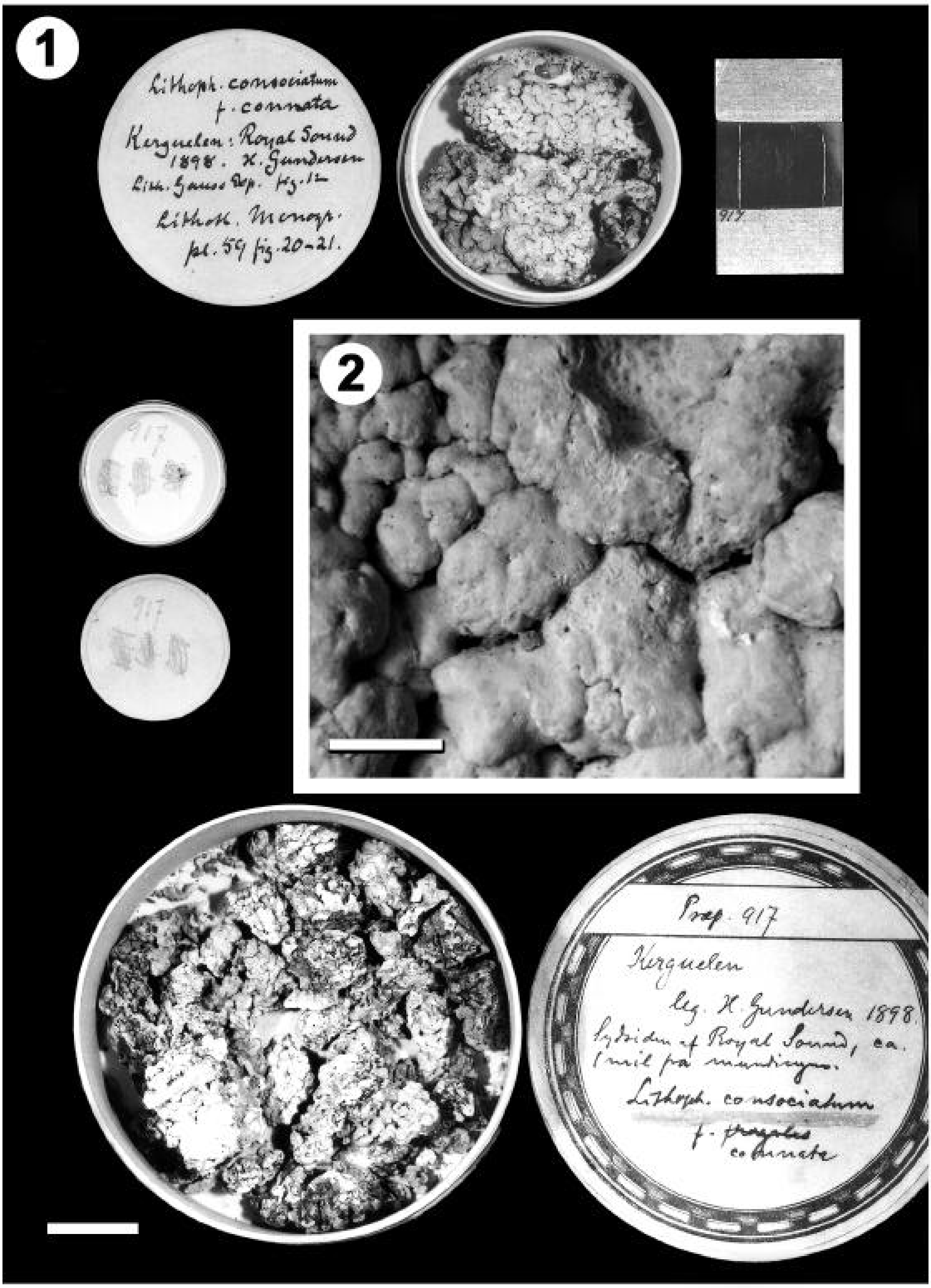
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Lithoph. consociatum
f. connata
Kerguelen: Royal Sound
1898. H. Gundersen
Lith. Gauss Exp. fig. 12
Lithoth. Monogr.
pl. 59 fig. 20–21.
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Kerguelen
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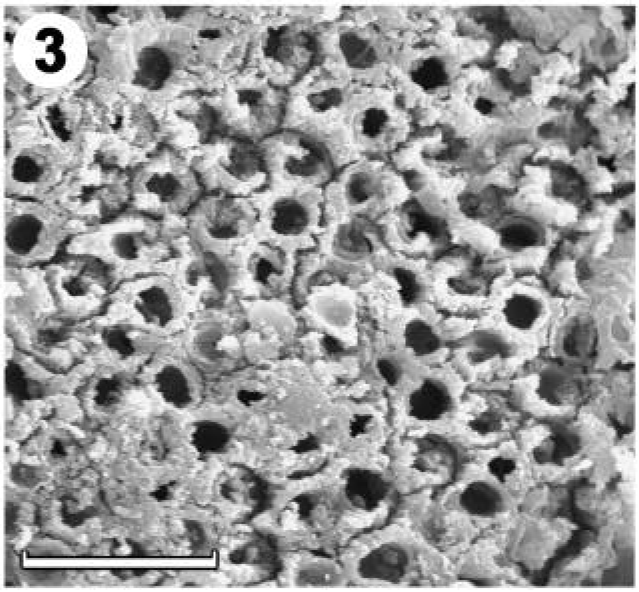
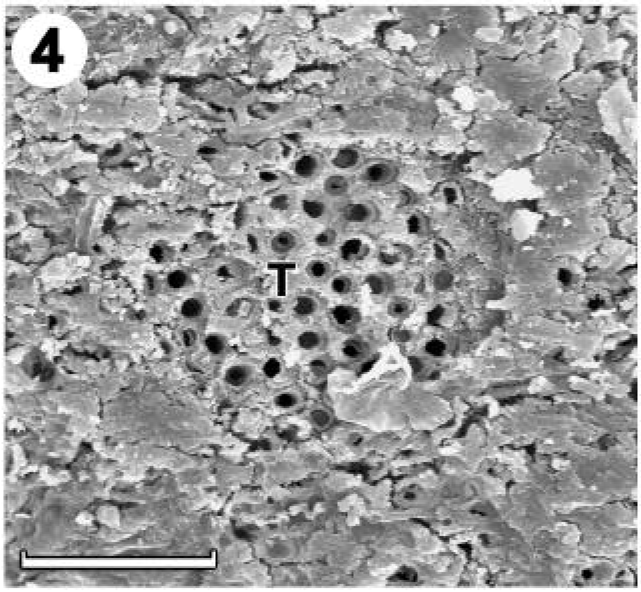
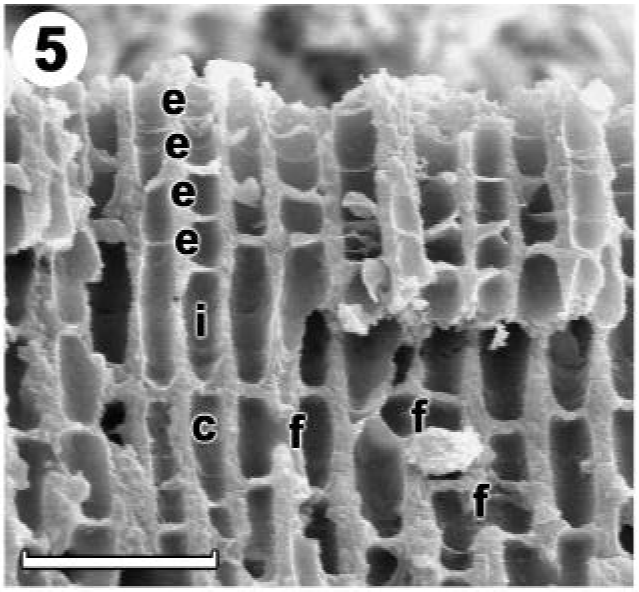
Lithoph. consociatum
f. ~~fragalis~~
connata

Plate 6







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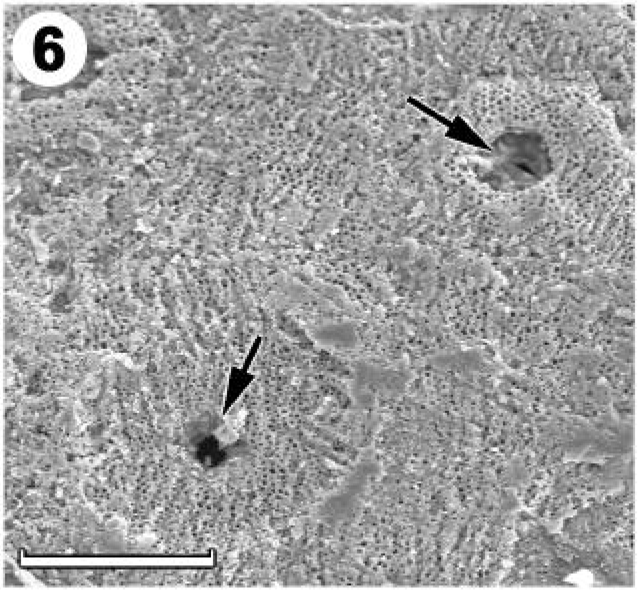
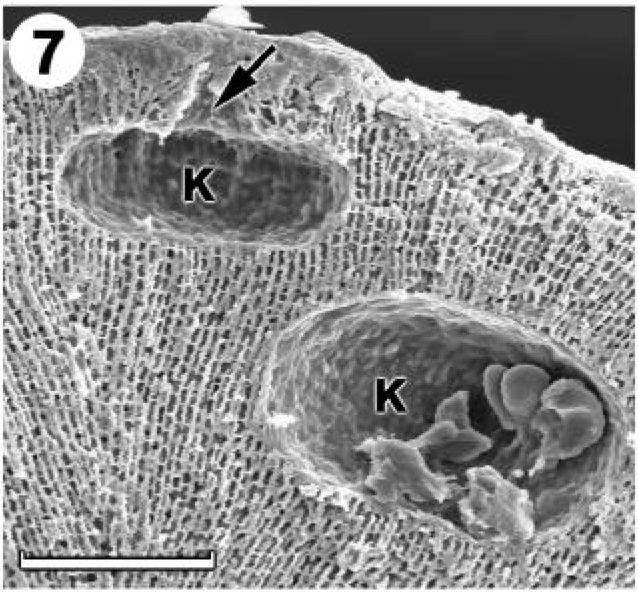
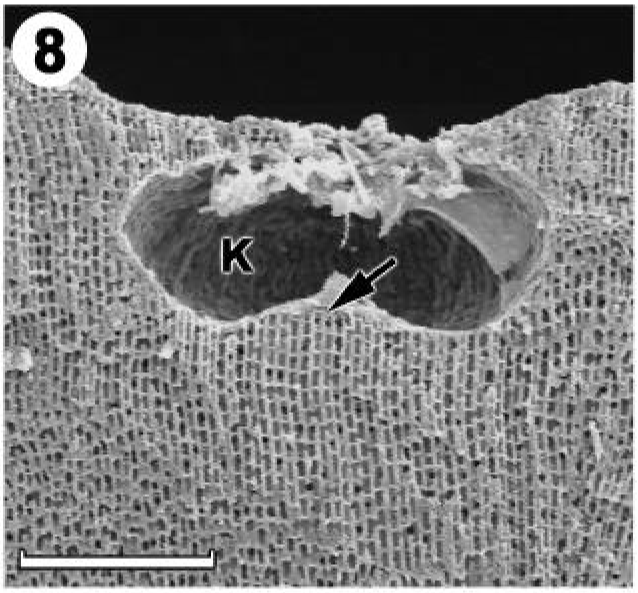
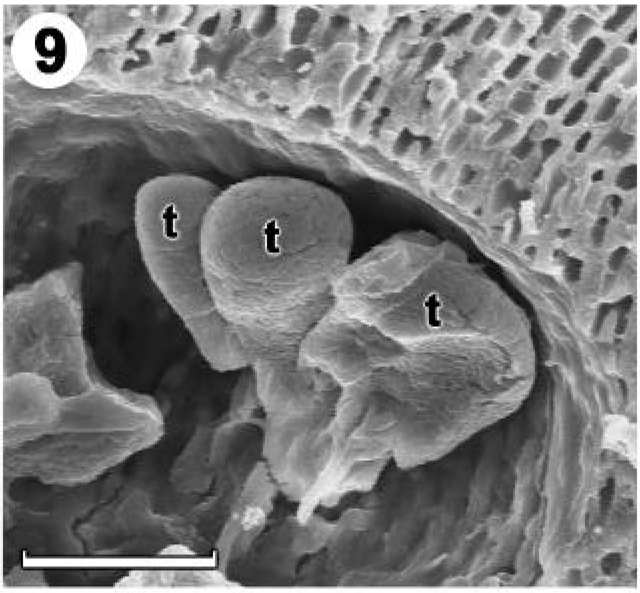
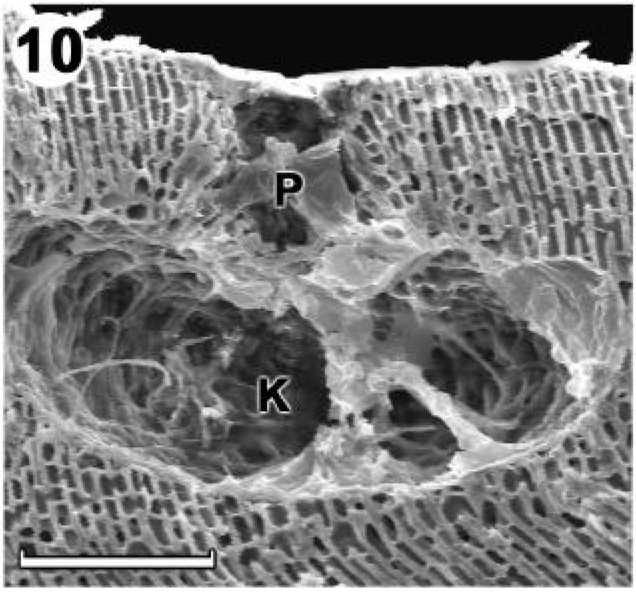










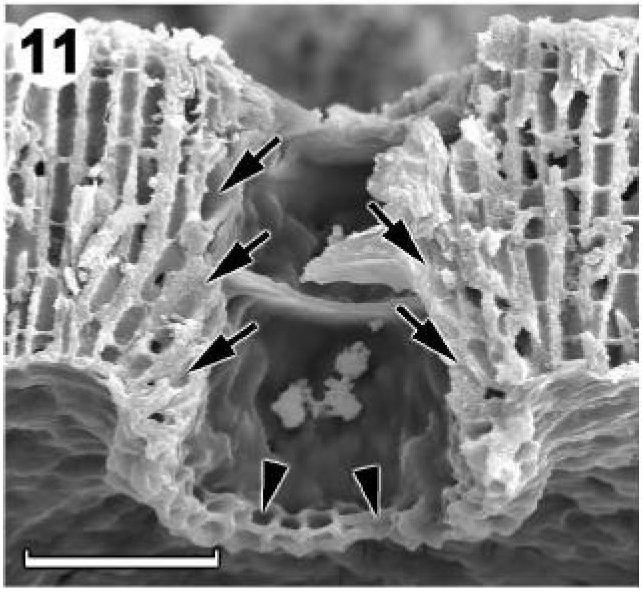
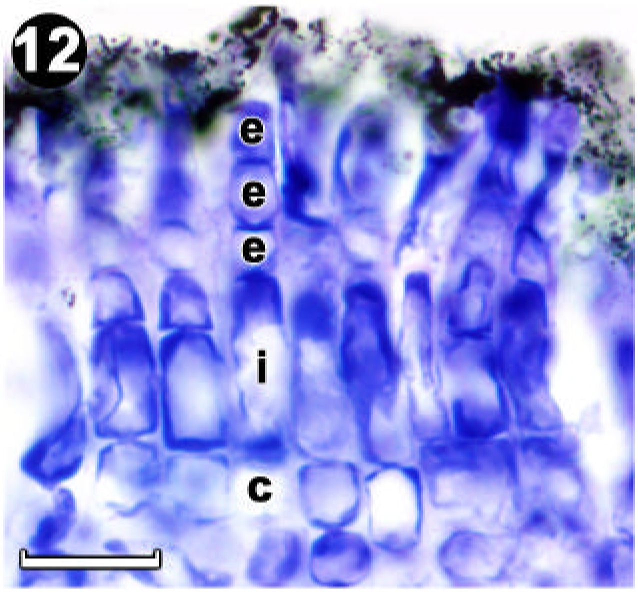
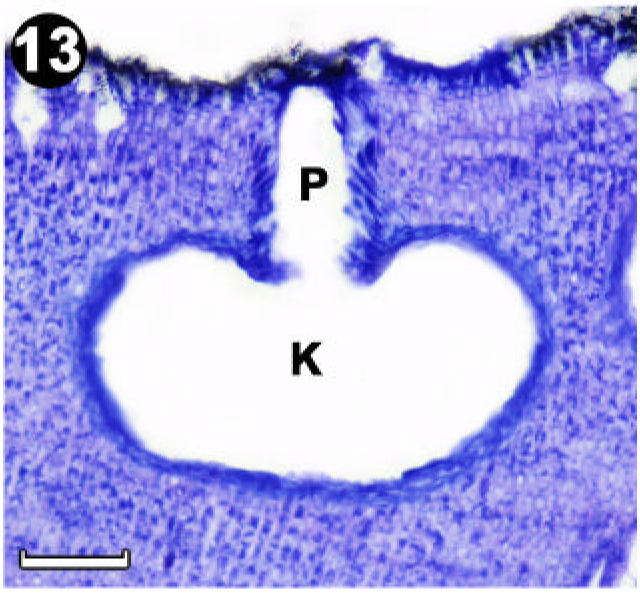
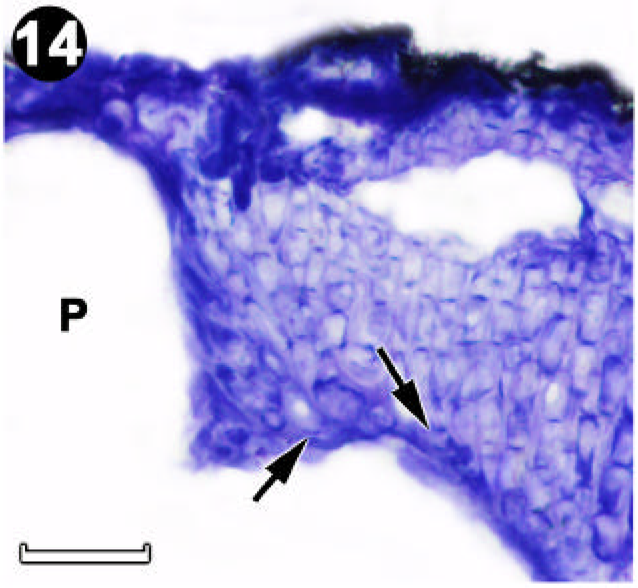


Plate 8







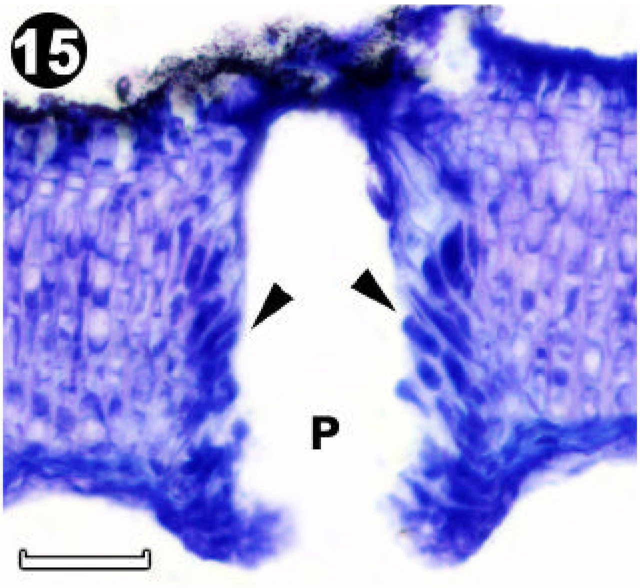


Plate 9

363

363

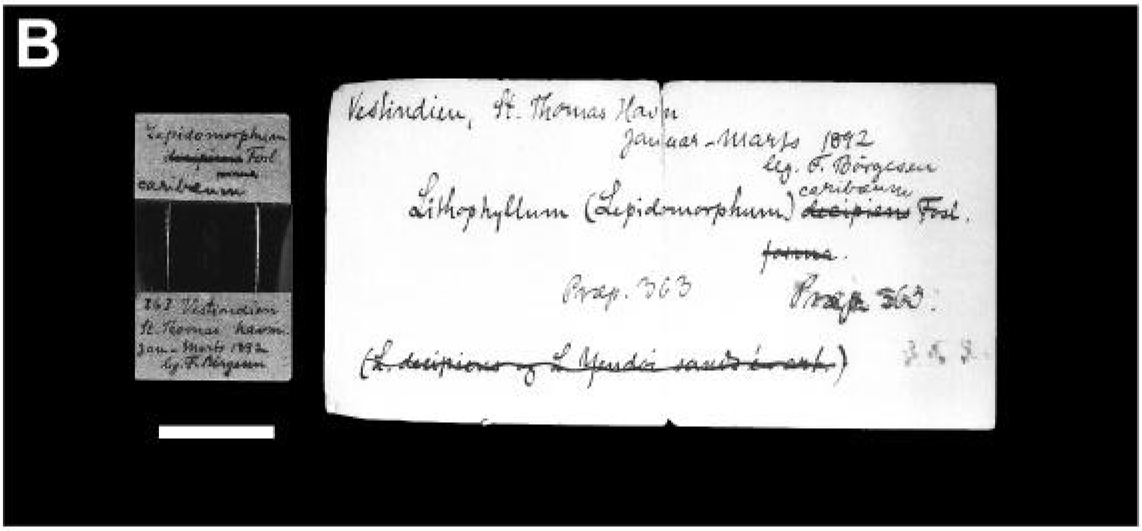
St. Thomas
præp. 363
L. caribaeum
[illegible]

Præp. 363

Lithoph. caribaeum

Vestindien
St. Thomas Havn
januar. Marts 1892
leg. F. Børgesen

Lithoth. Monogr. pl. 53 fig. 7.



Lepidomorphum
~~decipiens~~ Fosl.
~~forma~~
caribaeum

363 Vestindien
St. Thomas havn.
Jan.–Marts 1892
leg. F. Børgesen

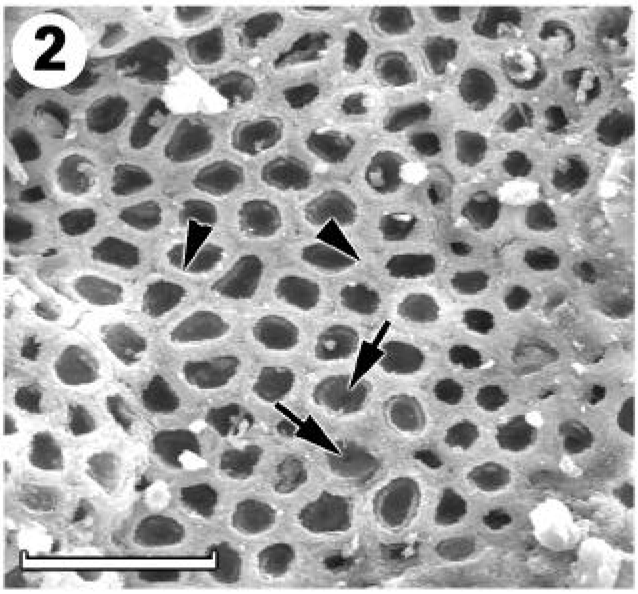
Vestindien, St. Thomas Havn
Januar–Marts 1892
leg. F. Børgesen

Lithophyllum (Lepidomorphum) ~~decipiens~~ caribaeum Fosl.
~~forma~~.

Præp. 363 Præp. 363.

(~~L. decipiens og L. Yendoi [illegible]~~) 363.

Plate 10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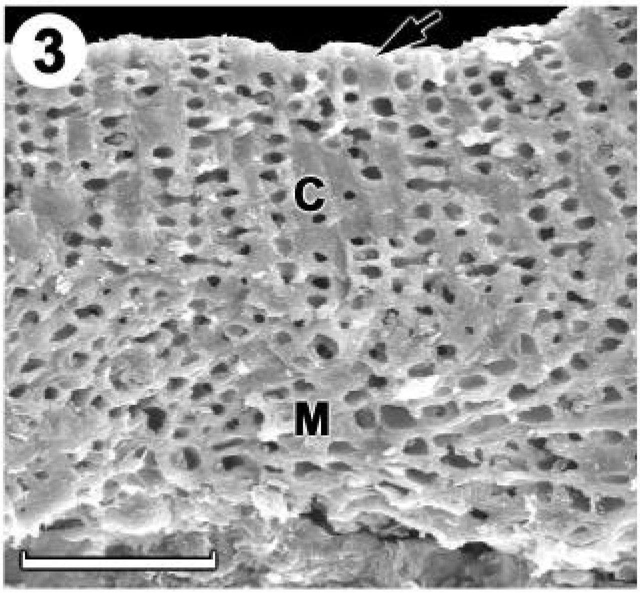
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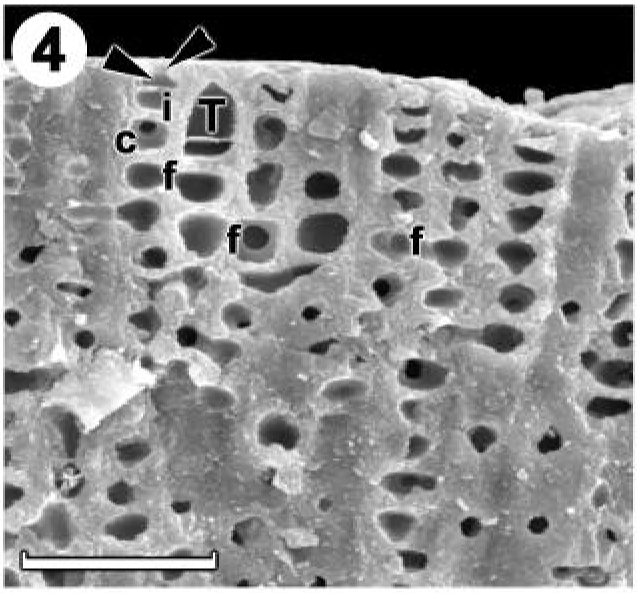
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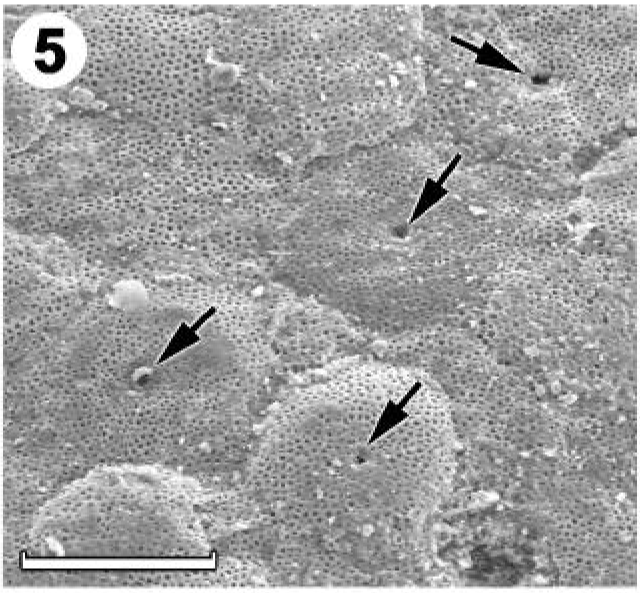
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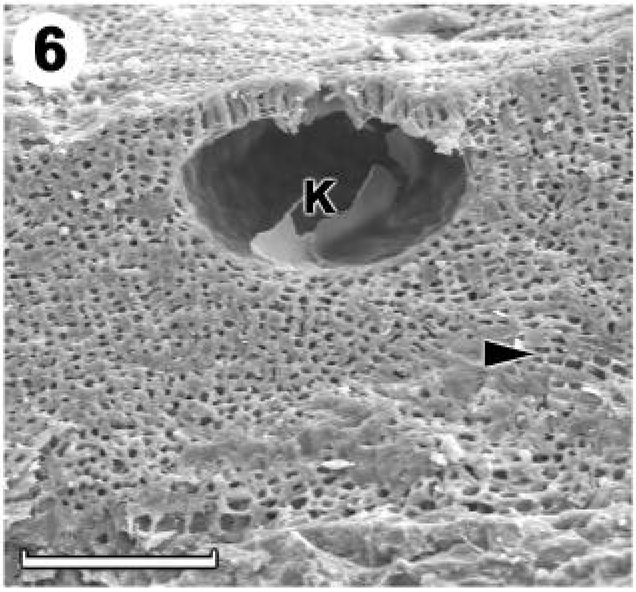
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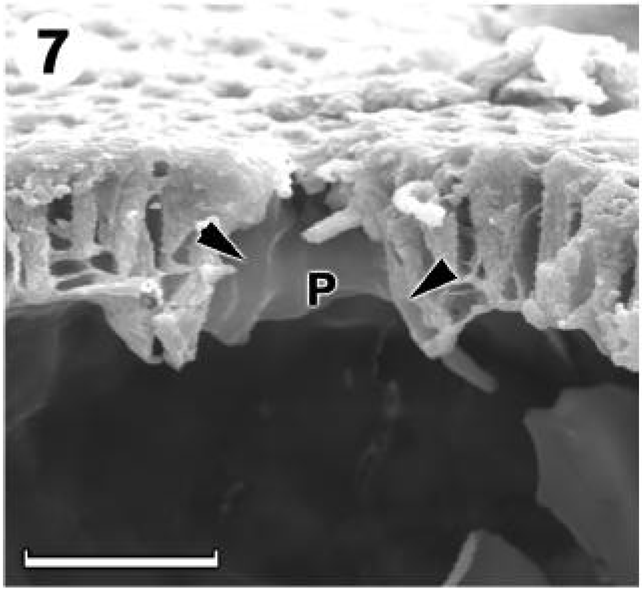
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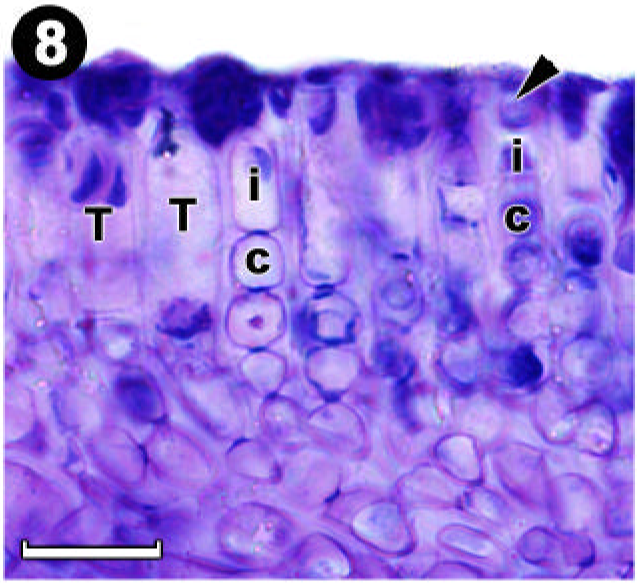
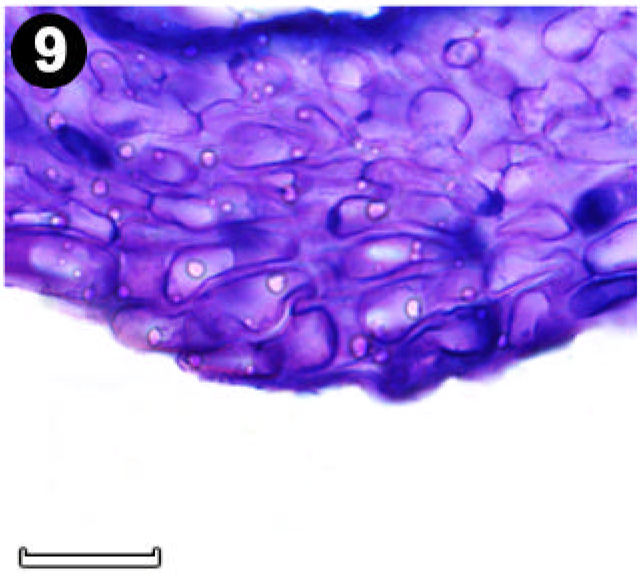
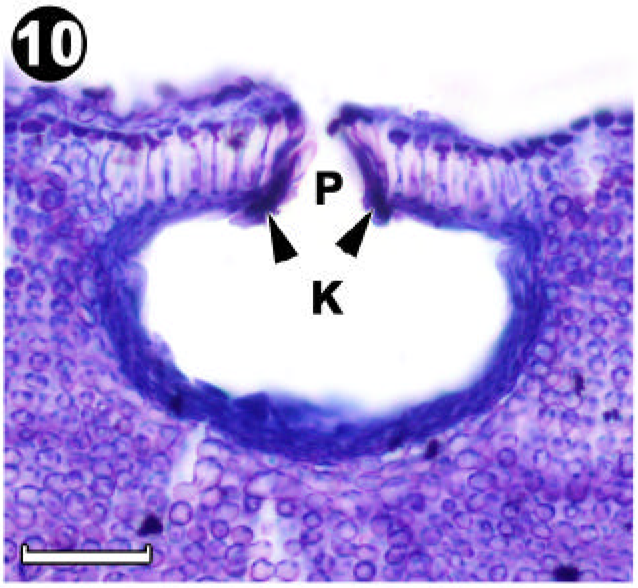
Plate 11







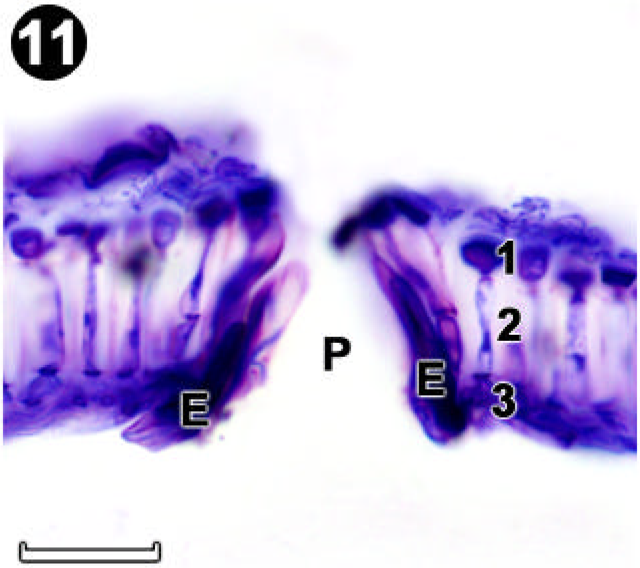


Plate 12

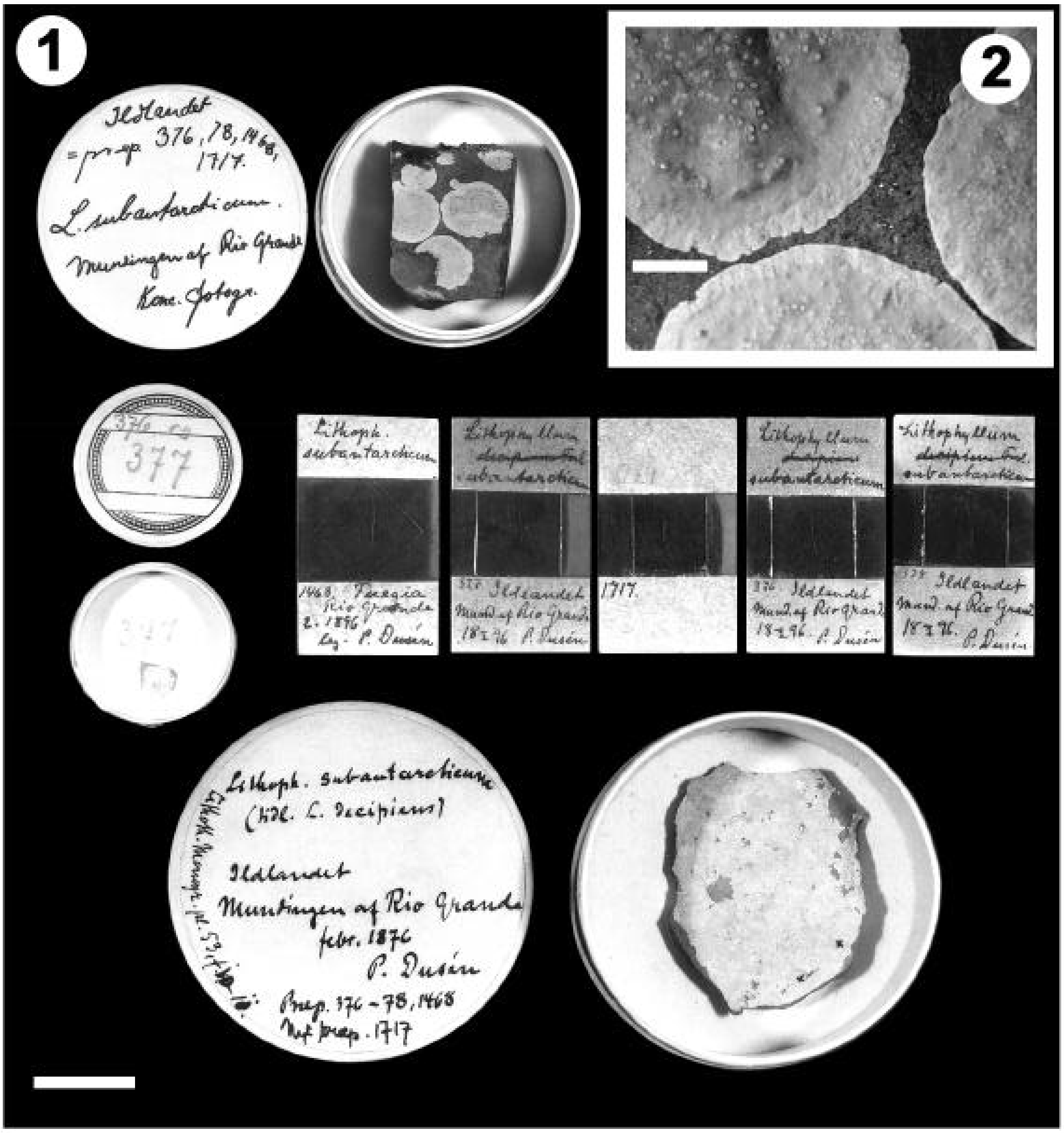
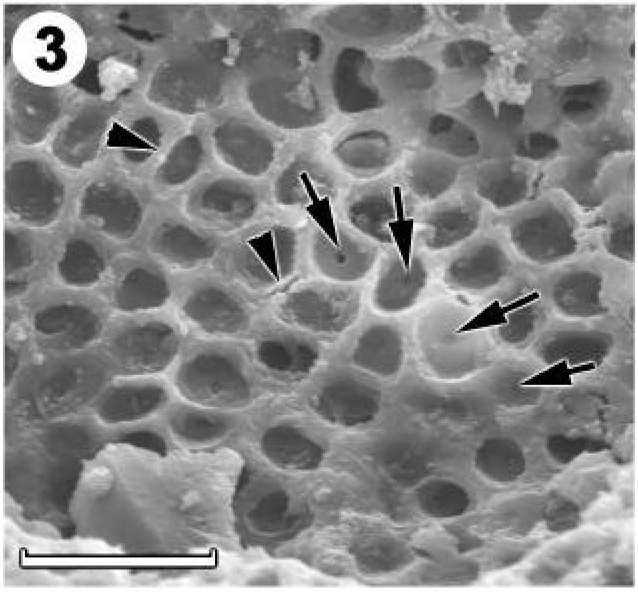
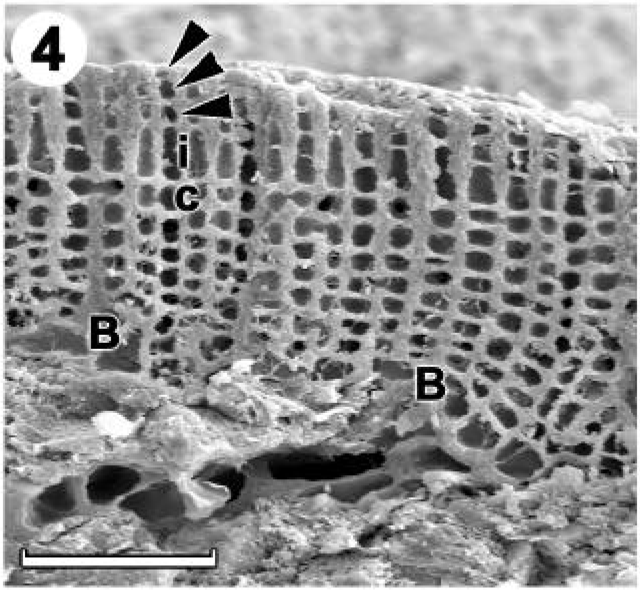
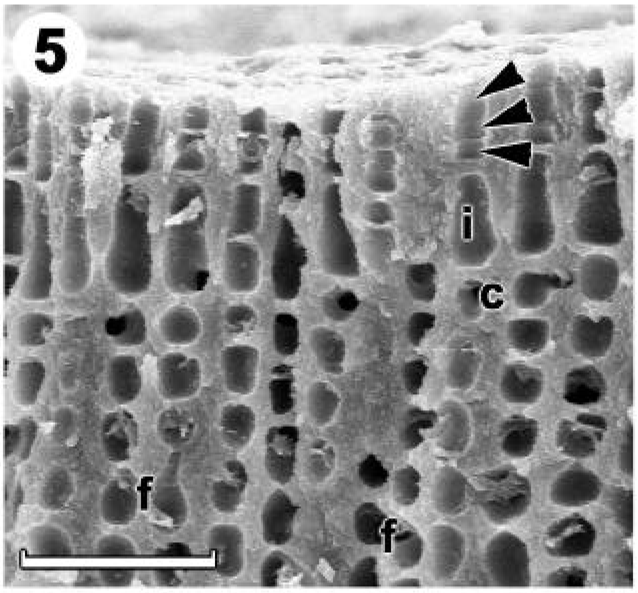

1
2
Ildlandet
= prep. 376, 78, 1468, 1717.
L. subantarcticum.
Mundingen af Rio Grande
Konc. fotogr.
376–79
377
Lithoph. subantarcticum
1468. Puegia Rio Grande 2. 1876 leg. P. Dusén
Lithophyllum ~~decipiens Fosl.~~ subantarcticum
377 Ildlandet Mund. af Rio Grande 18 2/76 P. Dusén
1717.
Lithophyllum ~~decipiens~~ subantarcticum
376. Ildlandet Mund. af Rio Grande 18 2/76 P. Dusén
Lithophyllum ~~decipiens Fosl.~~ subantarcticum
378 Ildlandet Mund. af Rio Grande 18 2/76 P. Dusén
Lithoph. subantarcticum
(Hkl. L. decipiens)
Ildlandet
Mundingen af Rio Grande
febr. 1876
P. Dusén
Prep. 376 – 78, 1468
Nyt prep. 1717

Plate 13







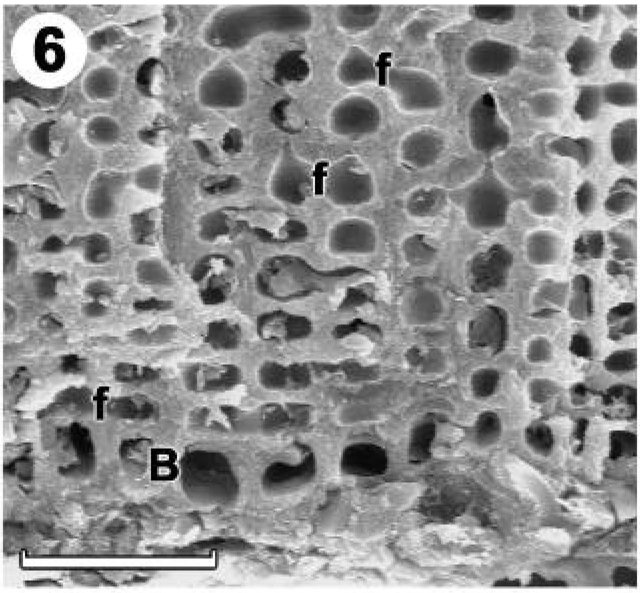
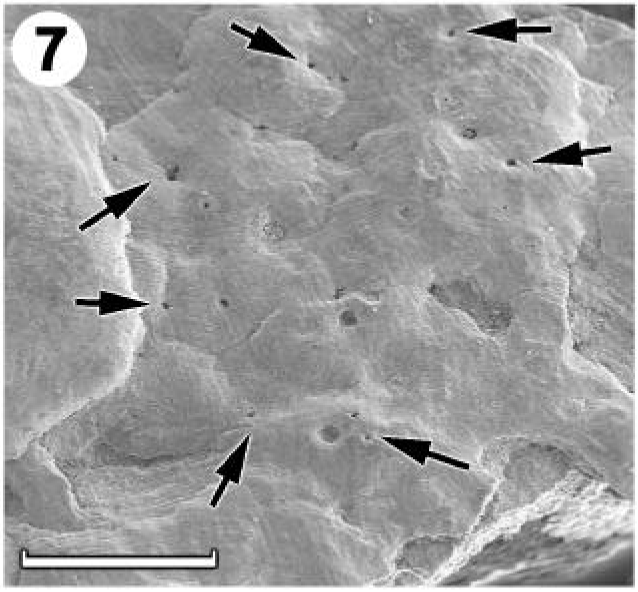
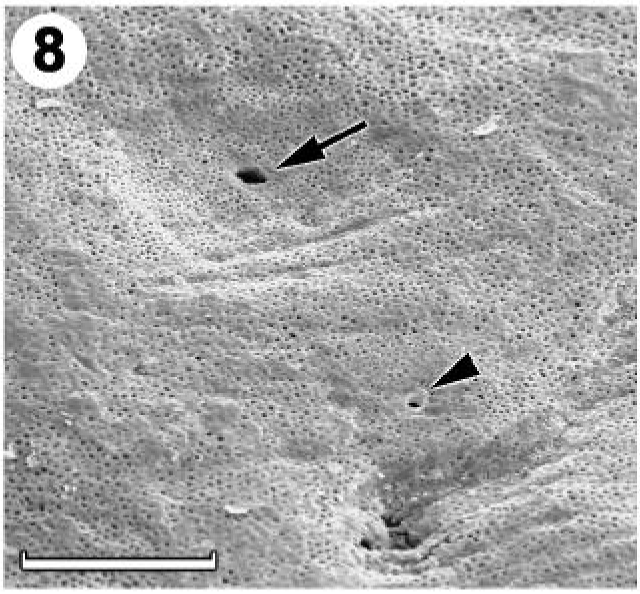
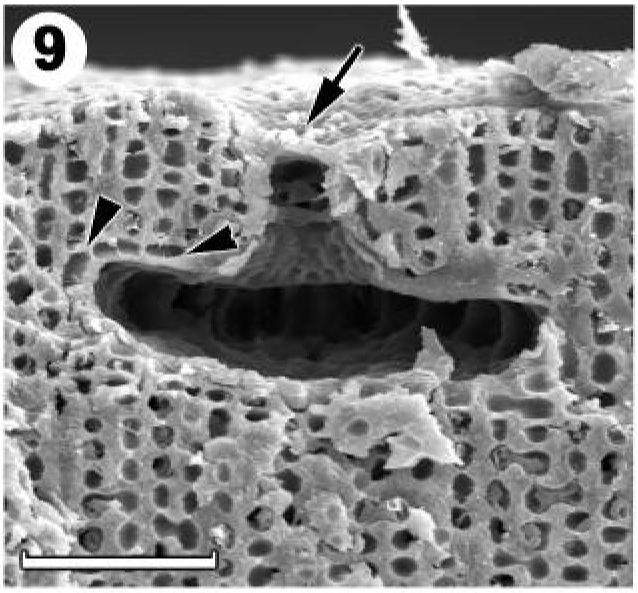


Plate 14







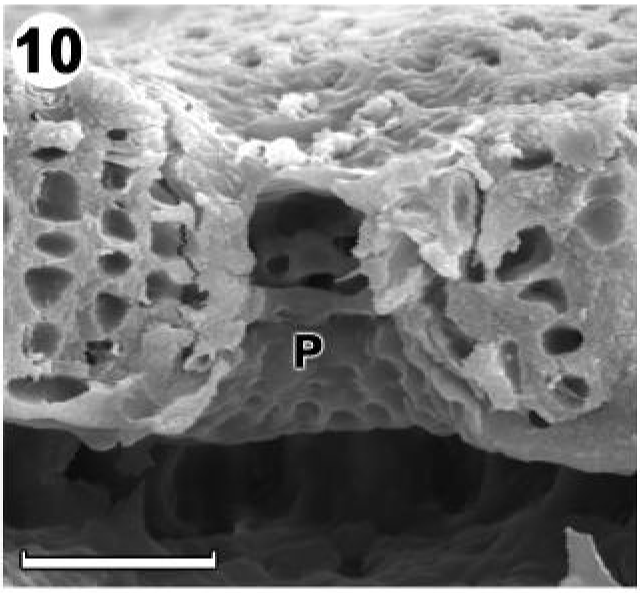
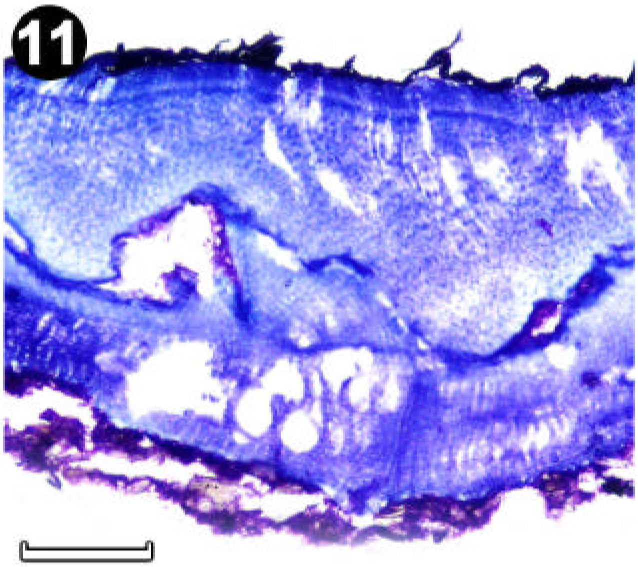


Plate 15

11


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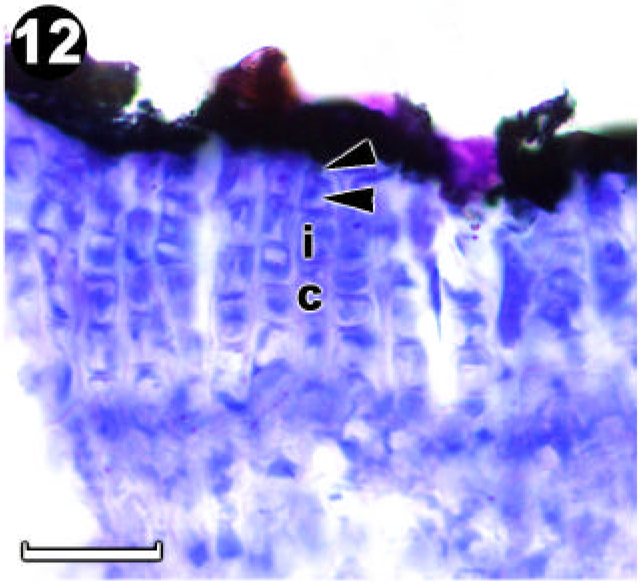

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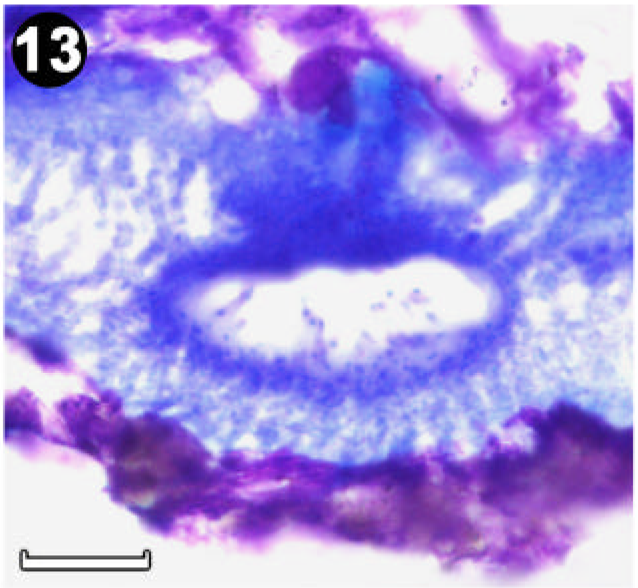

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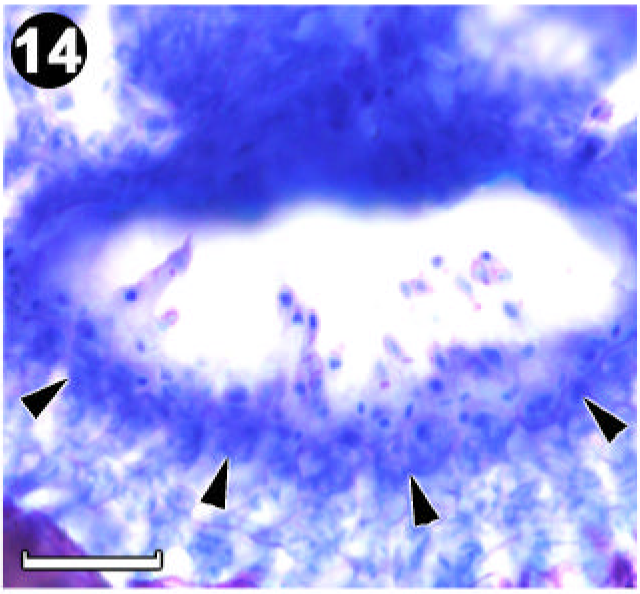


Plate 16

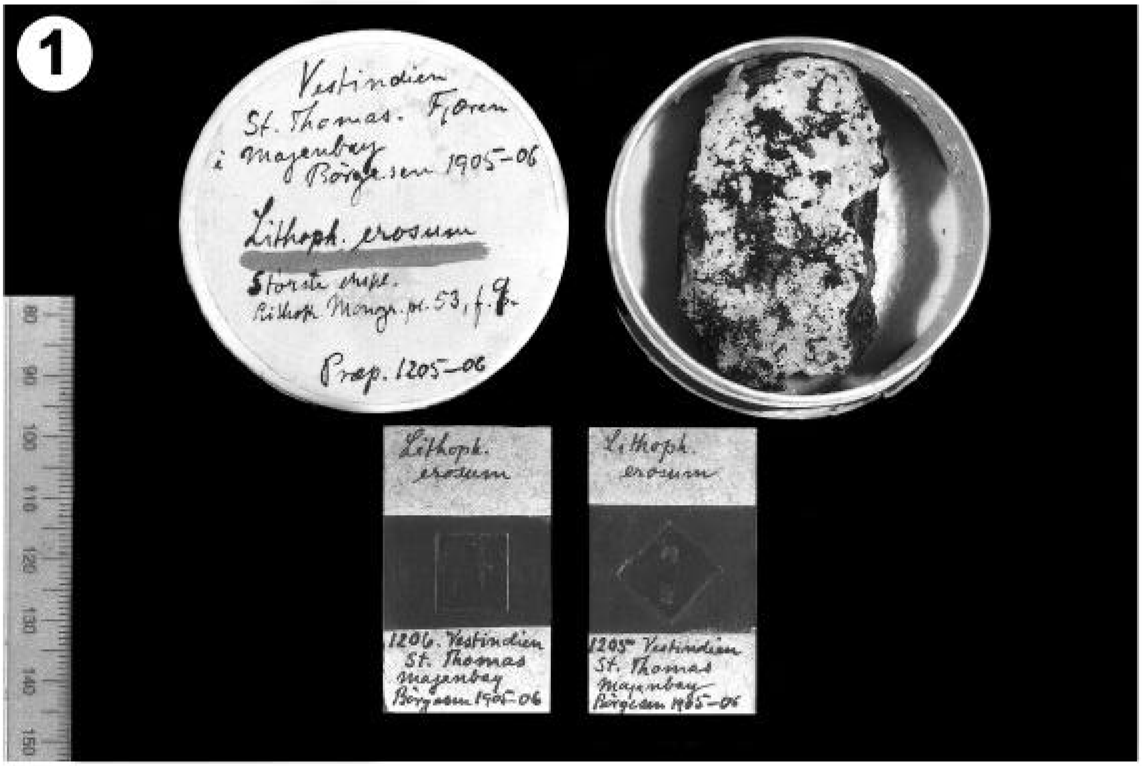

1
Vestindien
St. Thomas. Fjoren
i Mayenbay
Börgesen 1905–06
Lithoph. erosum
Störste ekspl.
Lithoph. Monogr. pl. 53, f. 9.
Prep. 1205–06
Lithoph. erosum
1206. Vestindien
St. Thomas
Mayenbay
Börgesen 1905–06
Lithoph. erosum
1205 Vestindien
St. Thomas
Mayenbay
Börgesen 1905–06
80
90
100
110
120
130
140
150

Plate 17

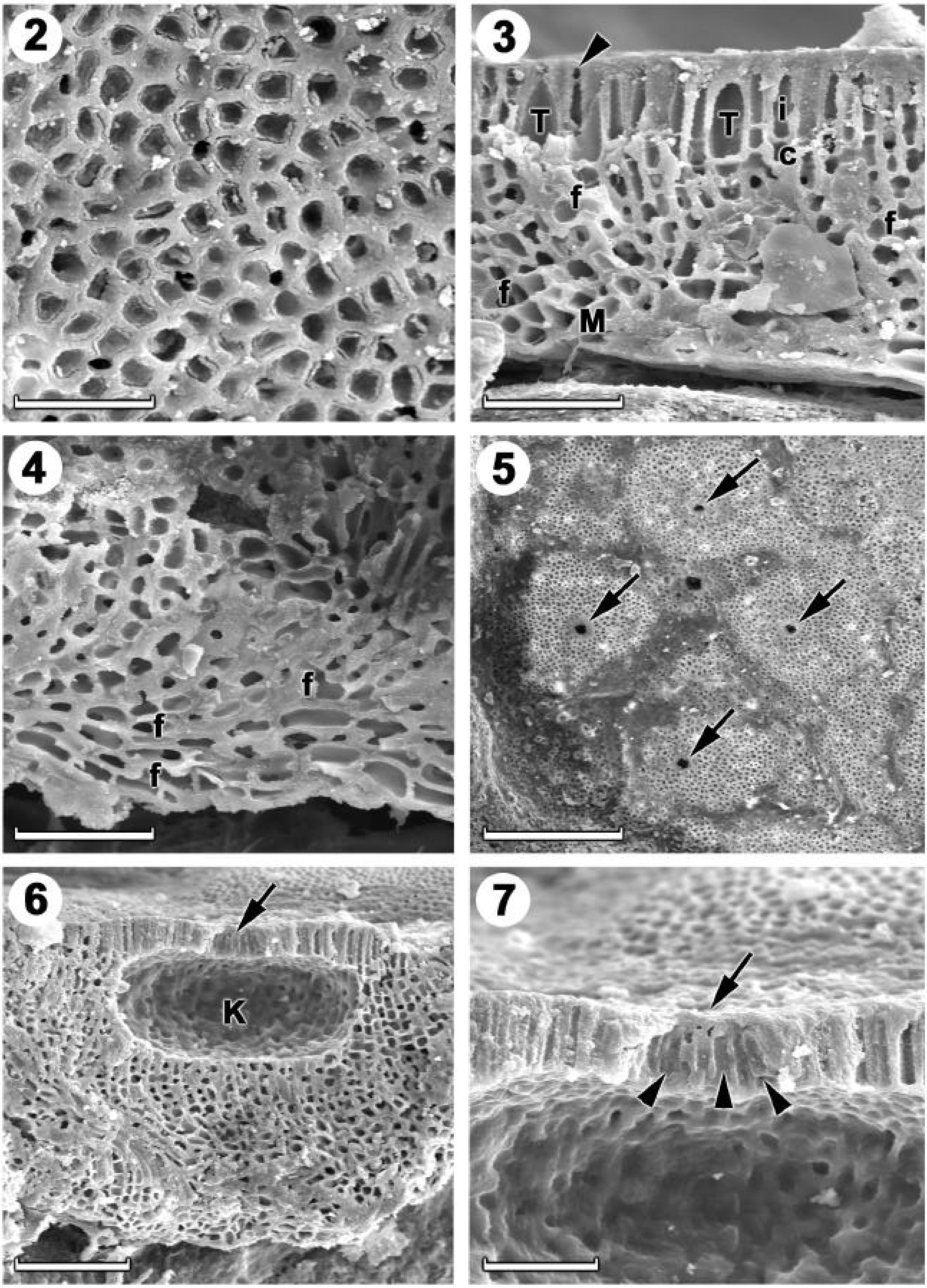
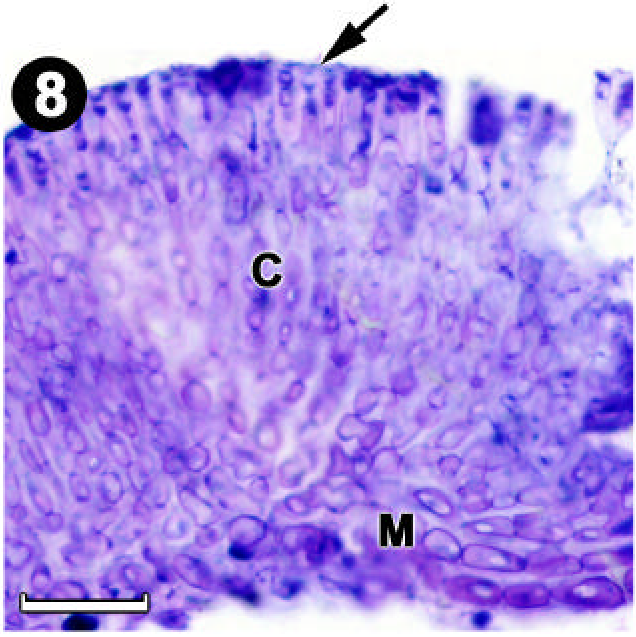
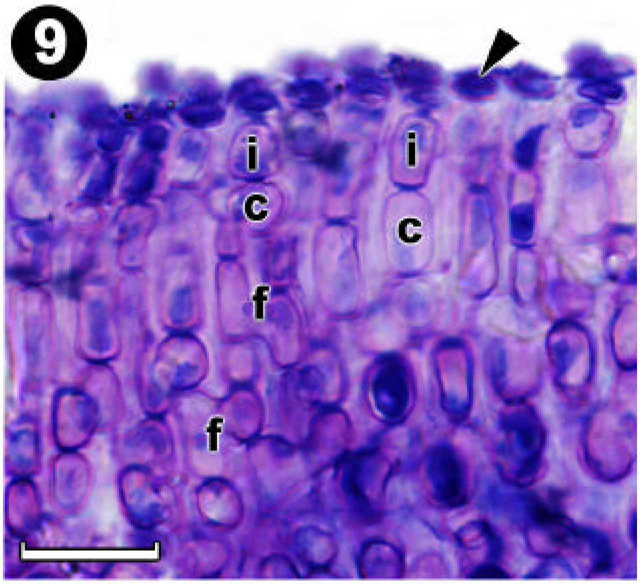
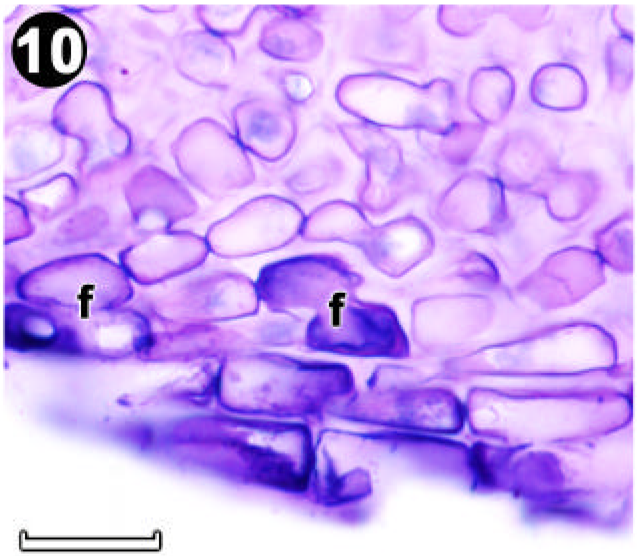
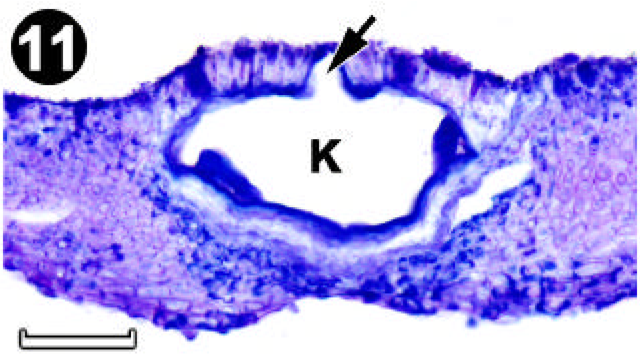


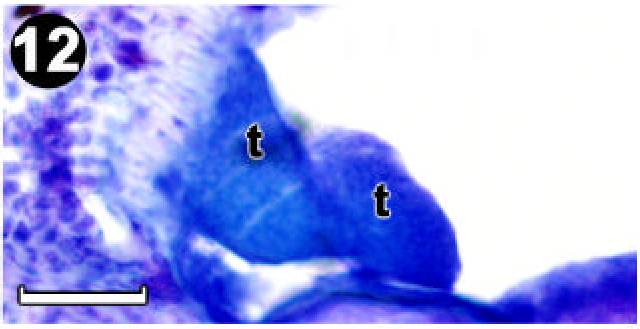
Plate 18

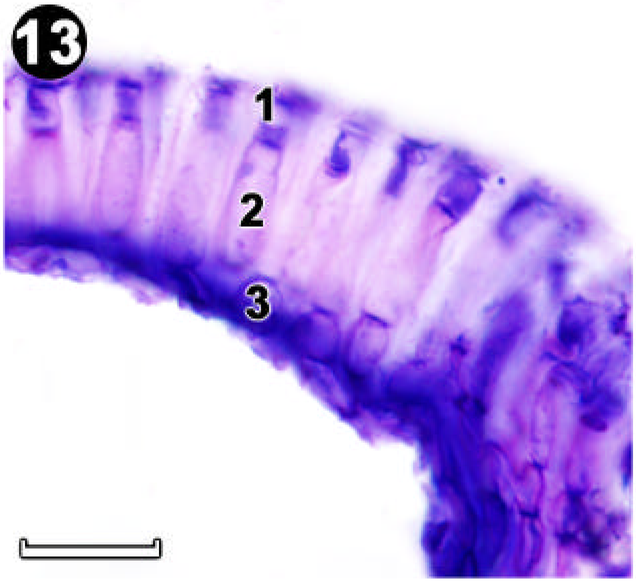












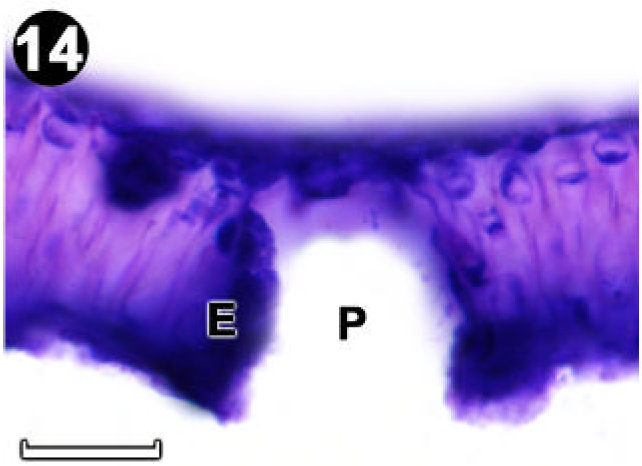
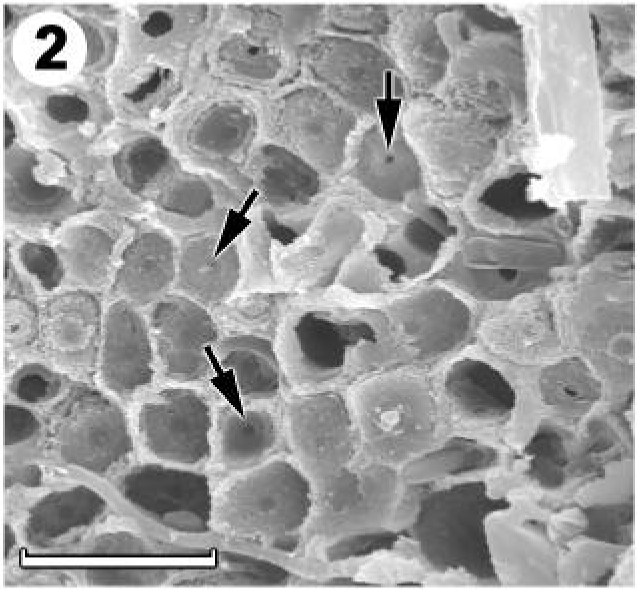
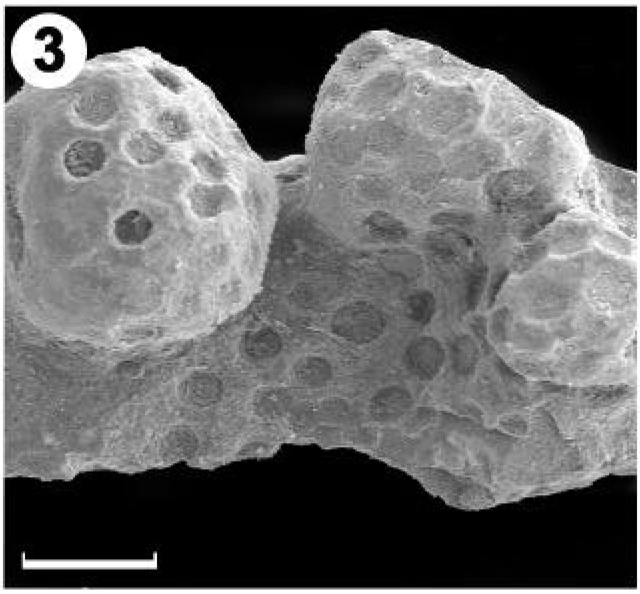


Plate 19


1
Sv. sydpeks. 1901–03
St. 35 Falklandsöarne
Berkeley Sound Port Louis
2/7 1902 leg. C. Skottsberg
Lithoph. falklandicum
Lith. Mon. pl. 94 f. 15–16
Prep. 940
Lithoph. falklandicum
940 Falklandsöarne
Berkeley Sound Port Louis
2/7 1902 leg. C. Skottsberg

Plate 20





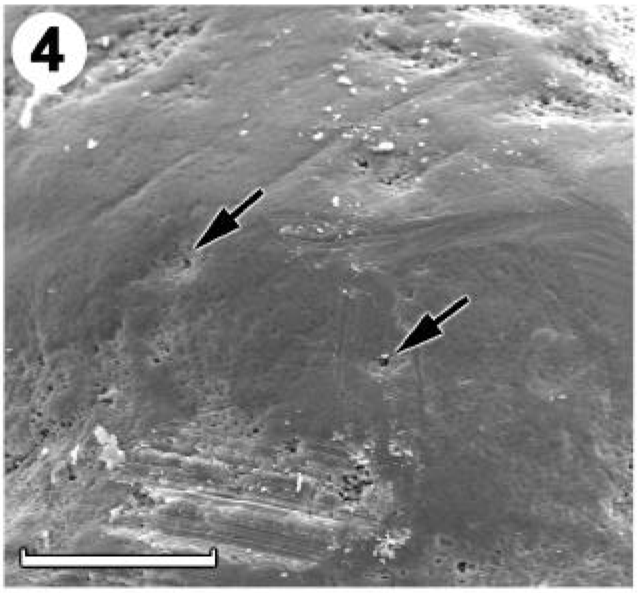
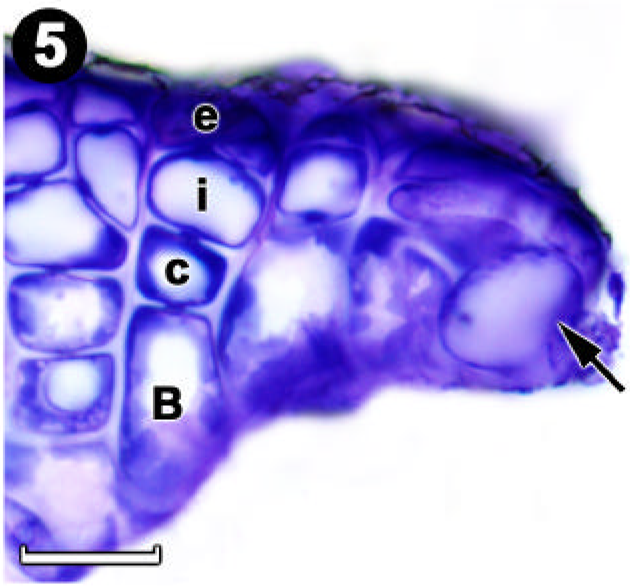
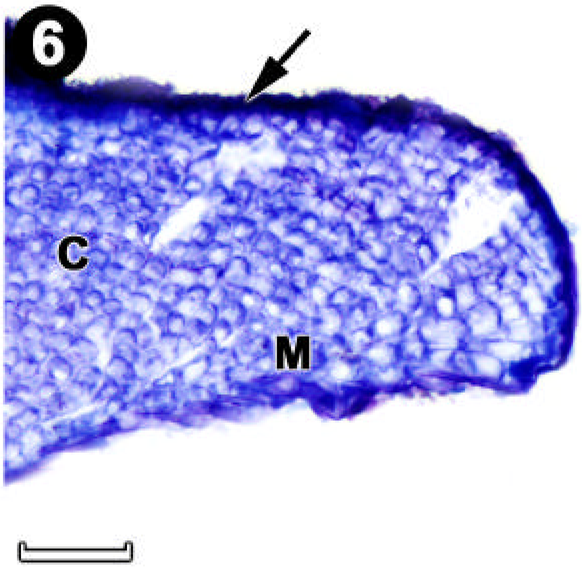
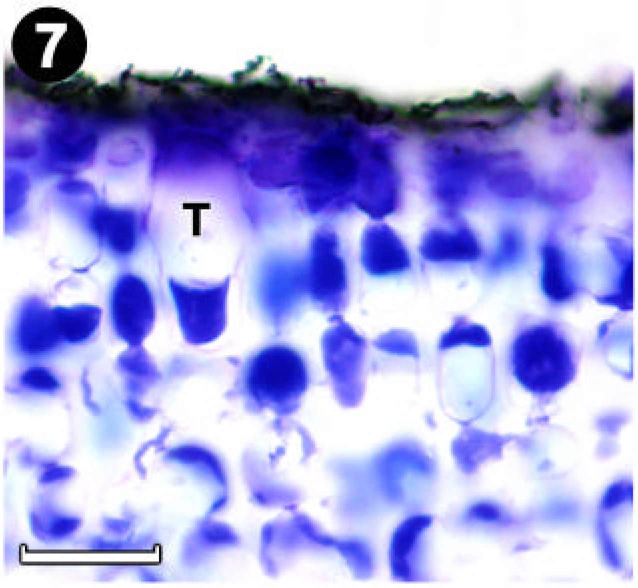
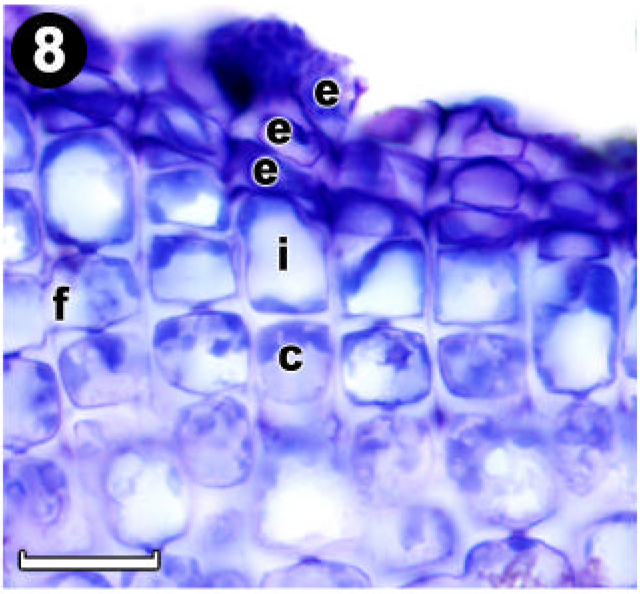


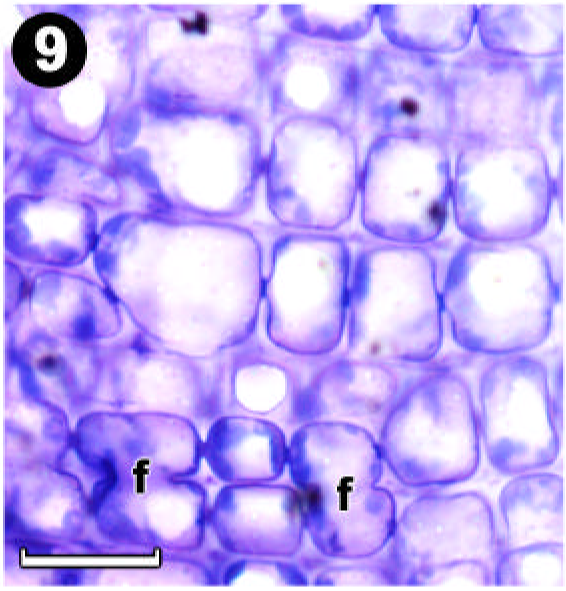
Plate 21











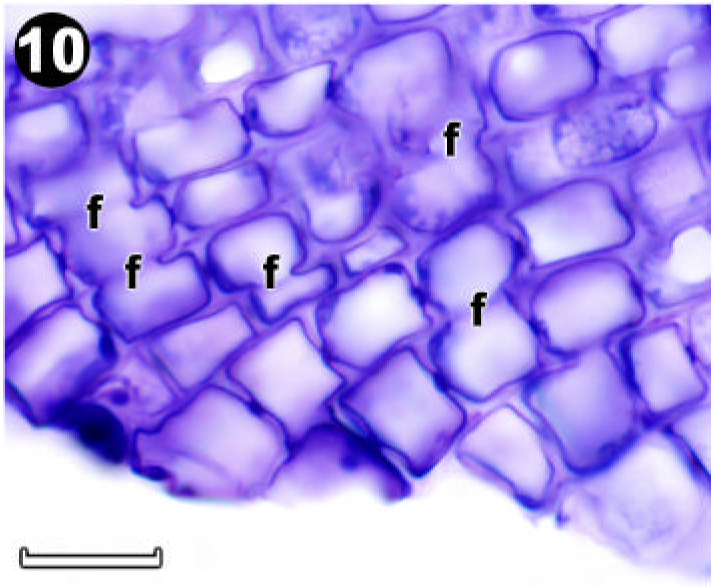
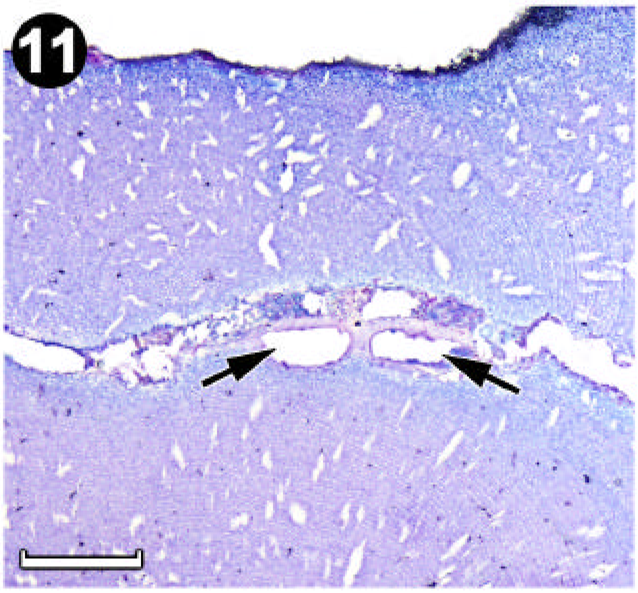
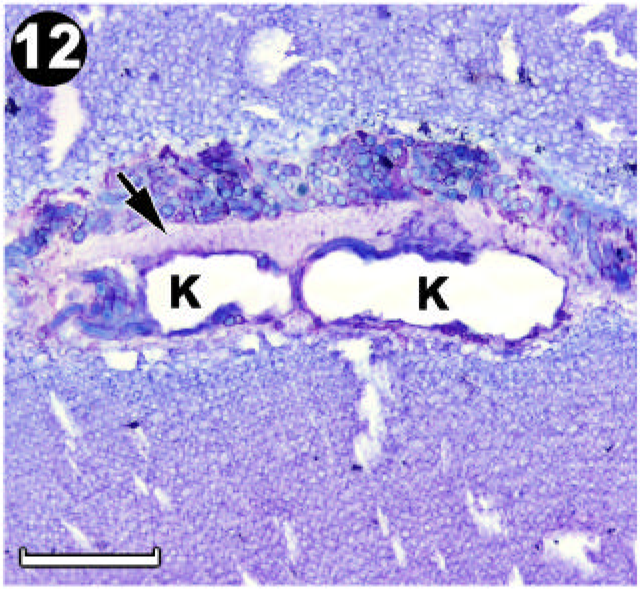


Plate 22





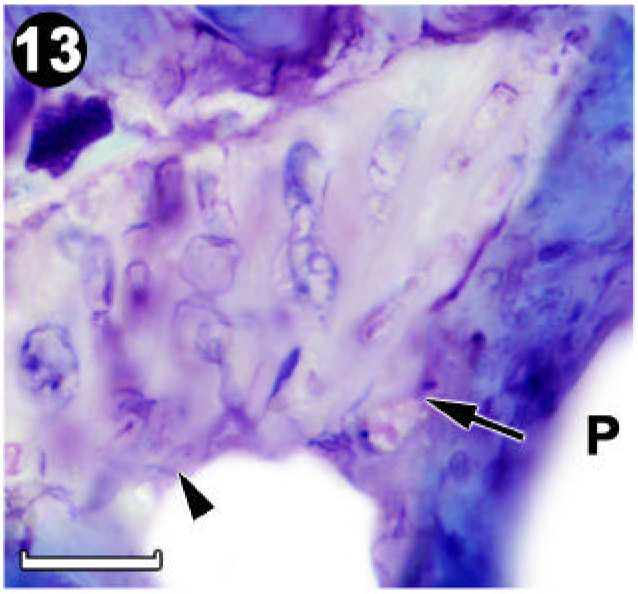


Plate 23

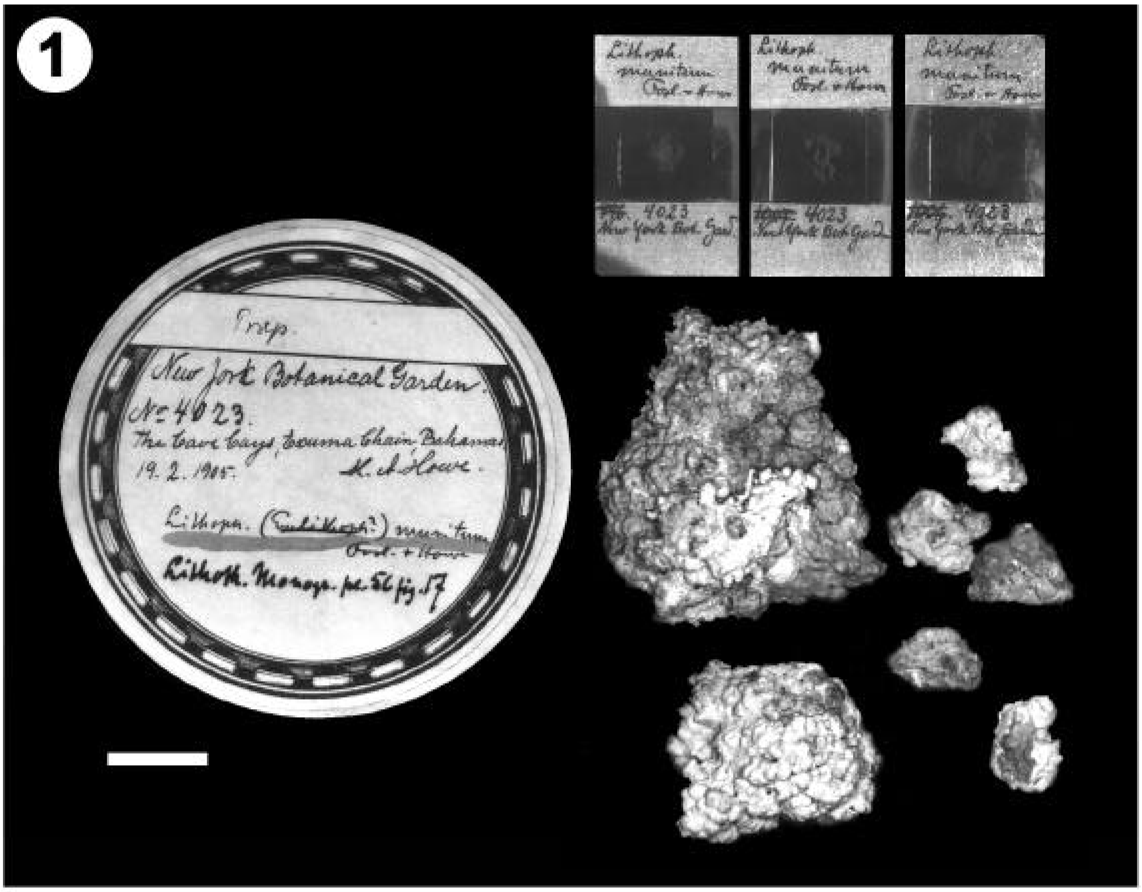
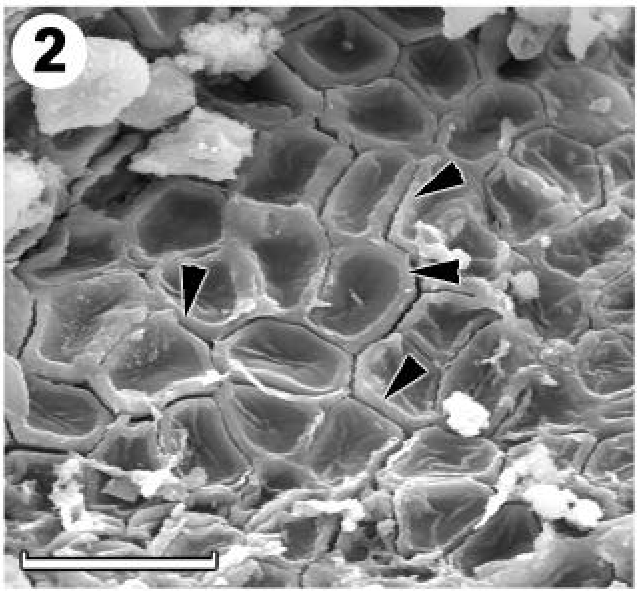
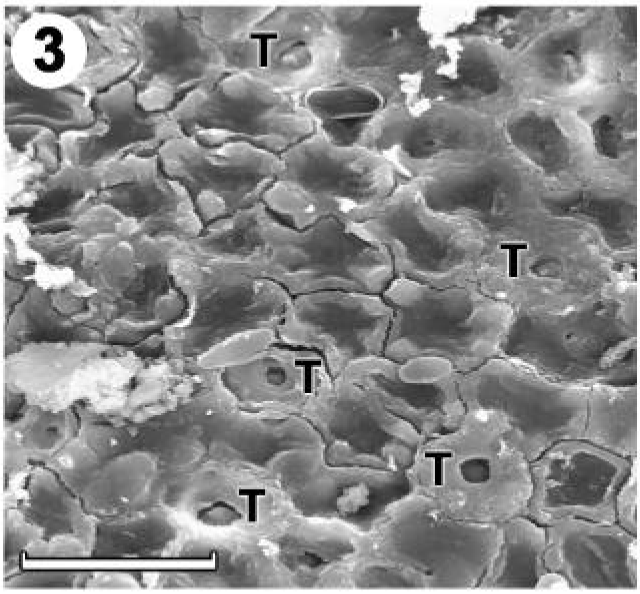

1
Prep.
New York Botanical Garden.
No. 4023.
The Cave Cays, Exuma Chain, Bahamas
19. 2. 1905.
M. A. Howe.
Lithoph. (Goniolith.?) munitum
Fosl. + Howe
Lithoth. Monogr. pl. 56 fig. 17
Lithoph. munitum Fosl. + Howe
4023 New York Bot. Gard.
Lithoph. munitum Fosl. + Howe
4023 New York Bot. Gard.
Lithoph. munitum Fosl. + Howe
4023 New York Bot. Garden

Plate 24





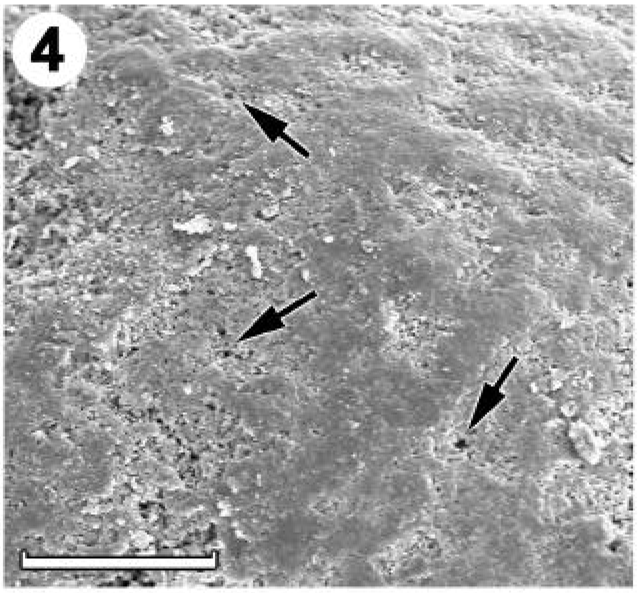
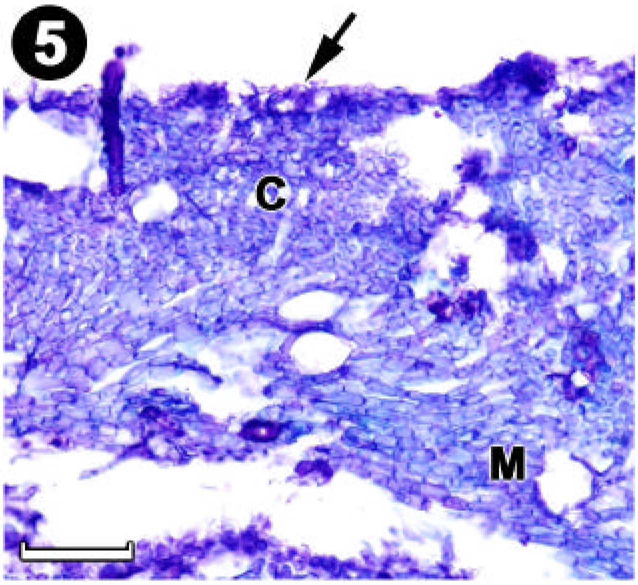
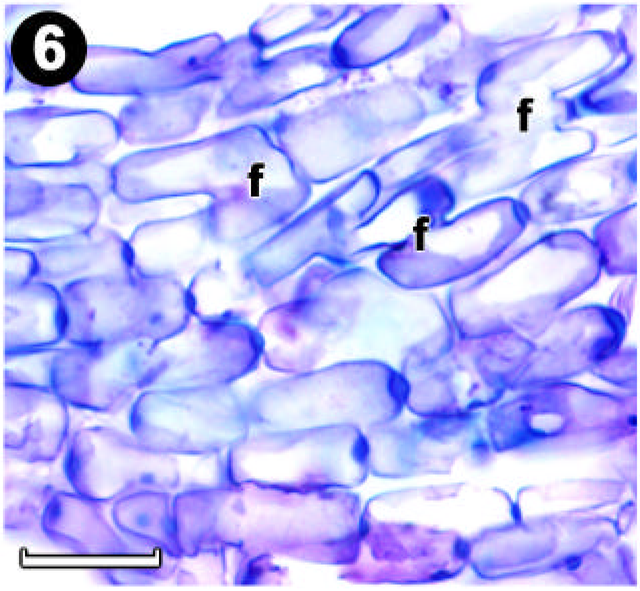
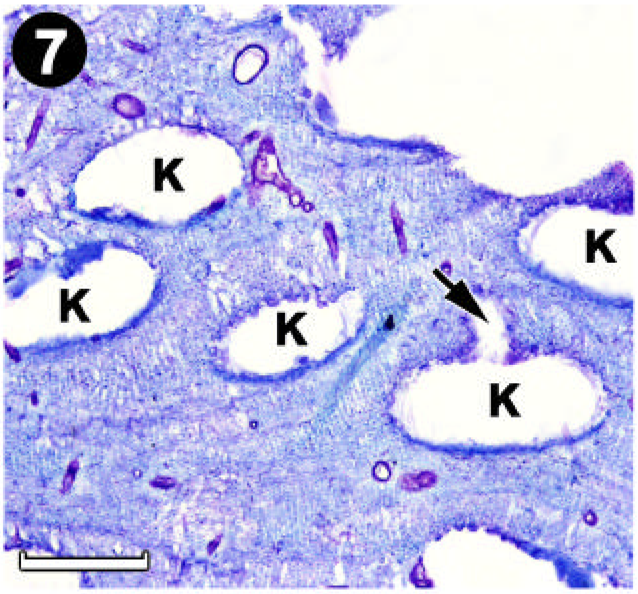


Plate 25







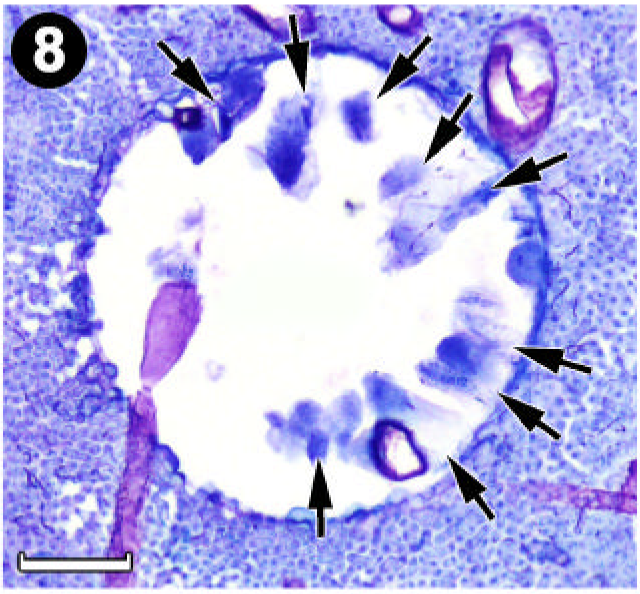


Plate 26

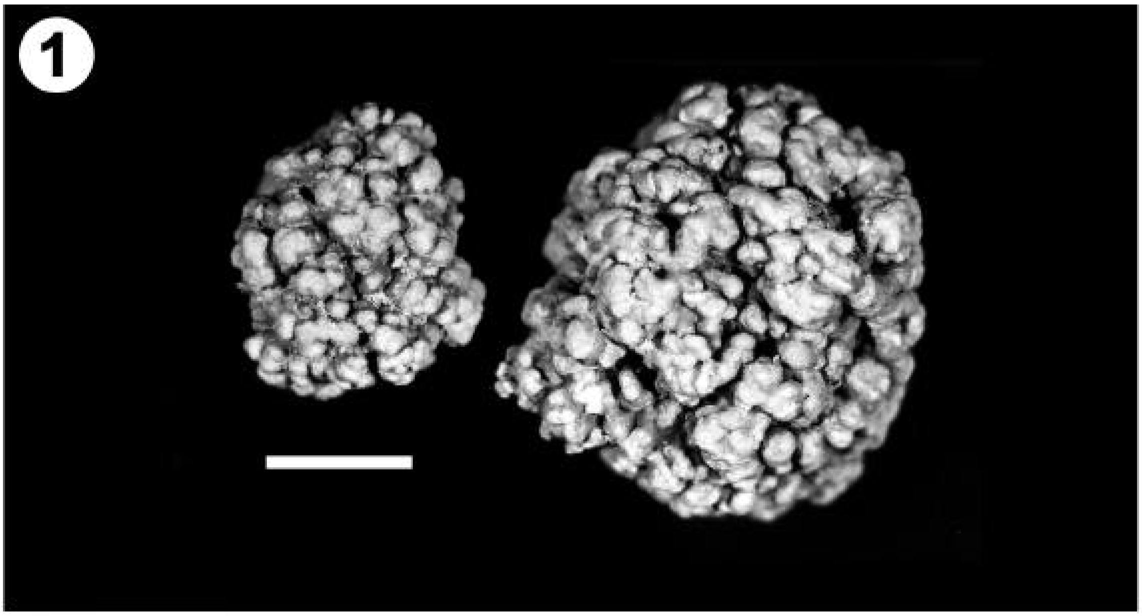
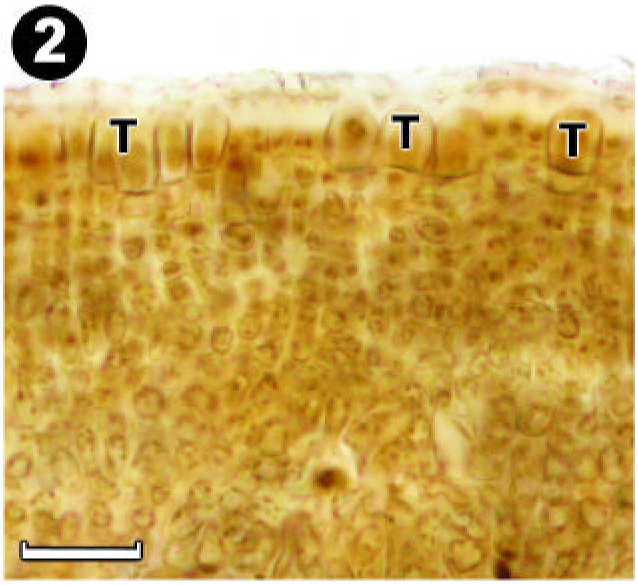
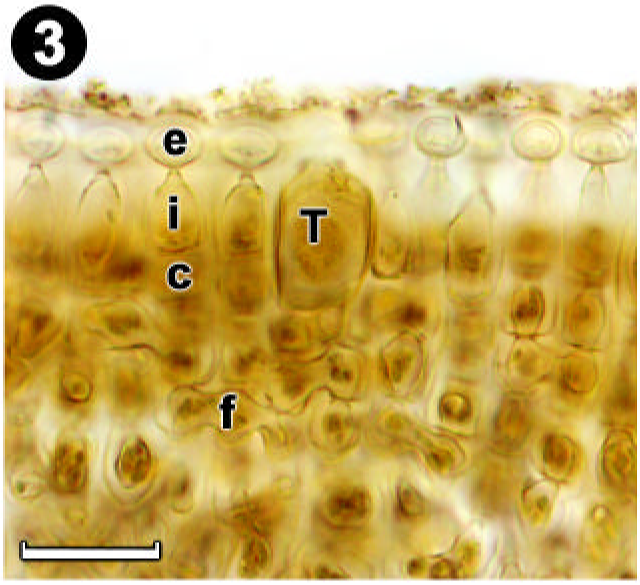
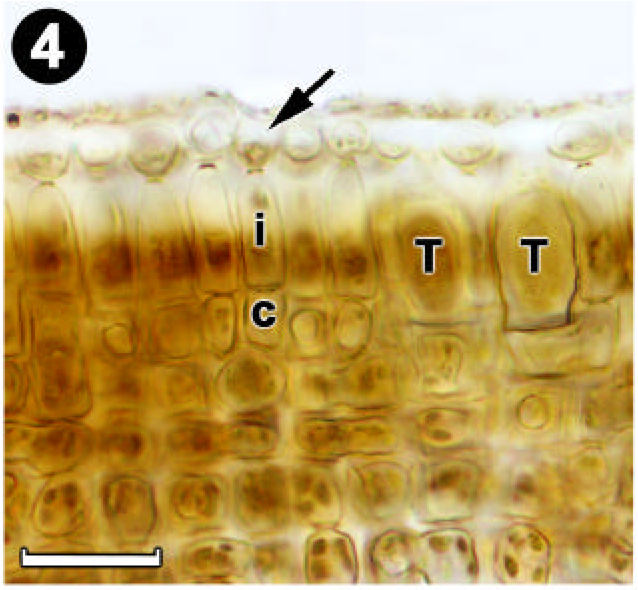


Plate 27







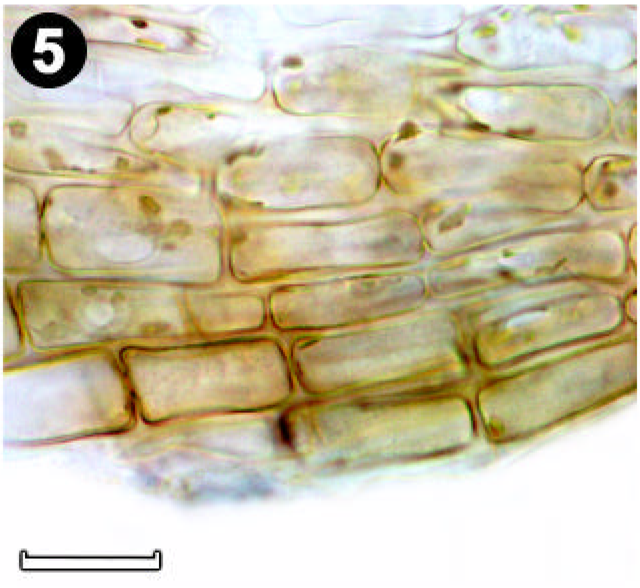
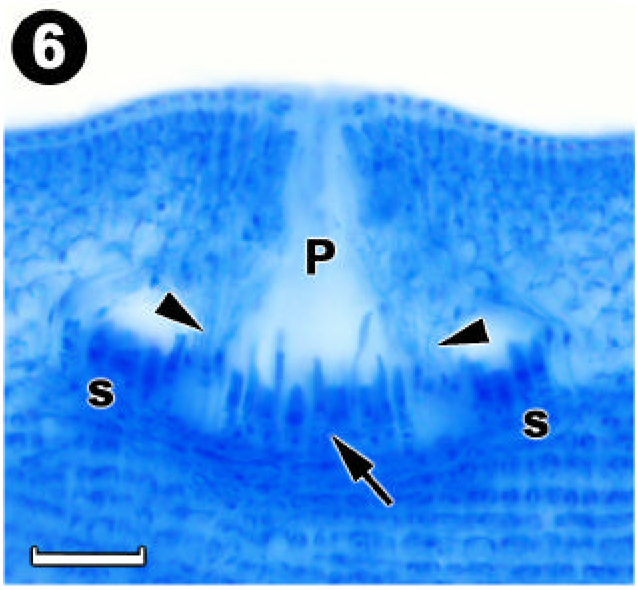


Plate 28

6



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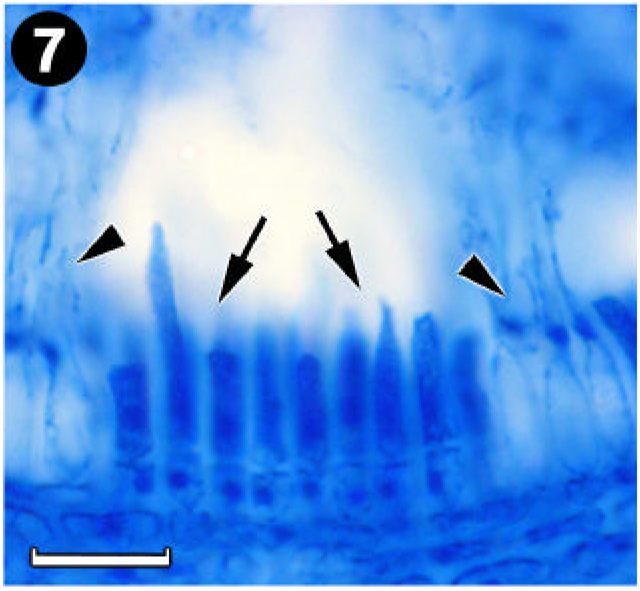

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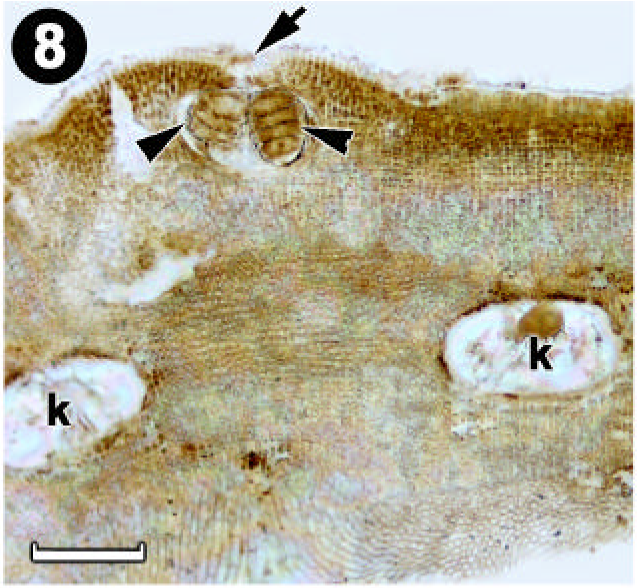

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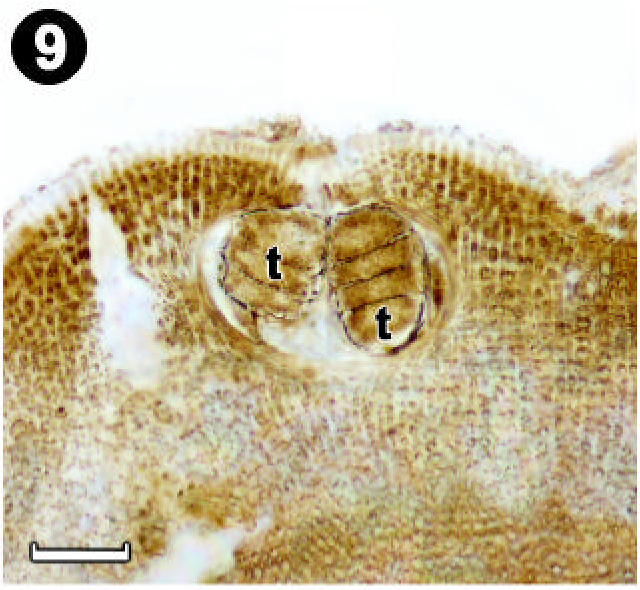

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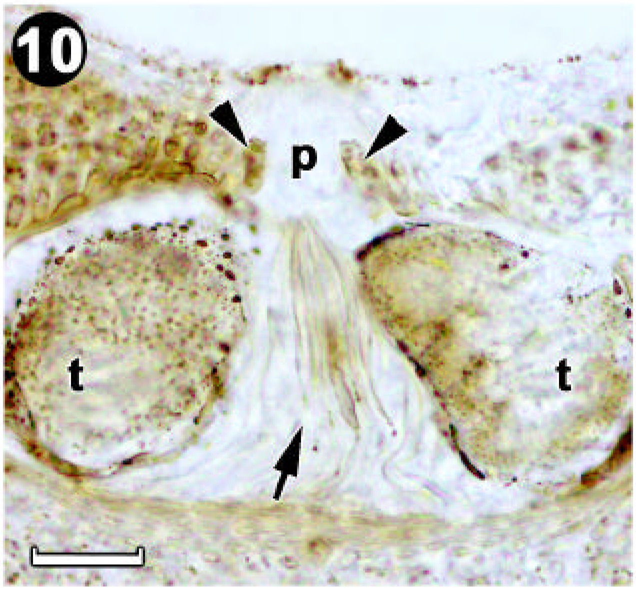

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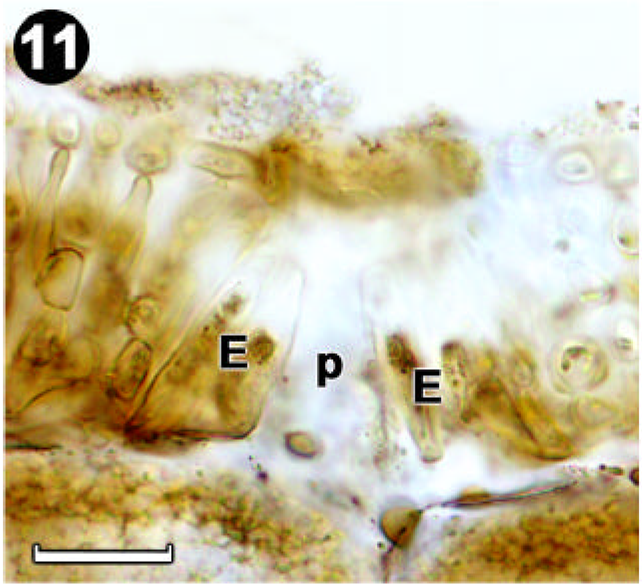
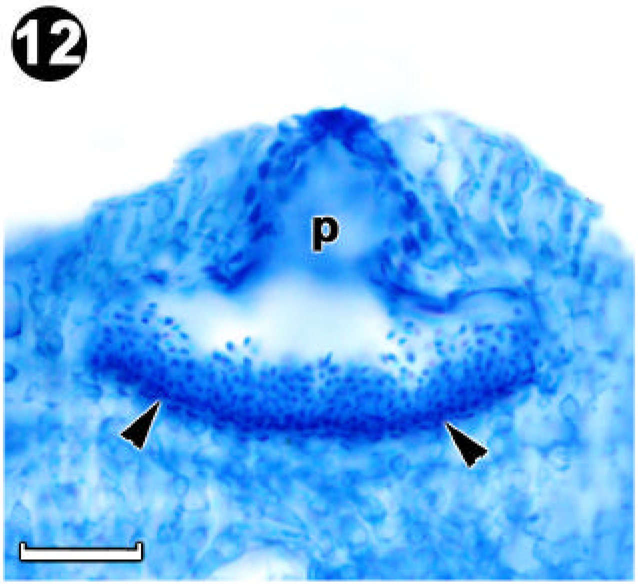


Plate 29



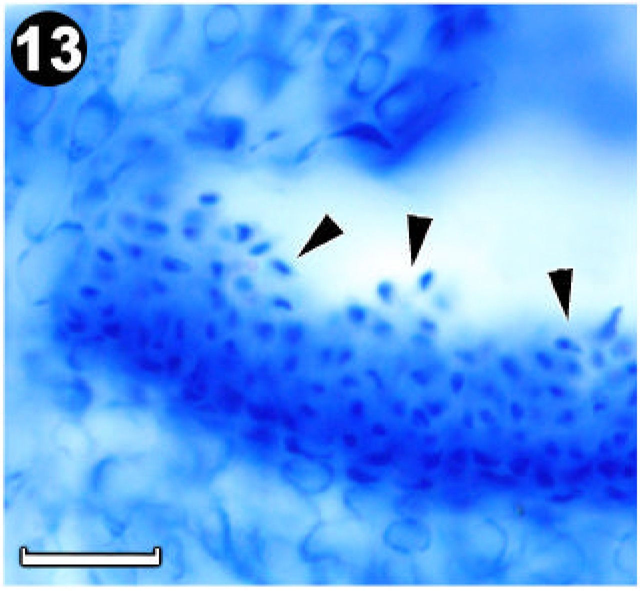
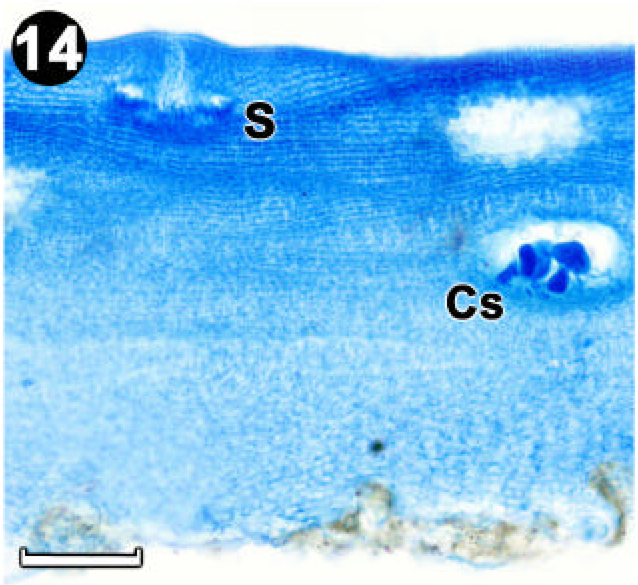
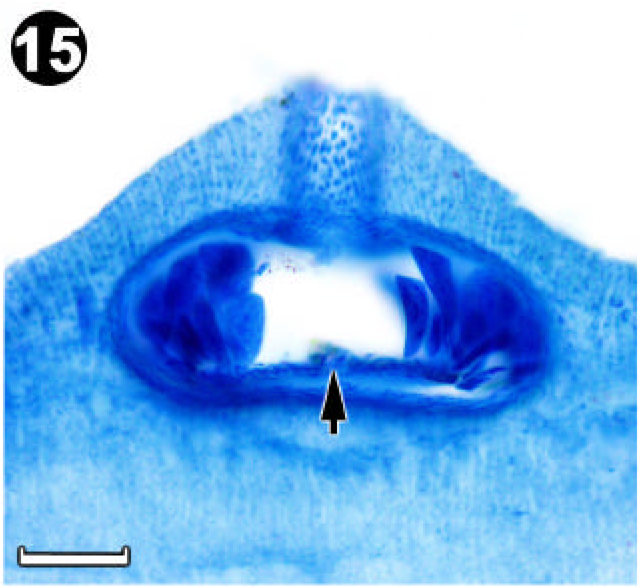
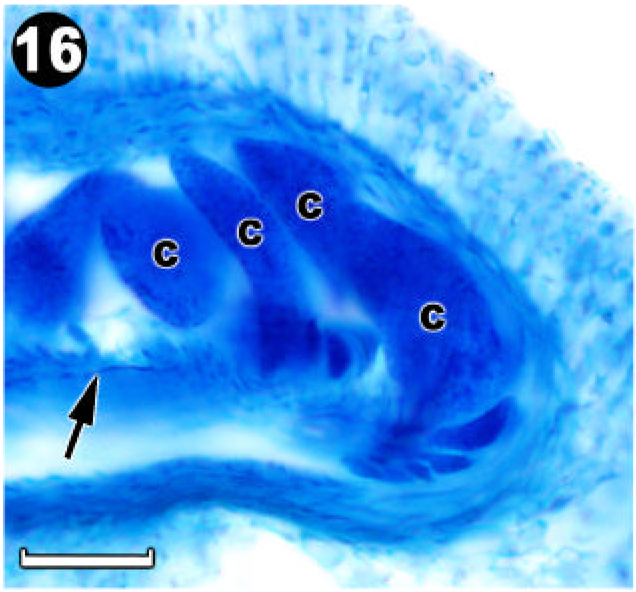


Plate 30







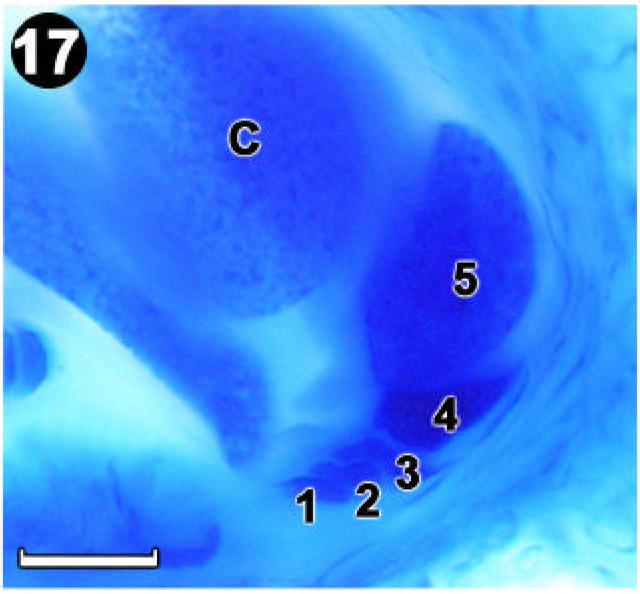


Plate 31

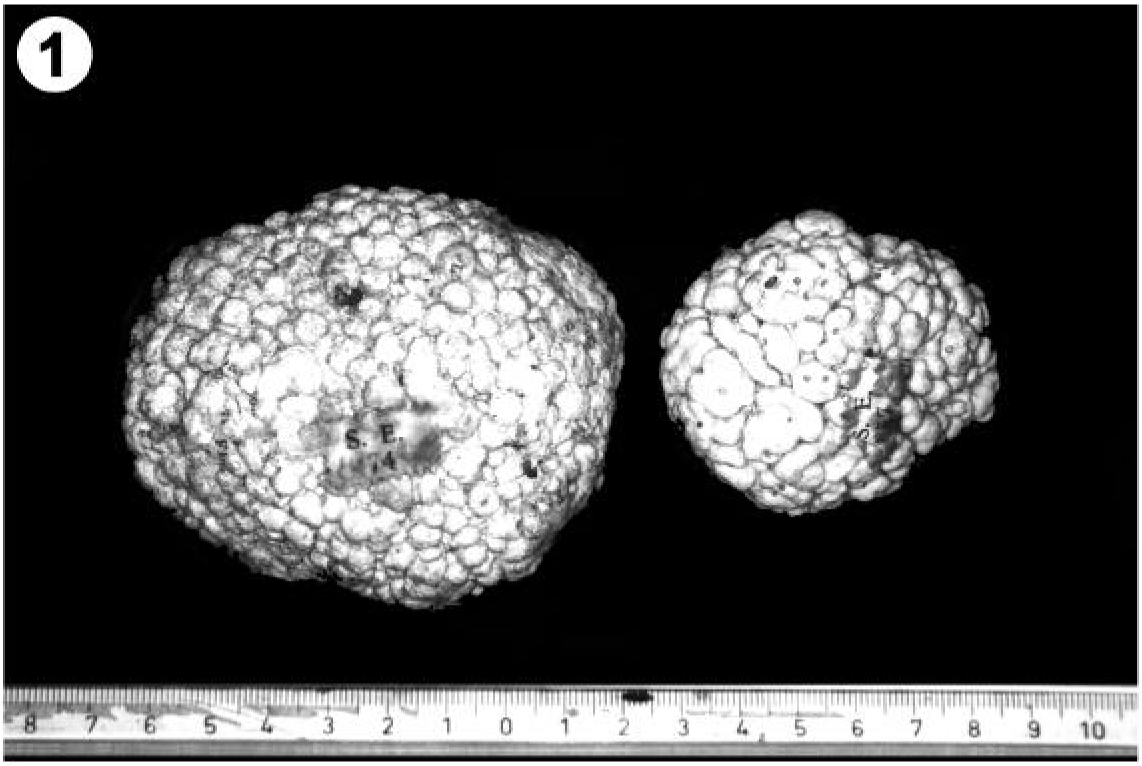
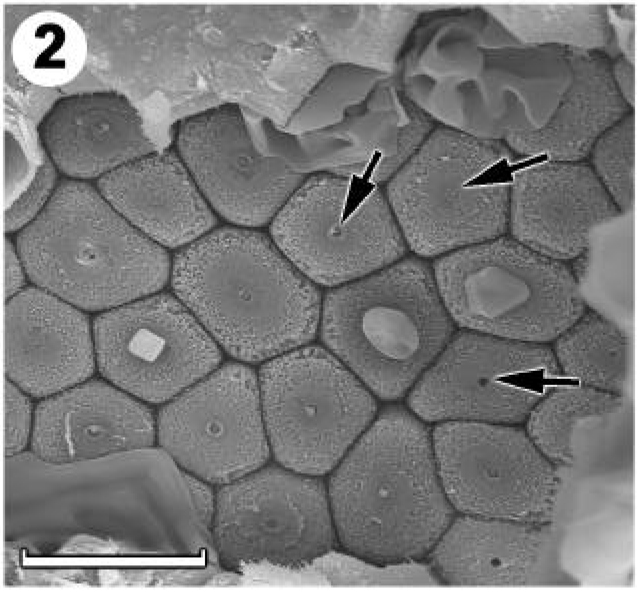
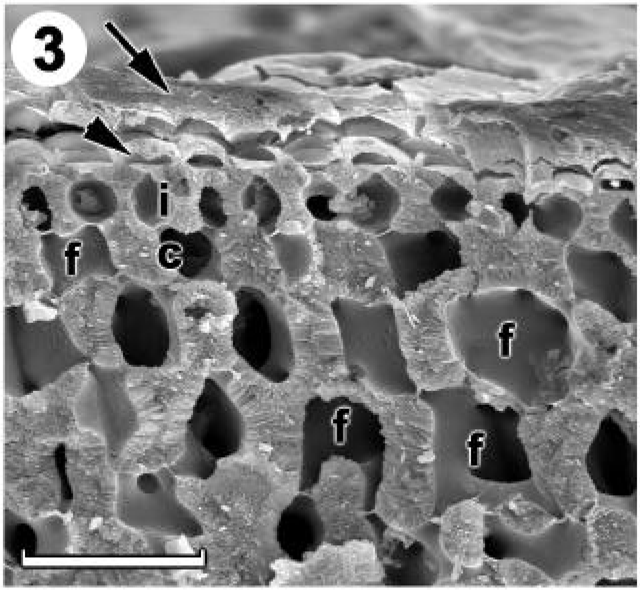
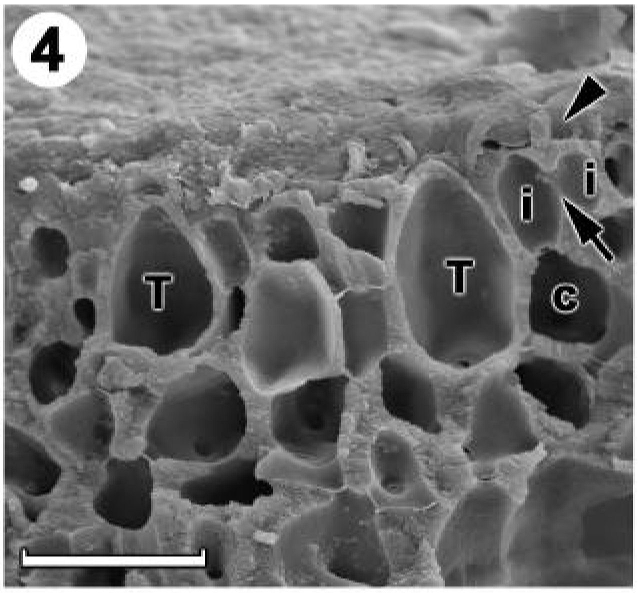
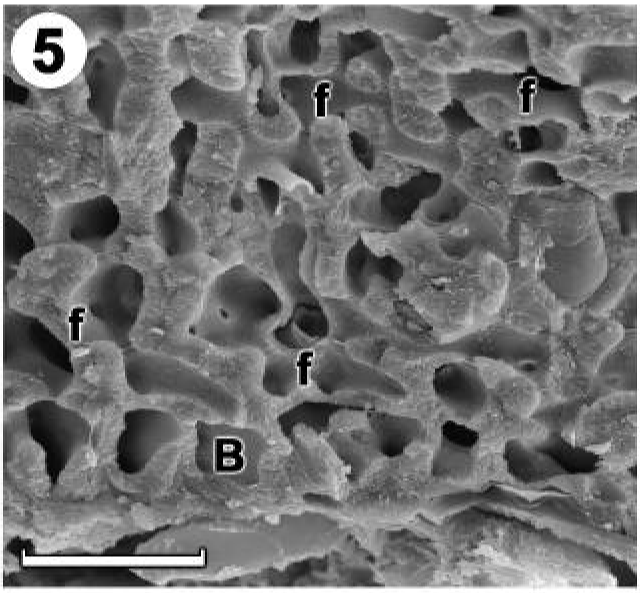


Plate 32









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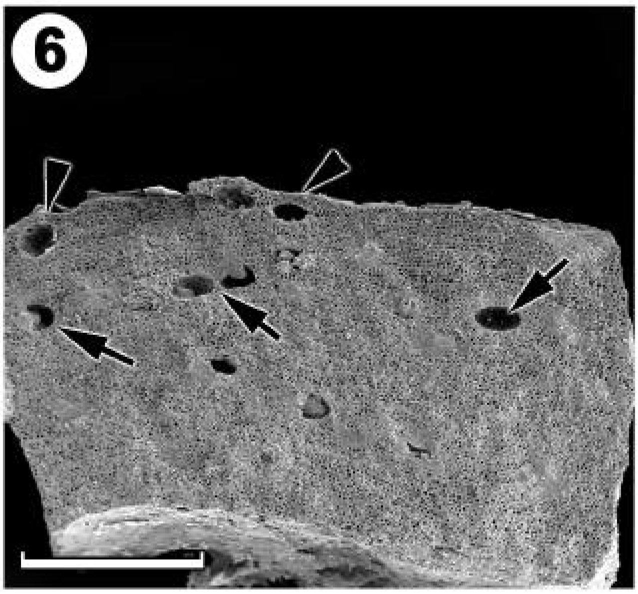

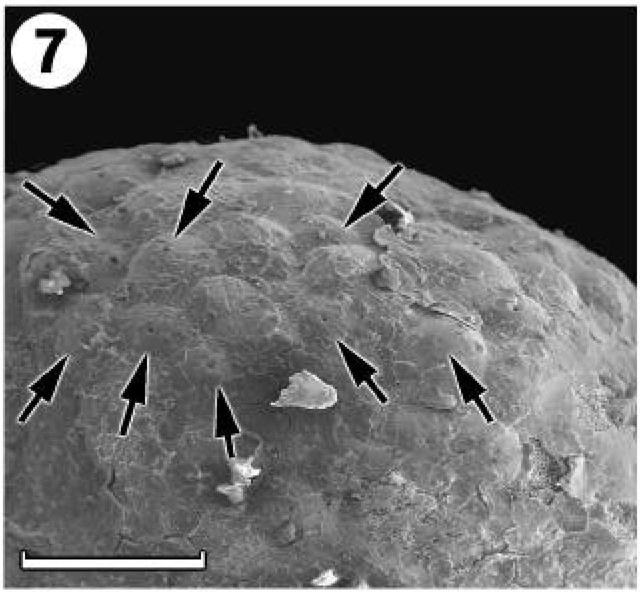

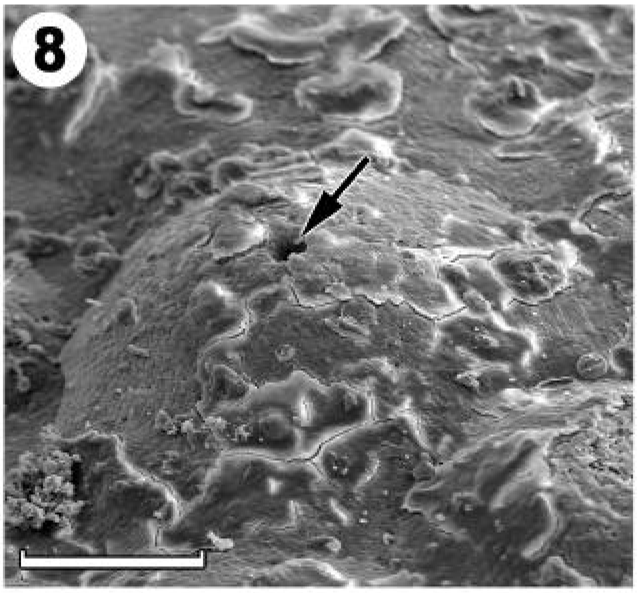

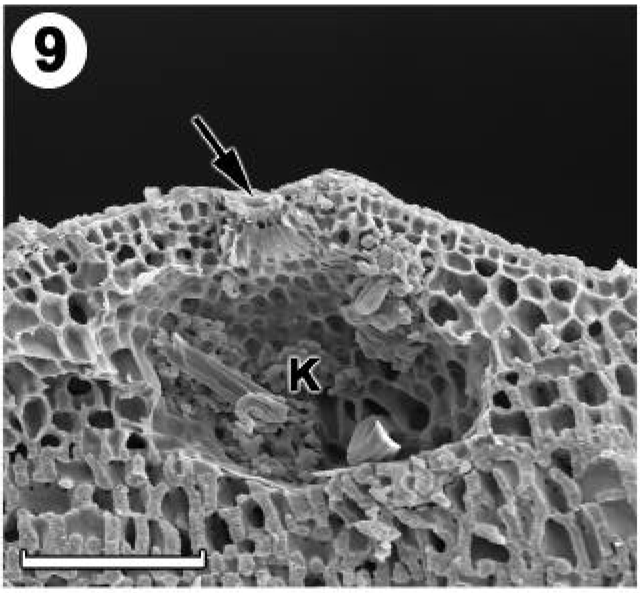

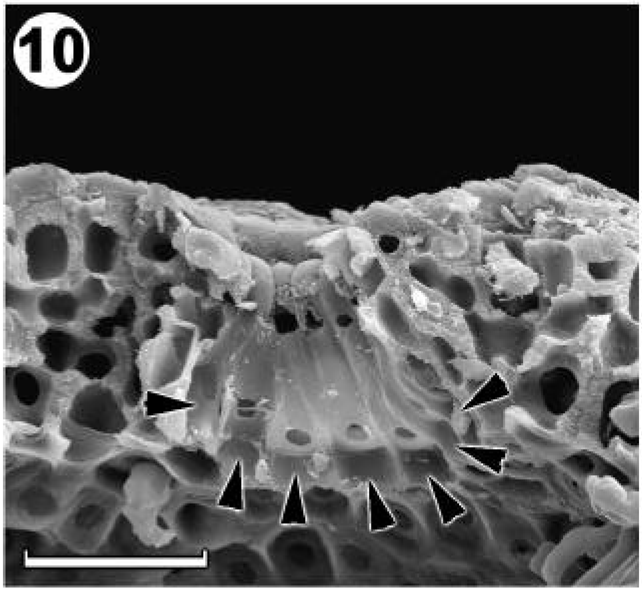

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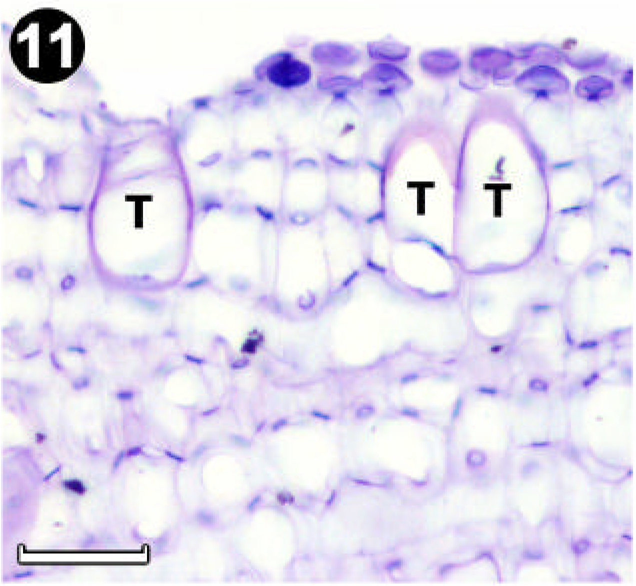

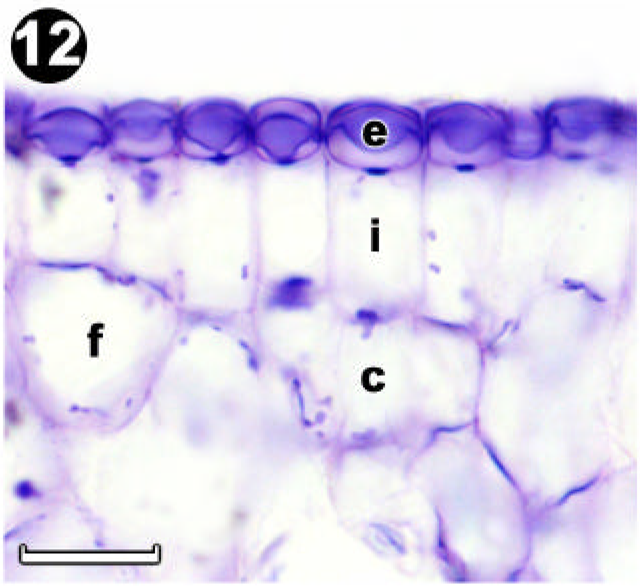

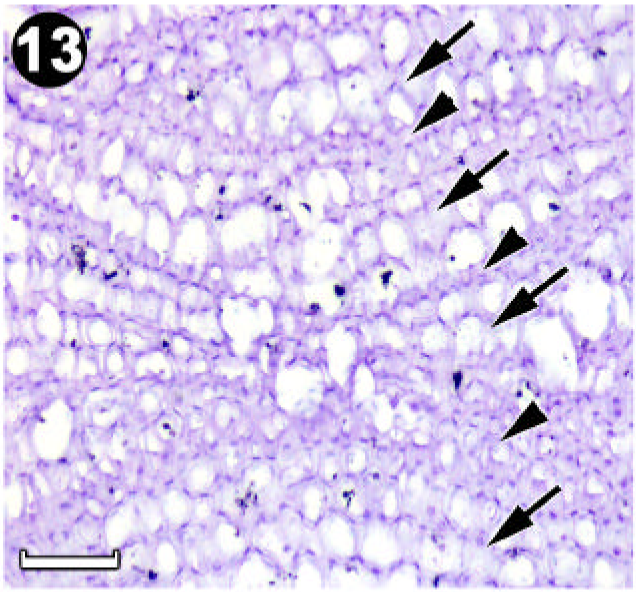

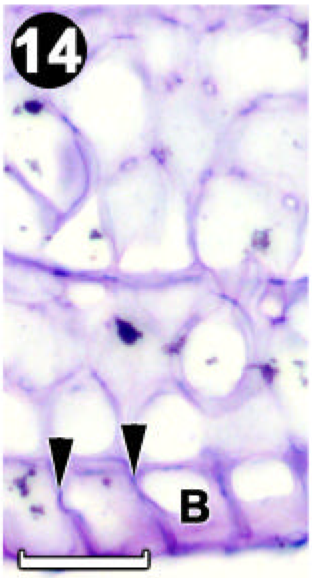

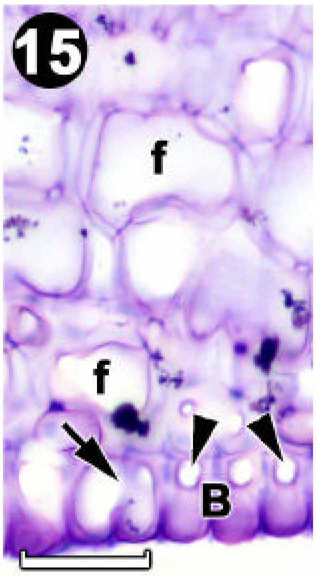

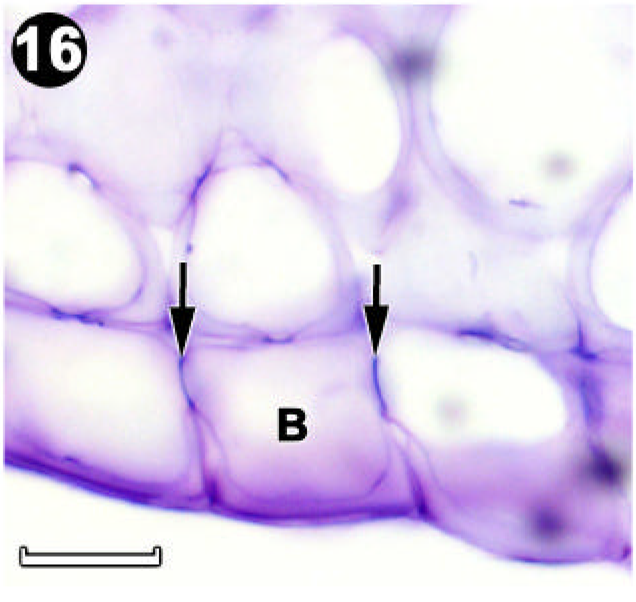

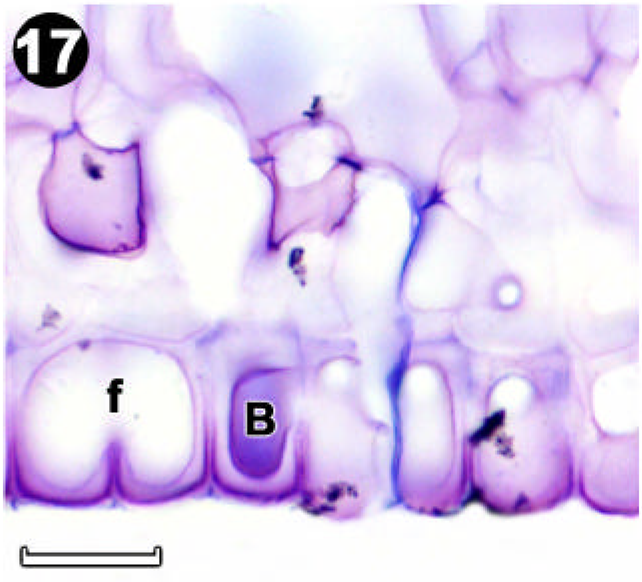

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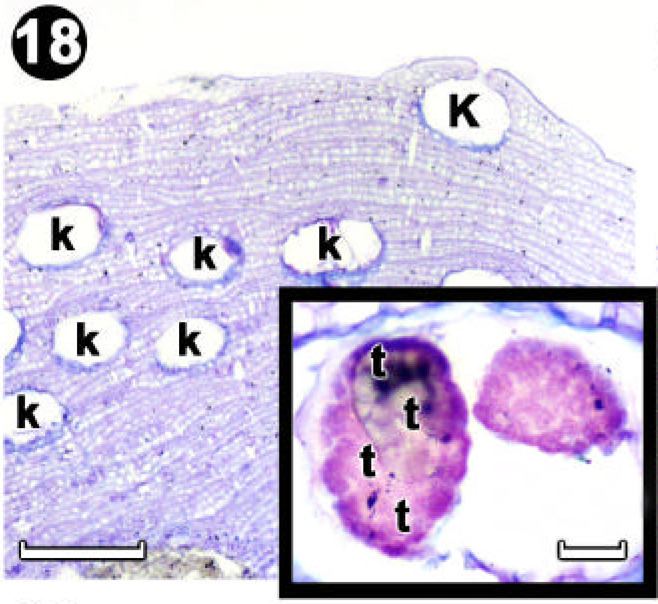

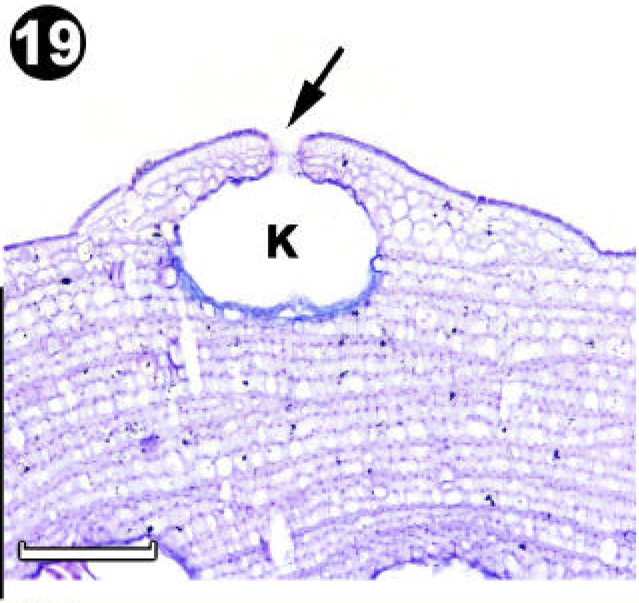

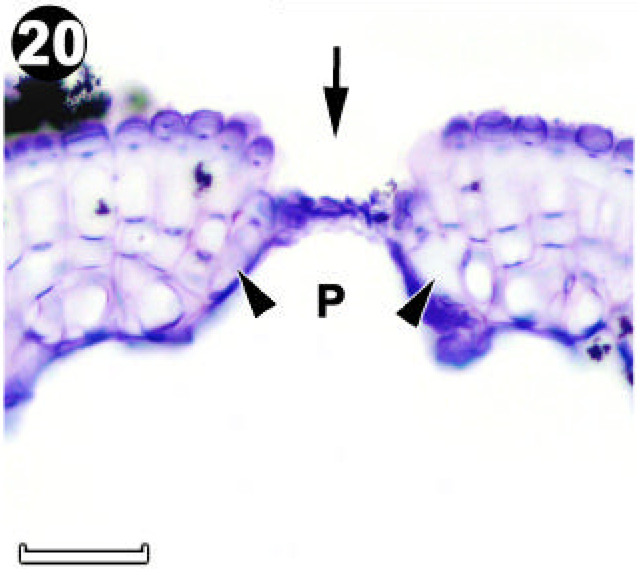

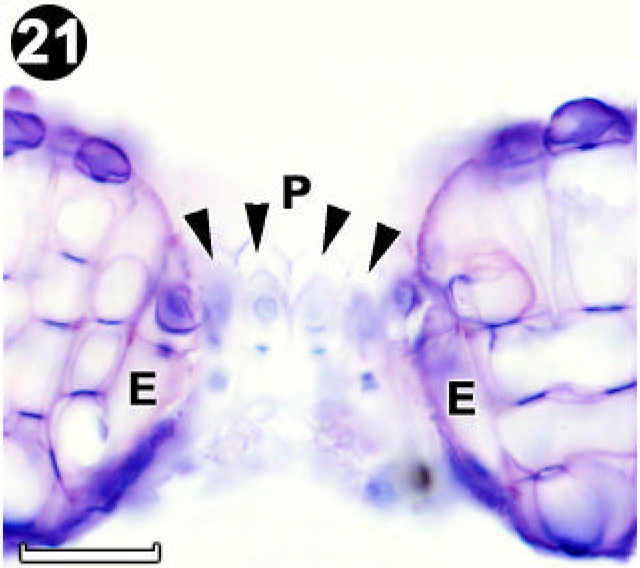

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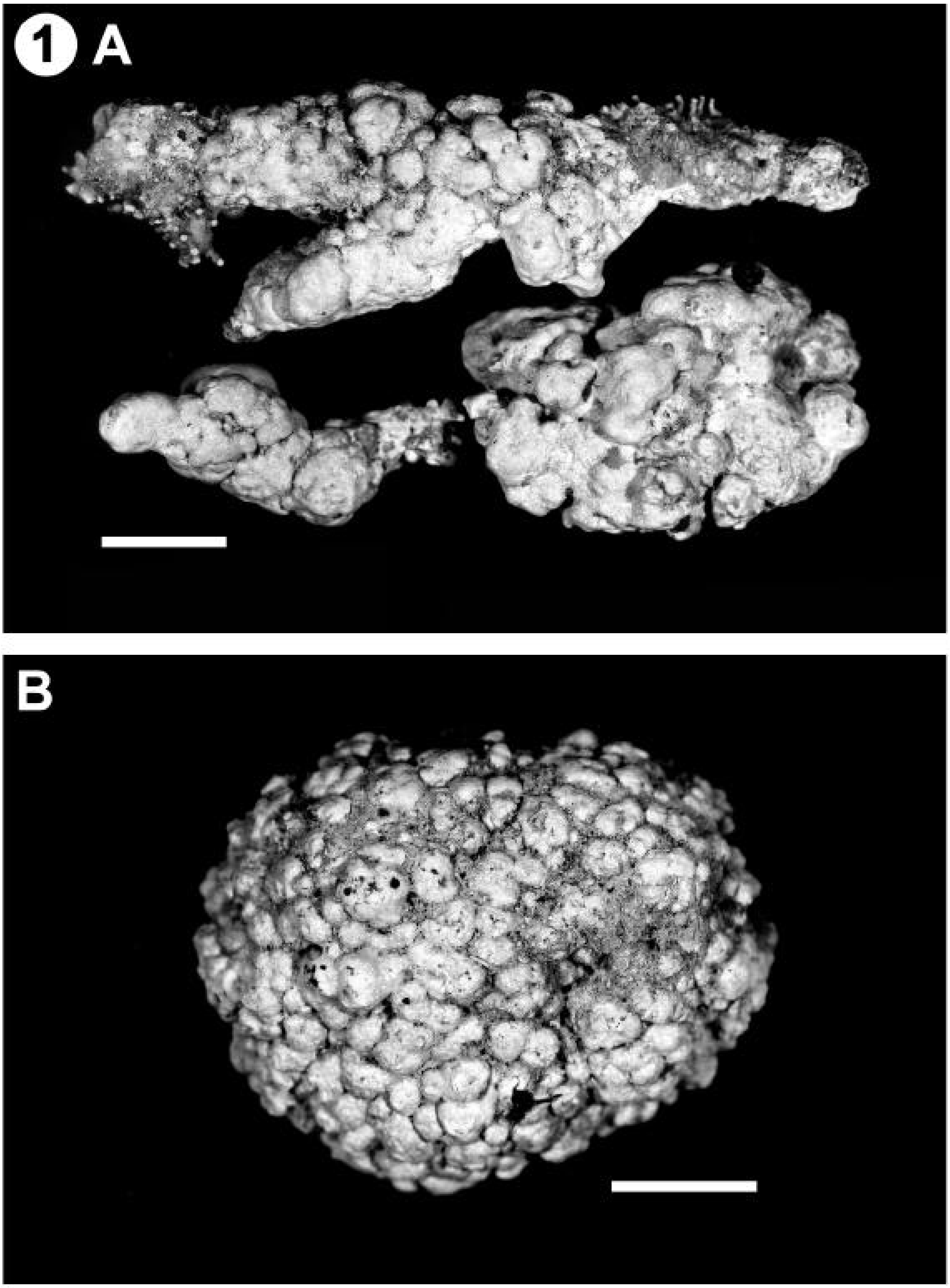

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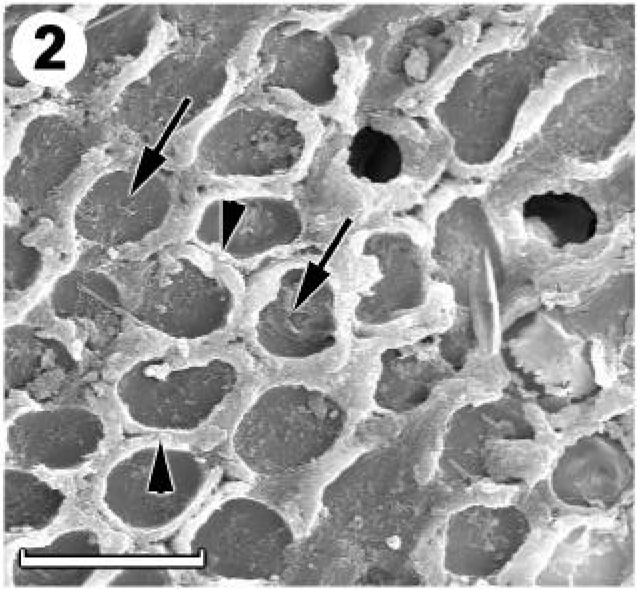

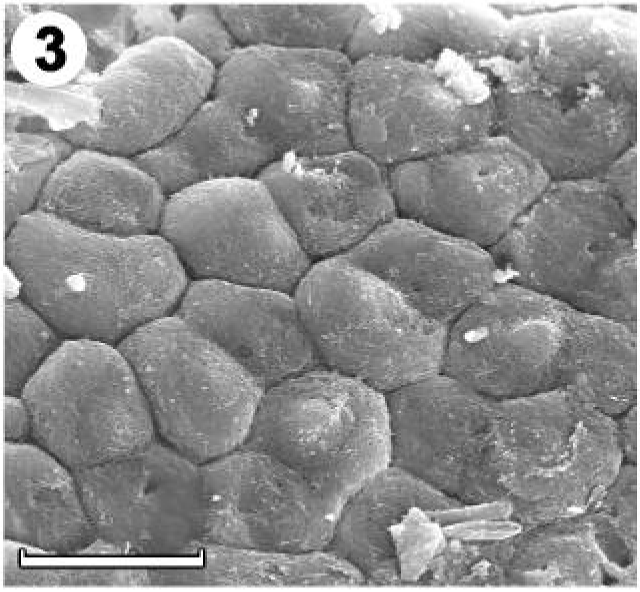

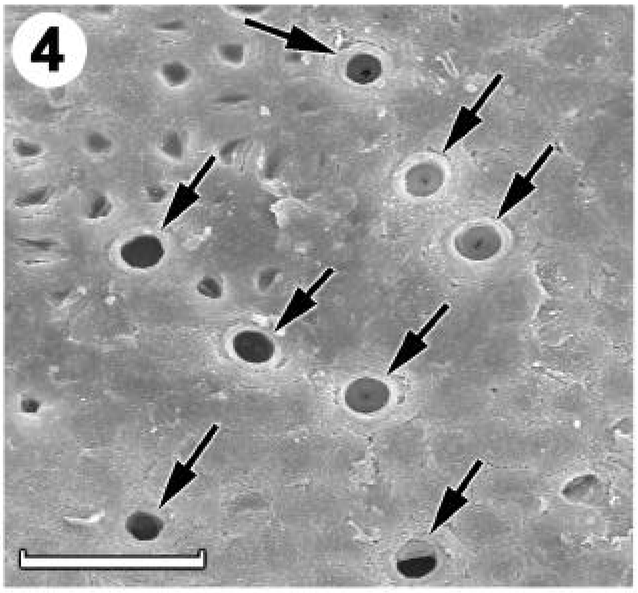

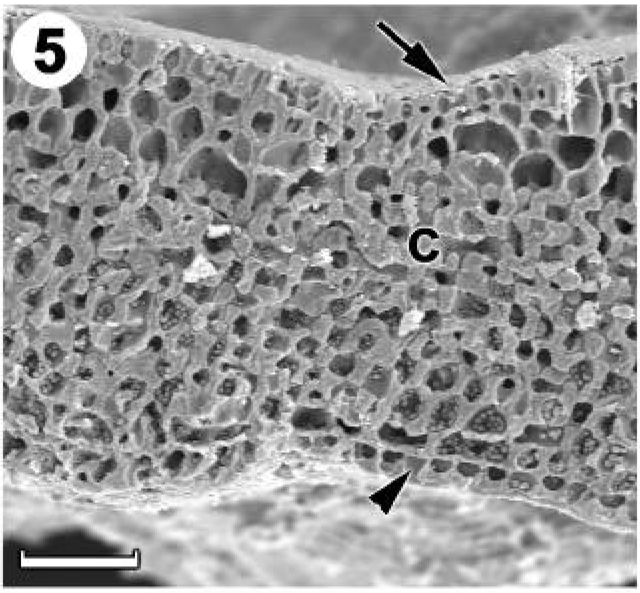

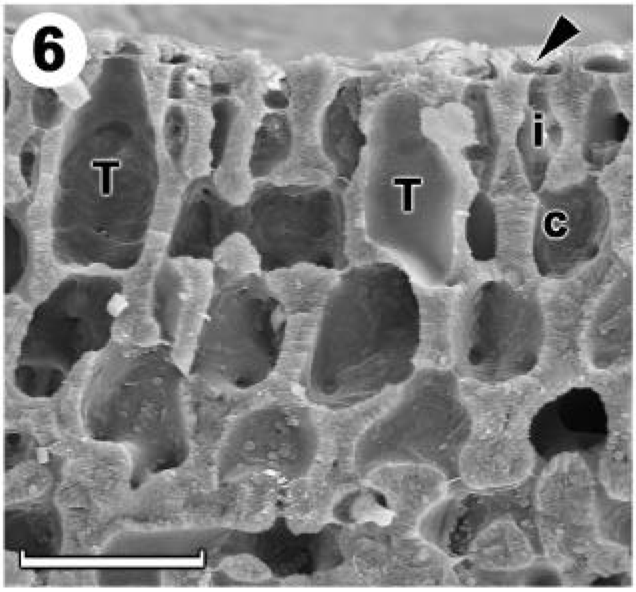

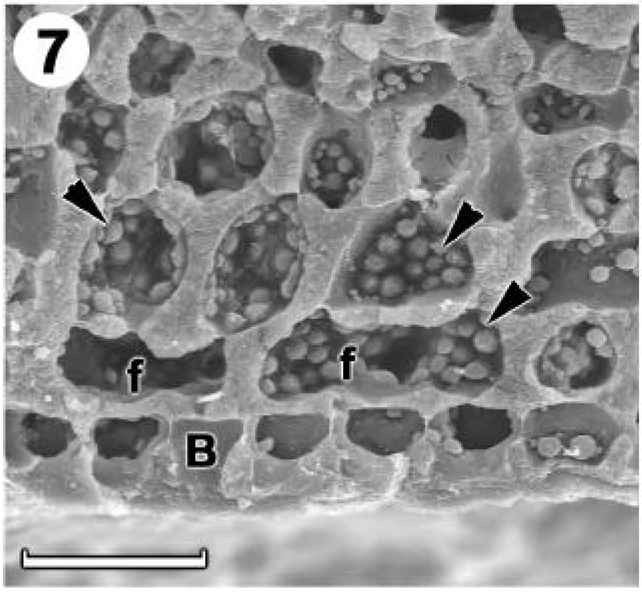

Plate 38

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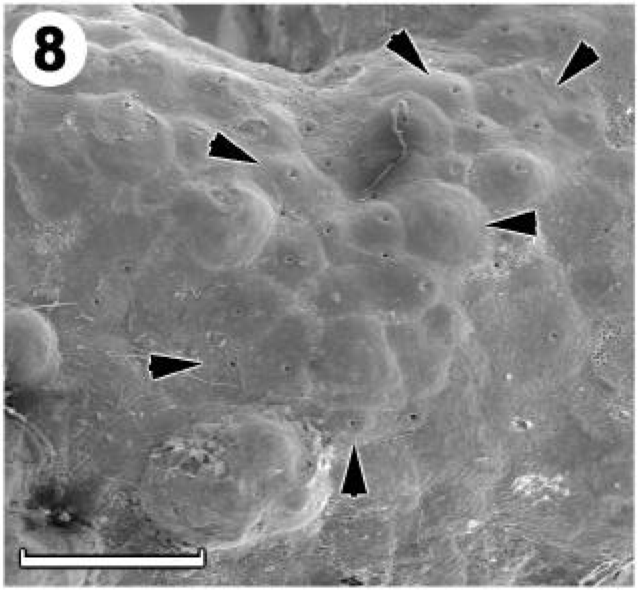

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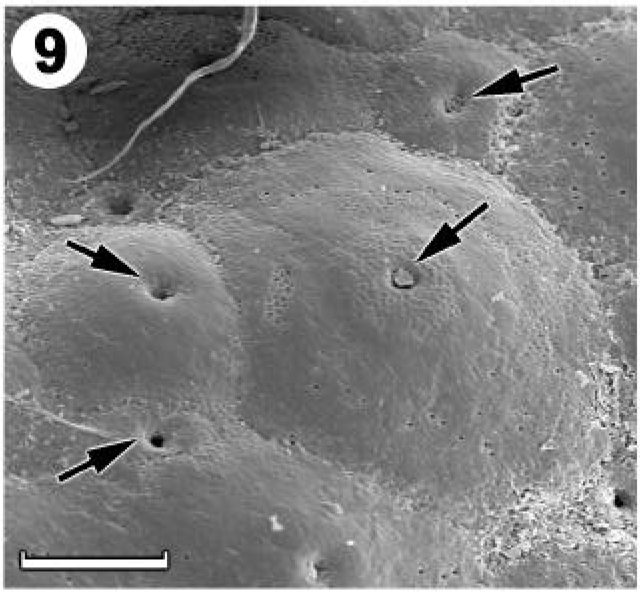

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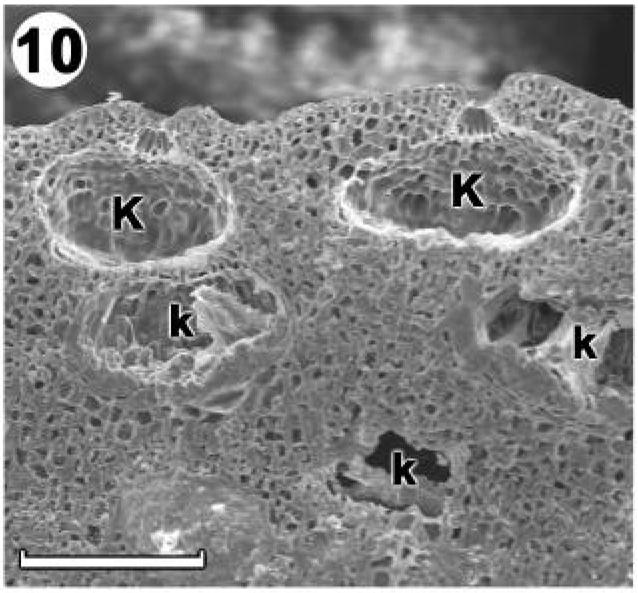

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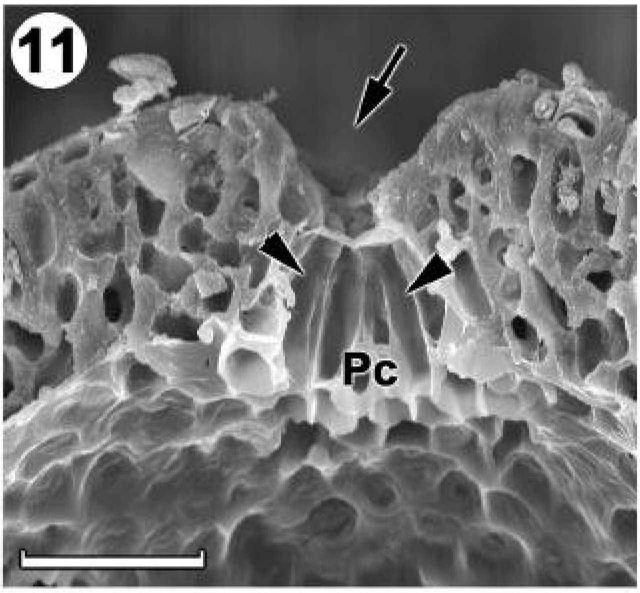

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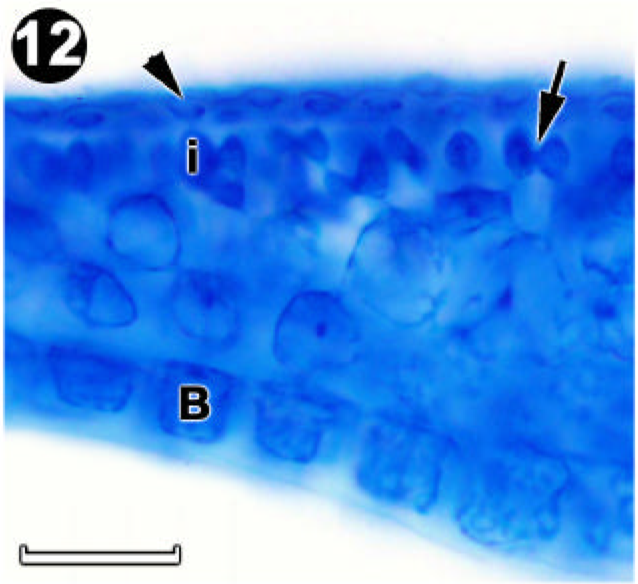
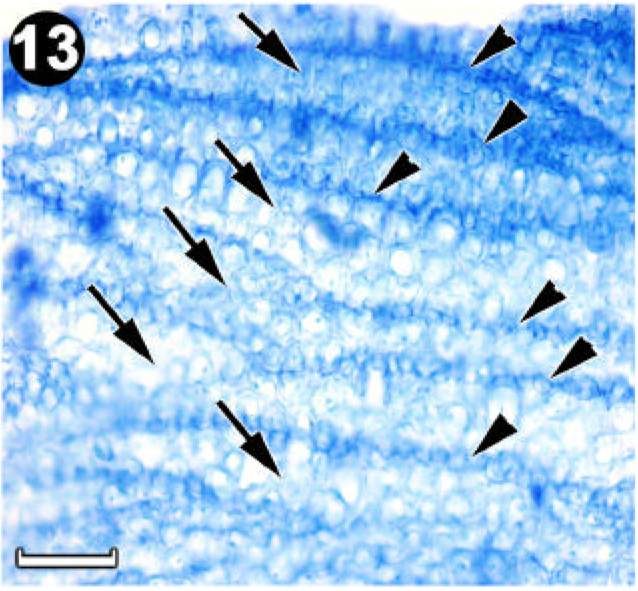
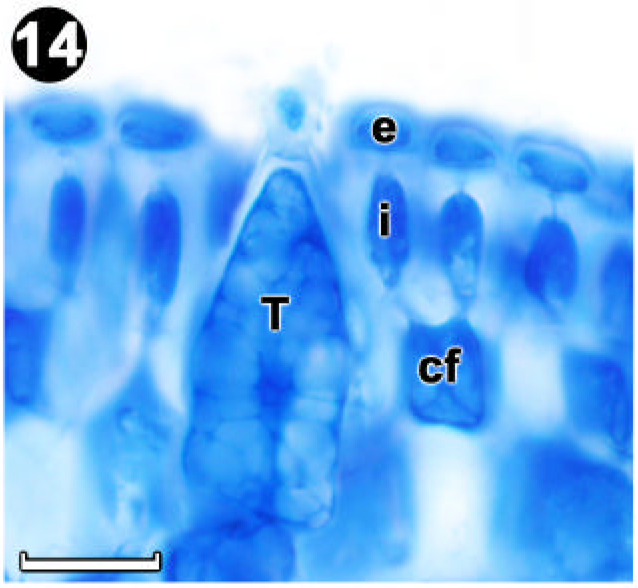
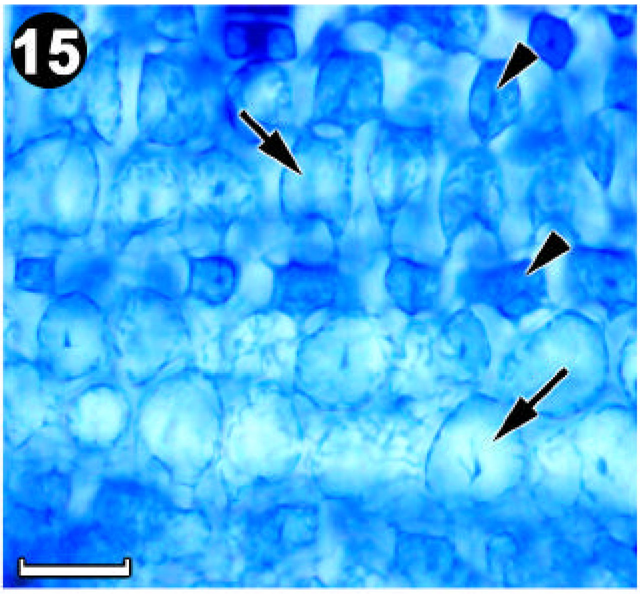
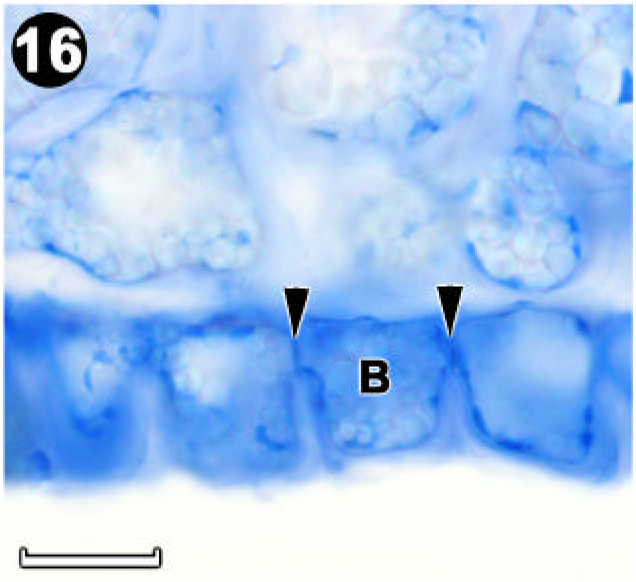










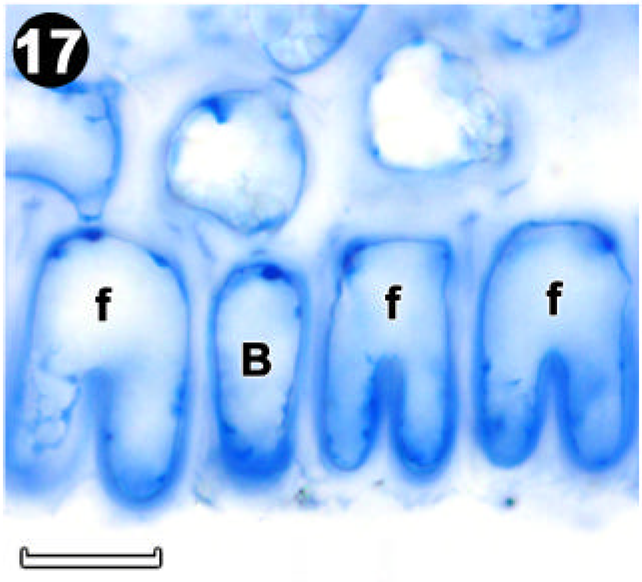
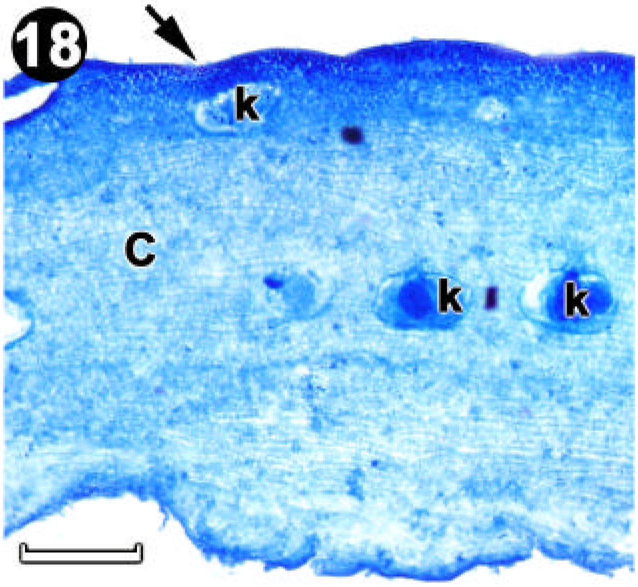
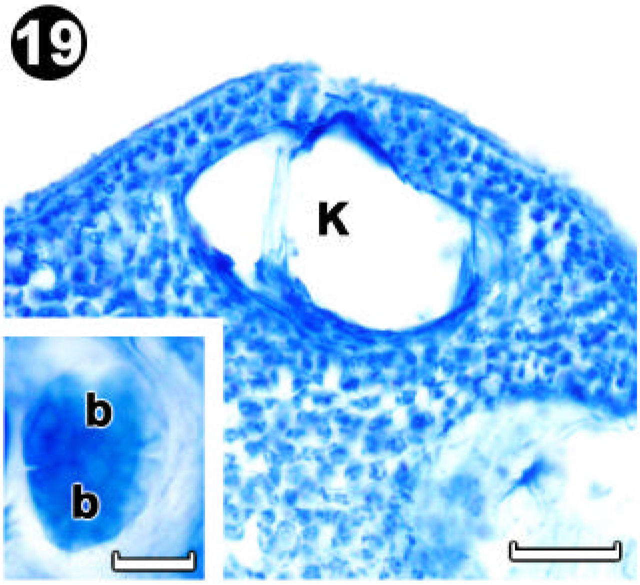
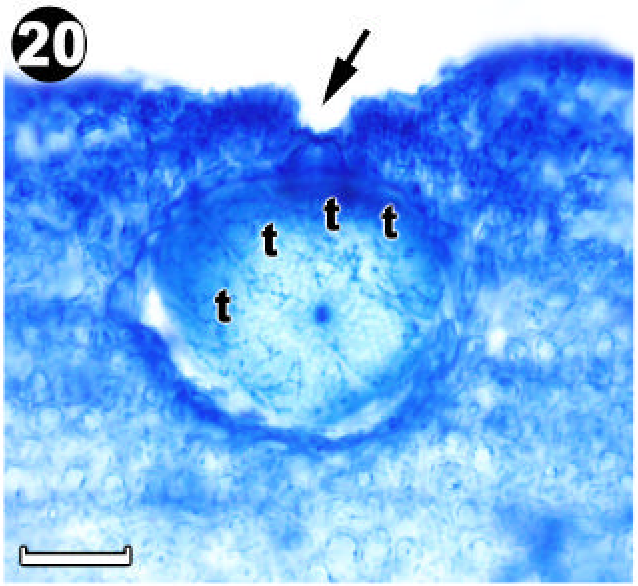
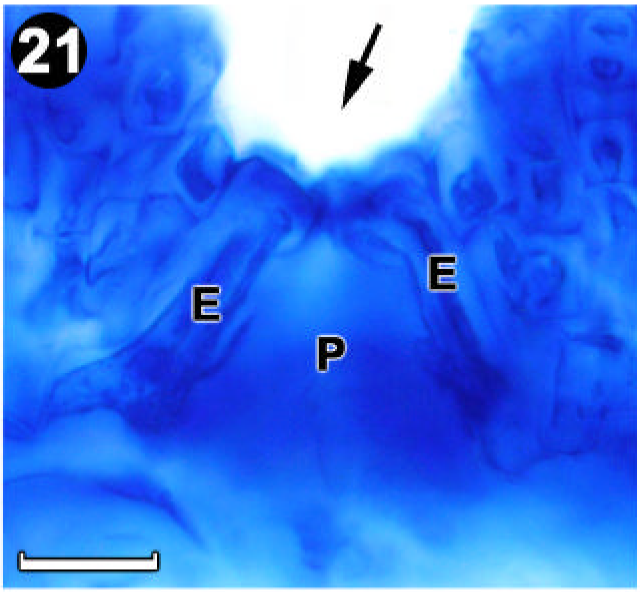


Plate 40









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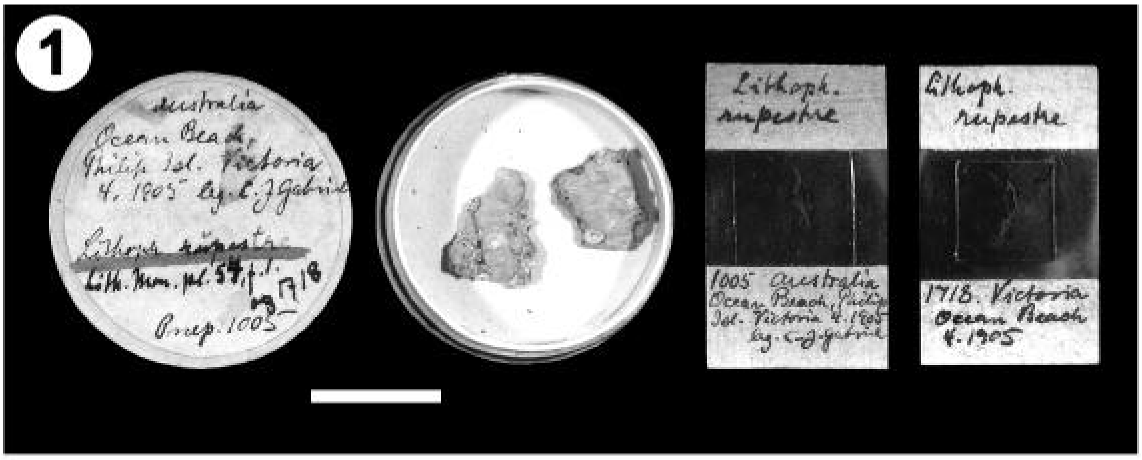
1
australia
Ocean Beach,
Philip Isl. Victoria
4. 1905 leg. C. J. Gabriel
~~Lithops rupestre~~
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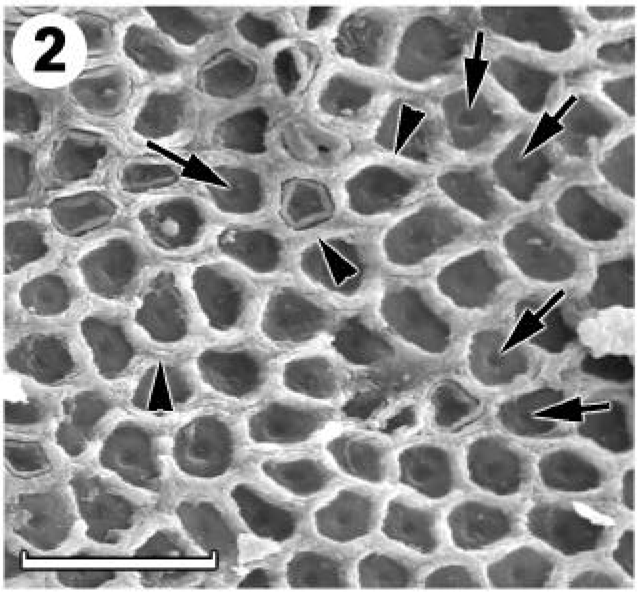
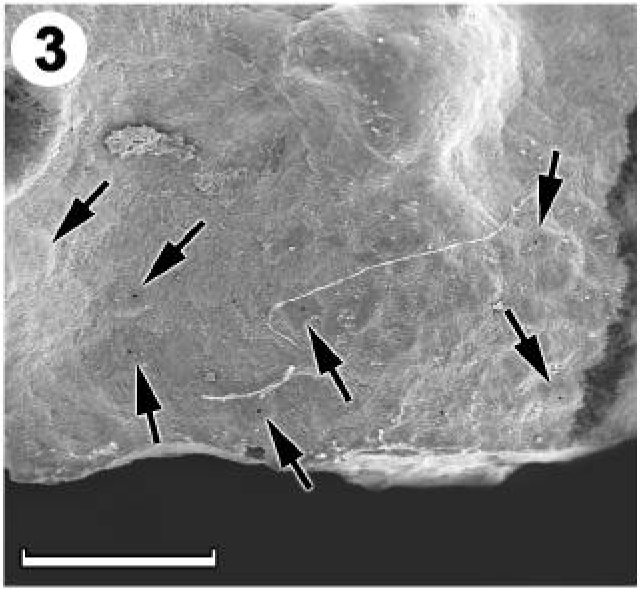
1005 australia Ocean Beach, Philip Isl. Victoria 4. 1905 leg. C. J. Gabriel
Lithoph. rupestre
1718. Victoria Ocean Beach 4. 1905

Plate 42





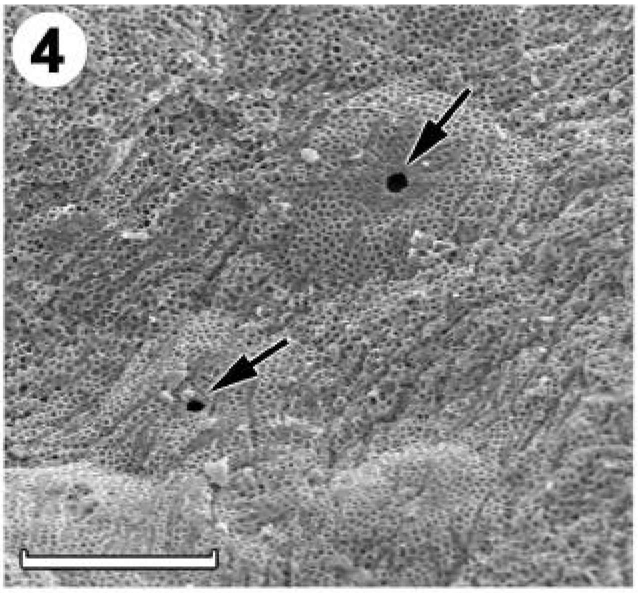
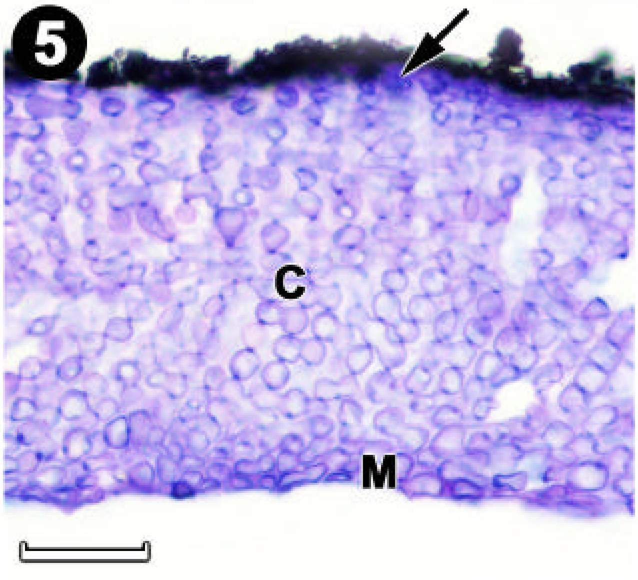
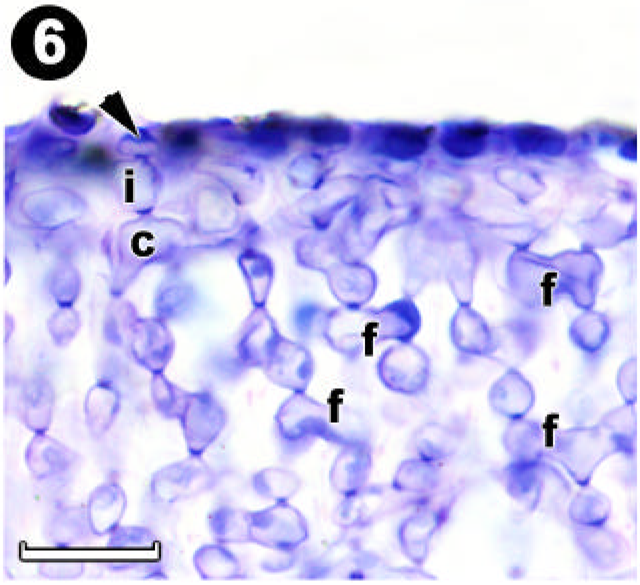
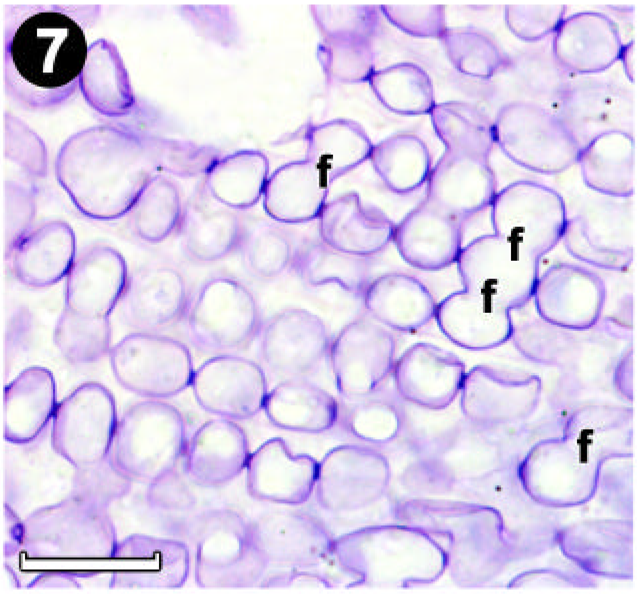


Plate 43







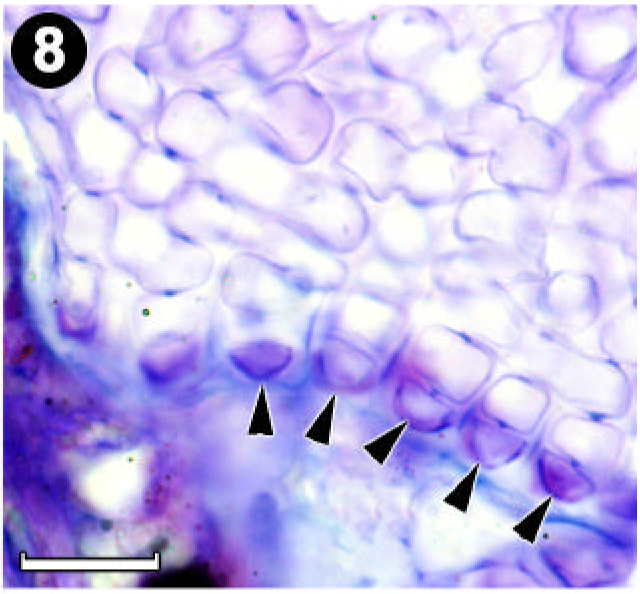
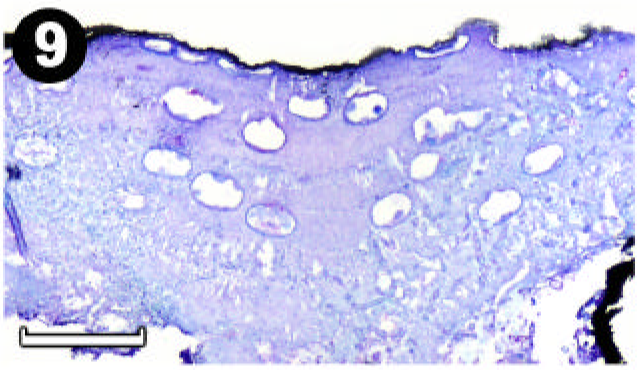


Plate 44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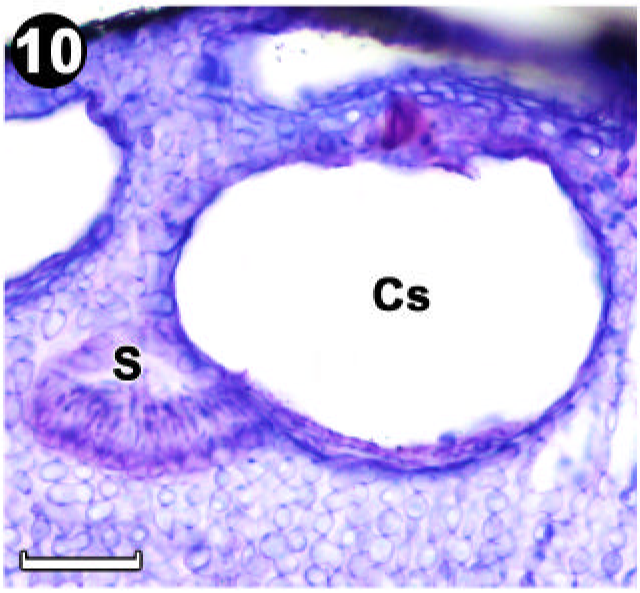
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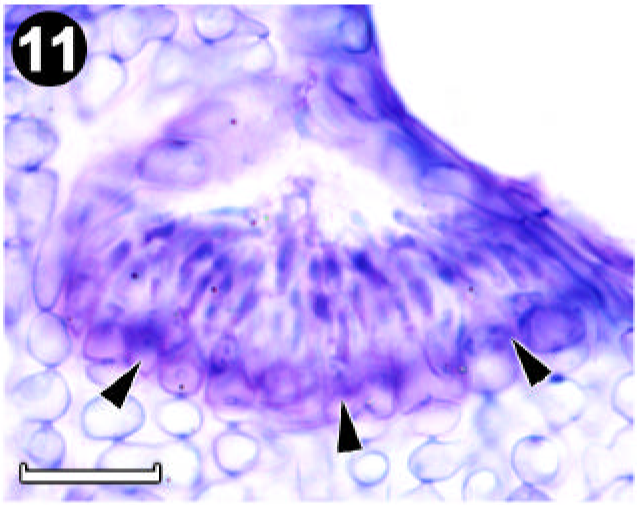
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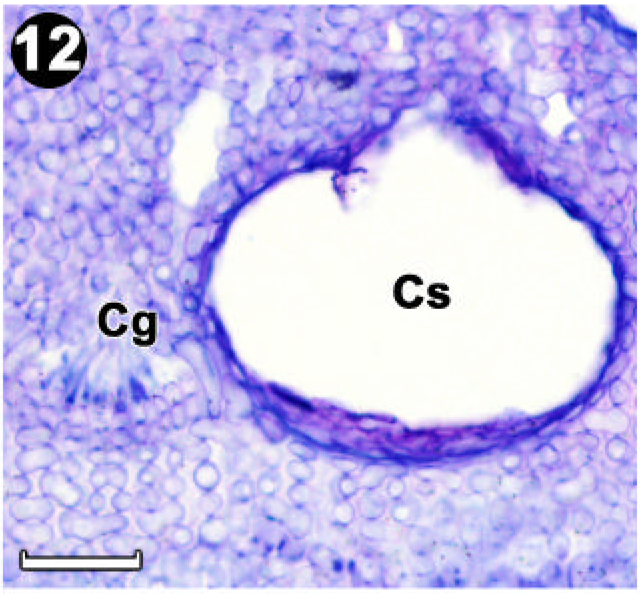
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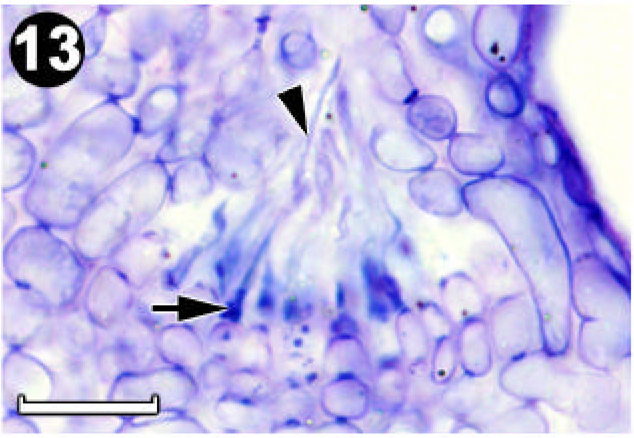
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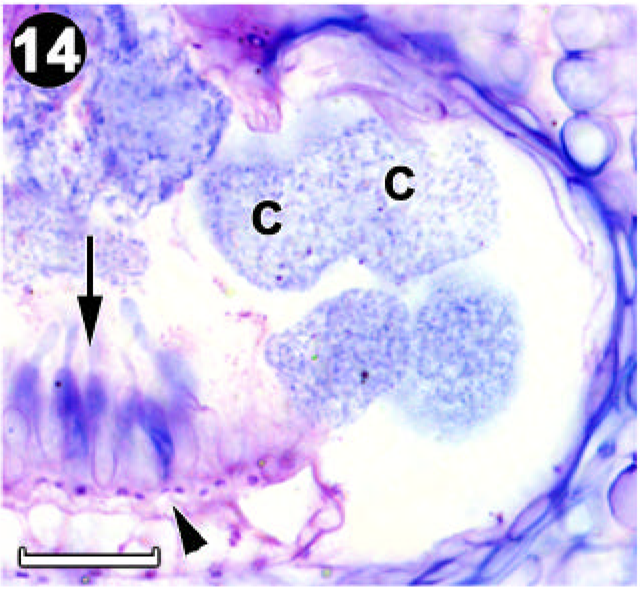
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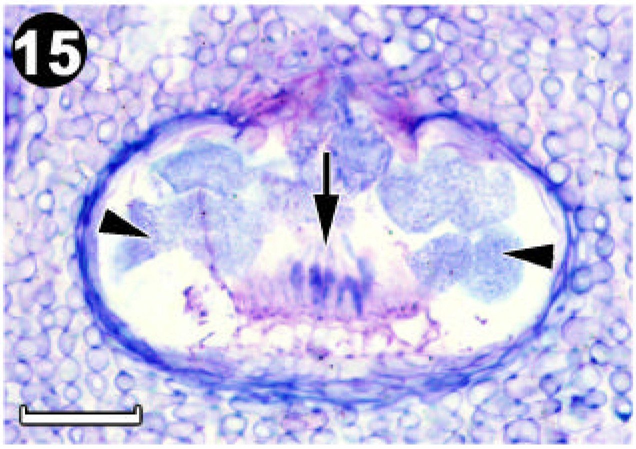
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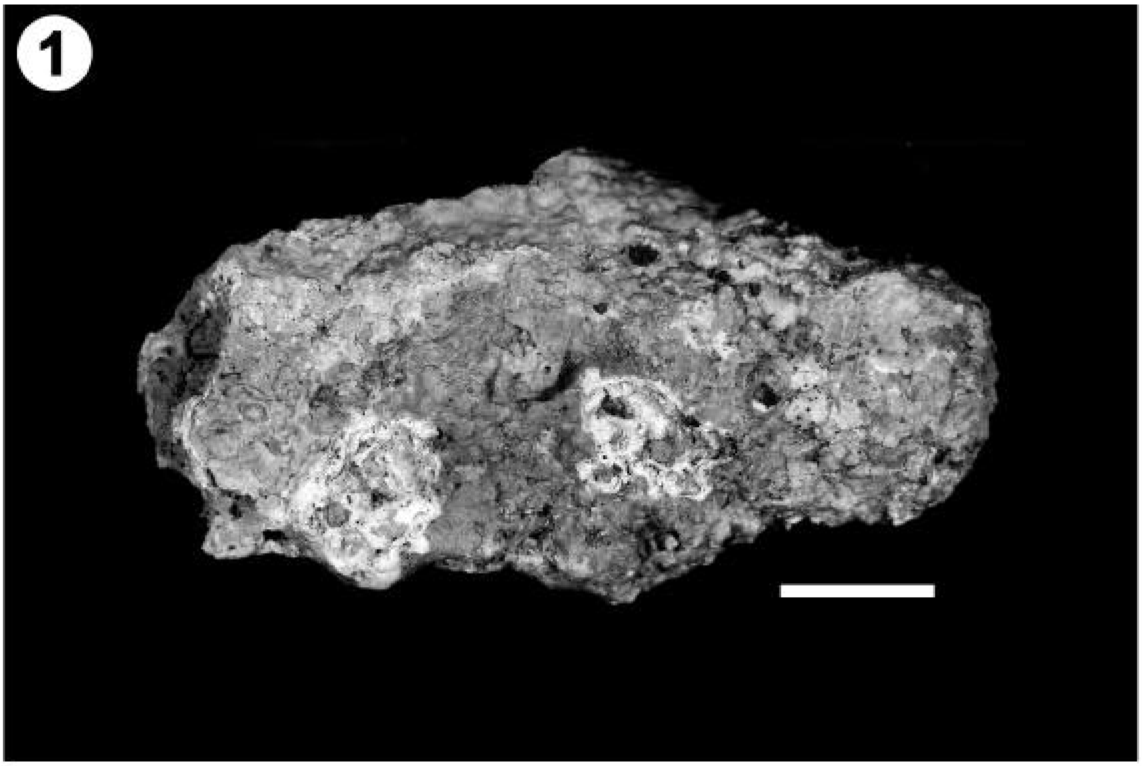
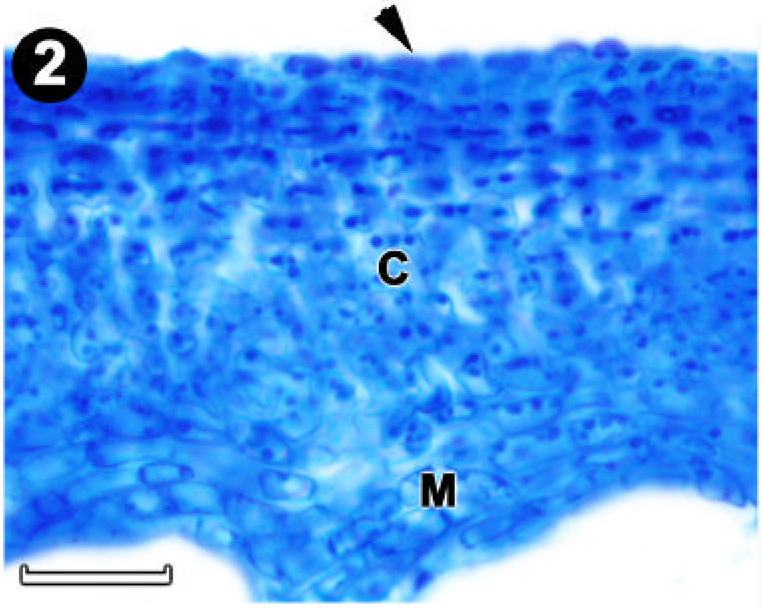
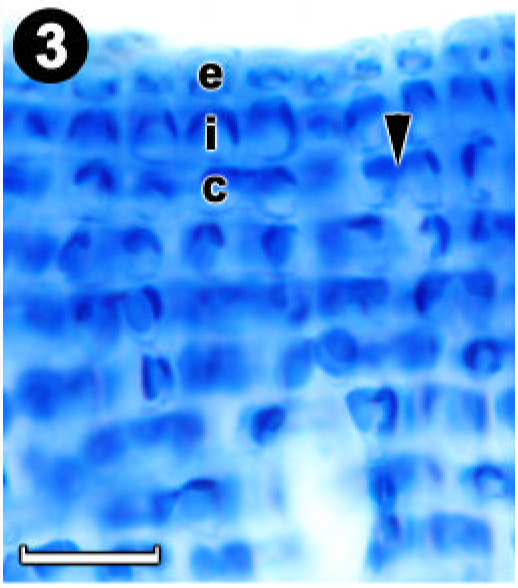
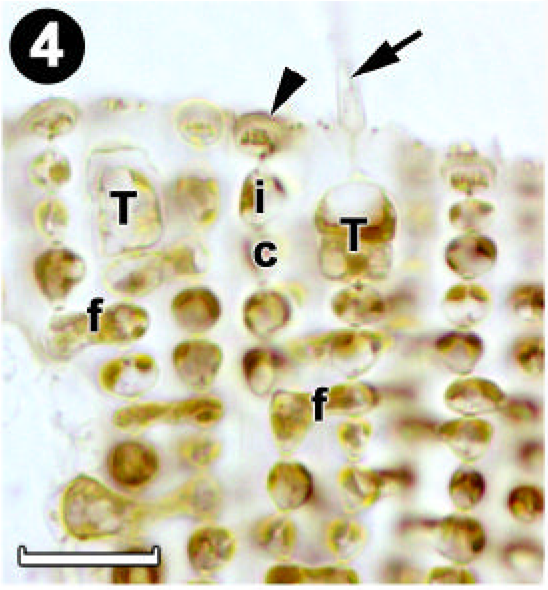
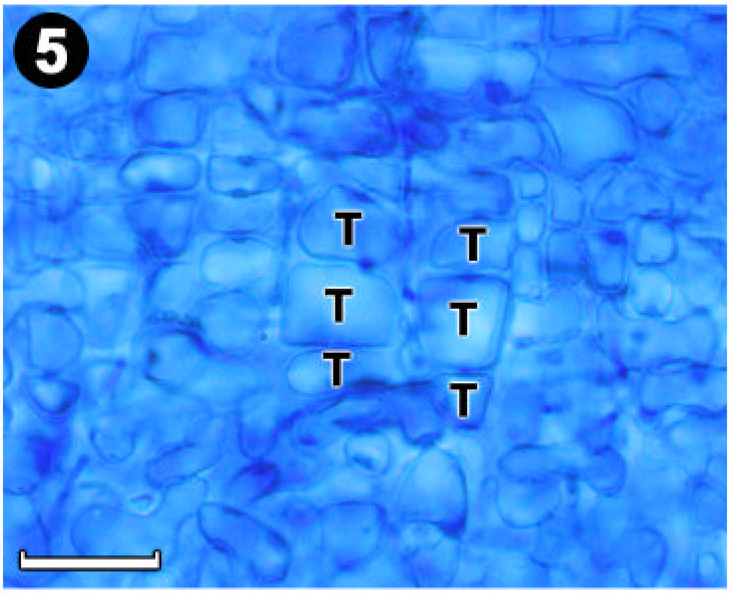


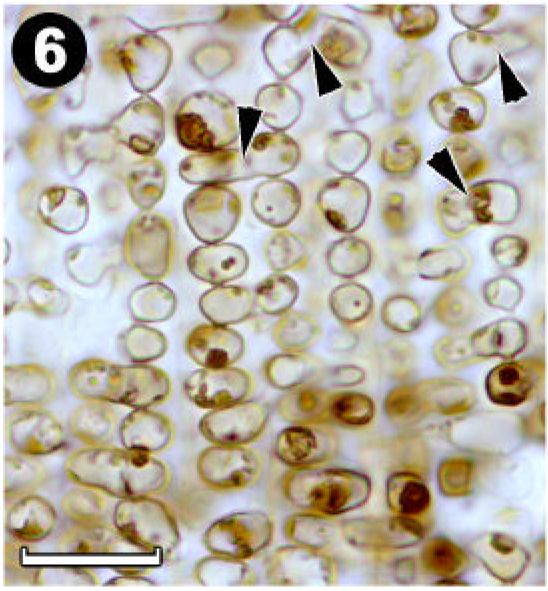
Plate 46











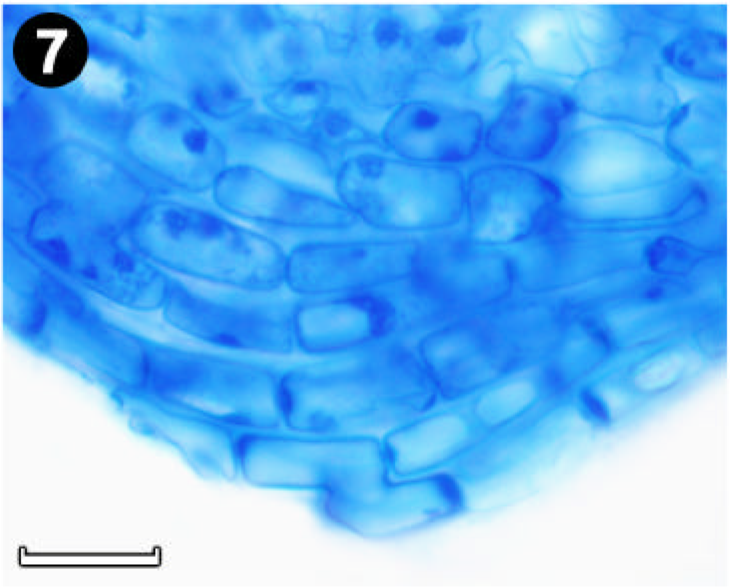
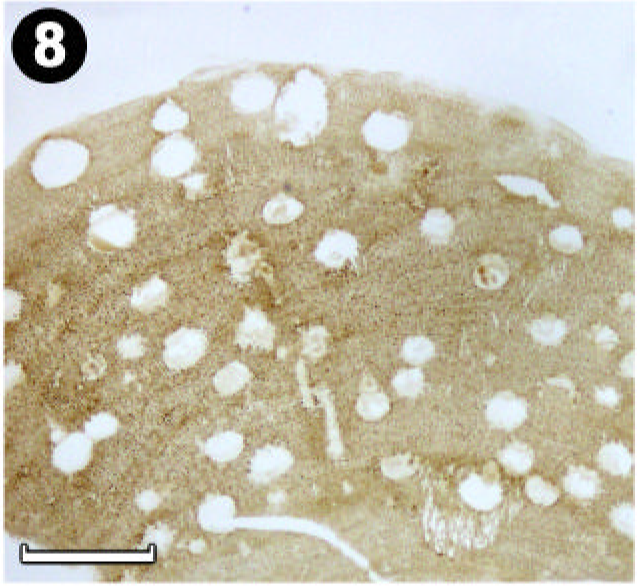
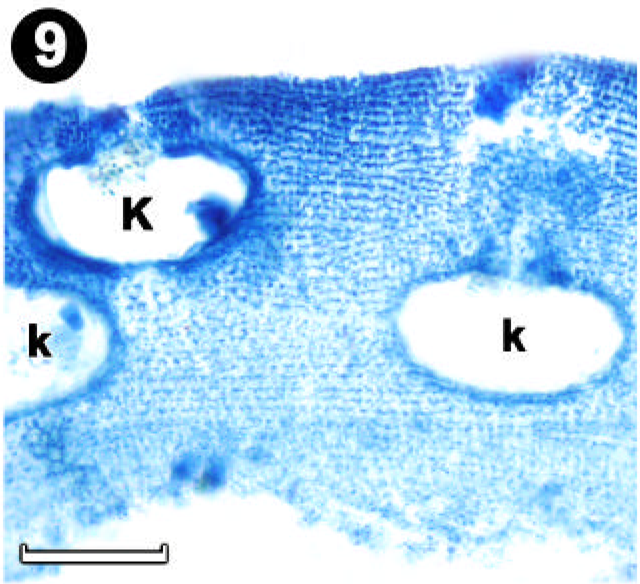
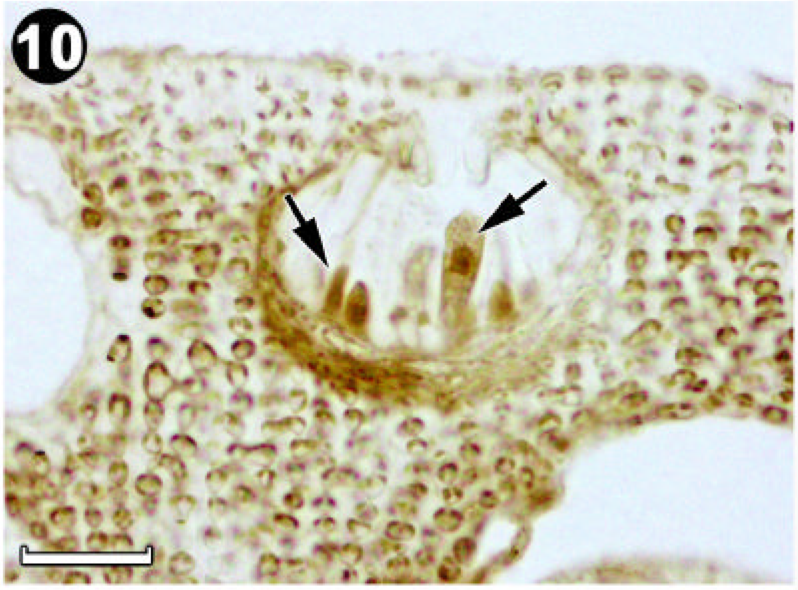
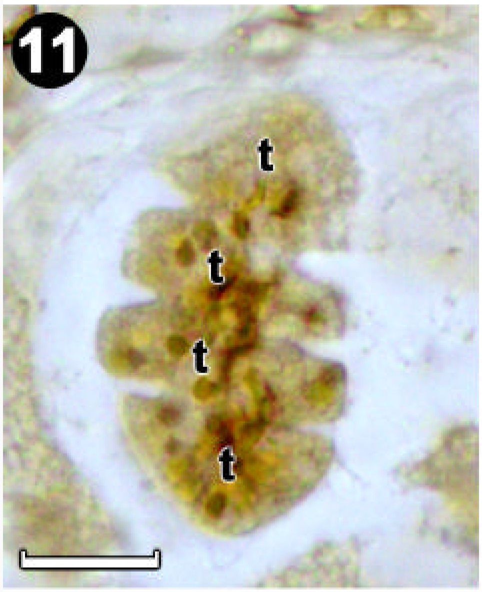


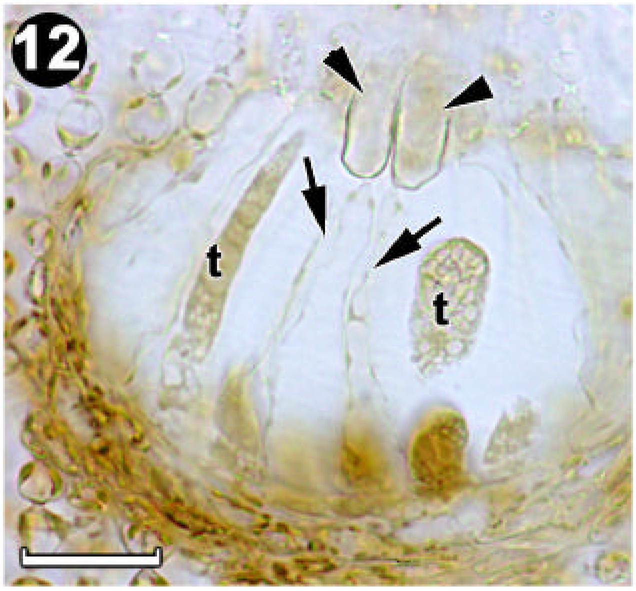
Plate 47











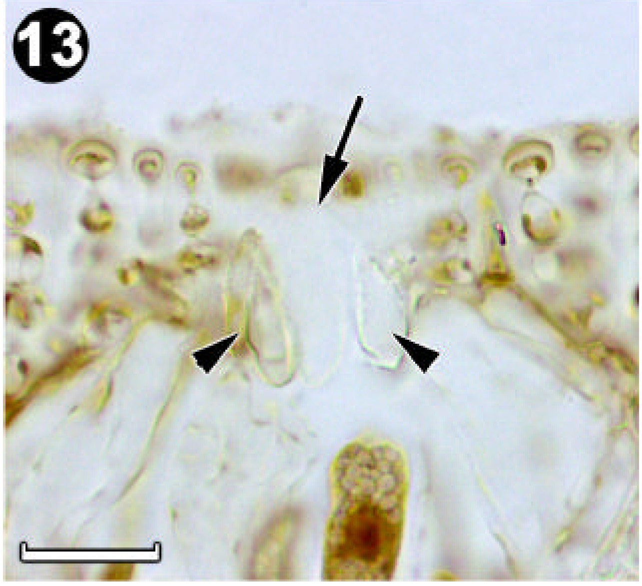
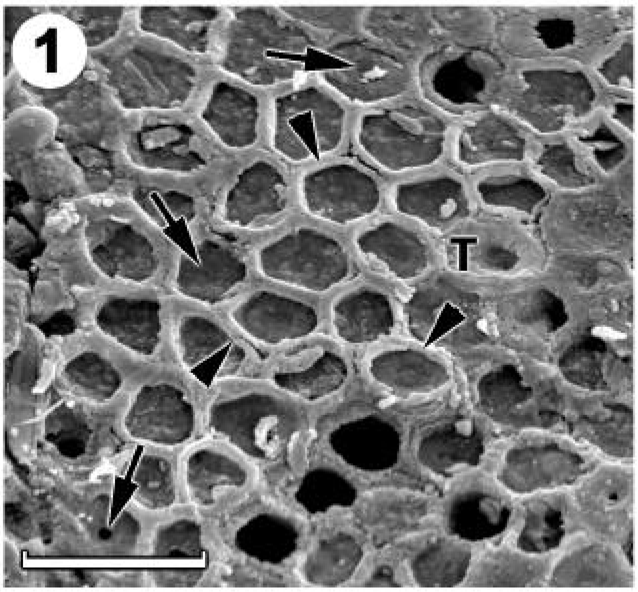
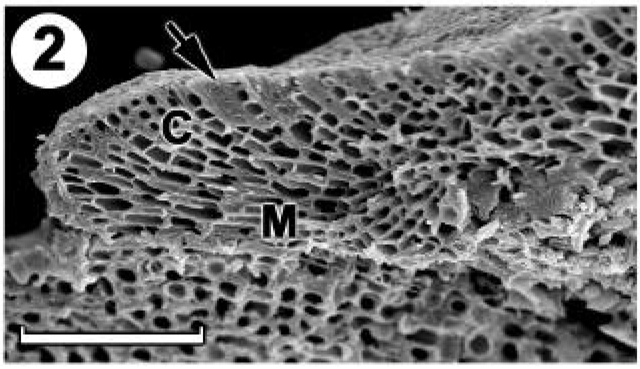
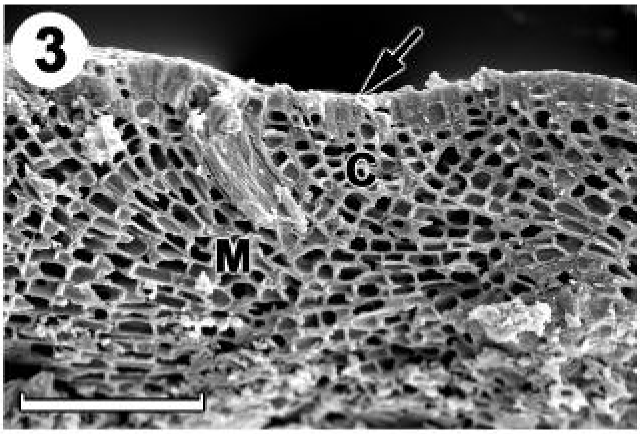
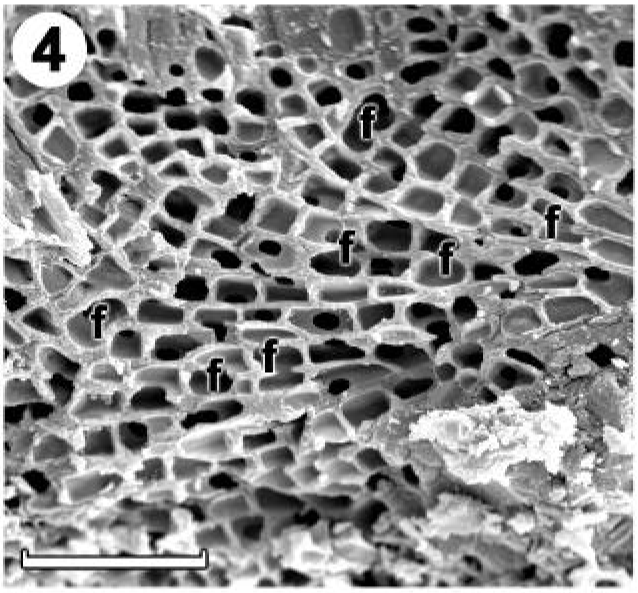


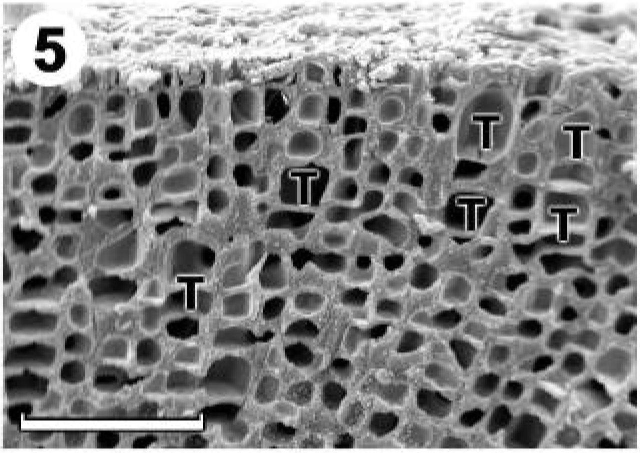
Plate 48











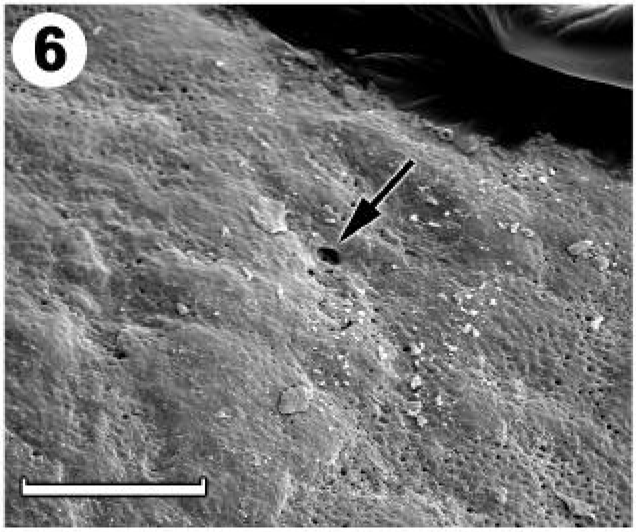
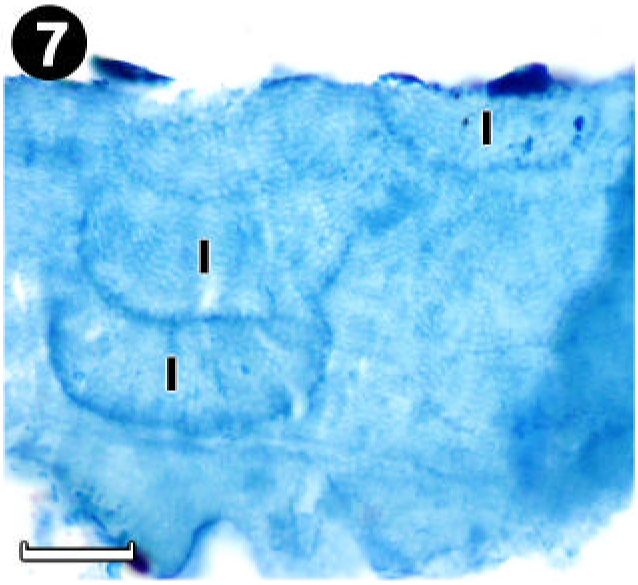
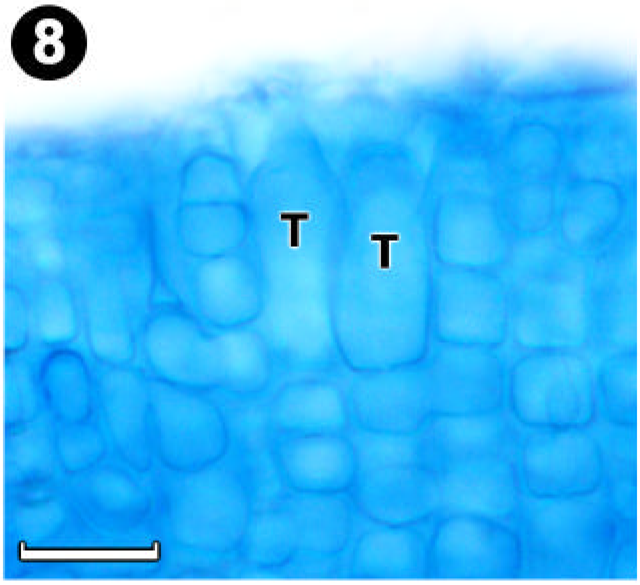
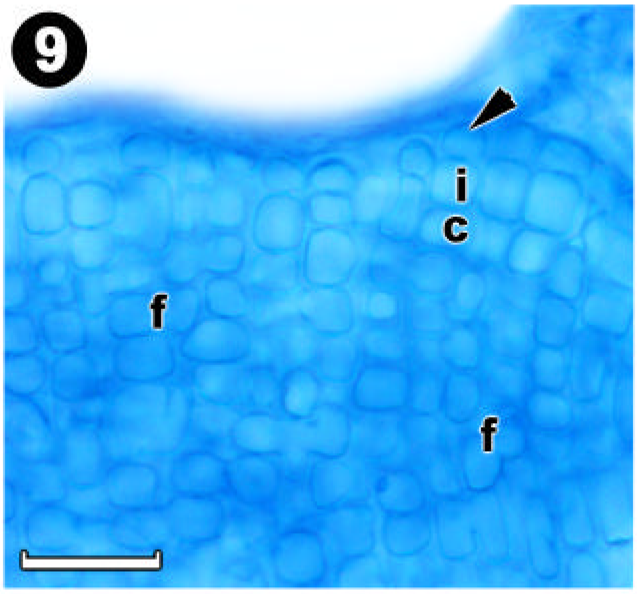
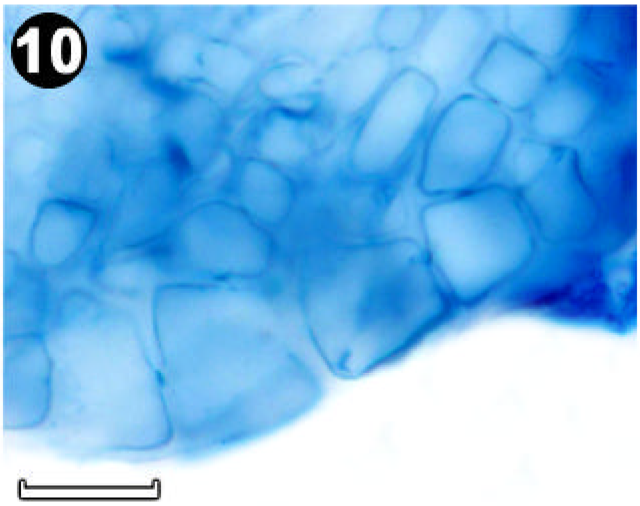


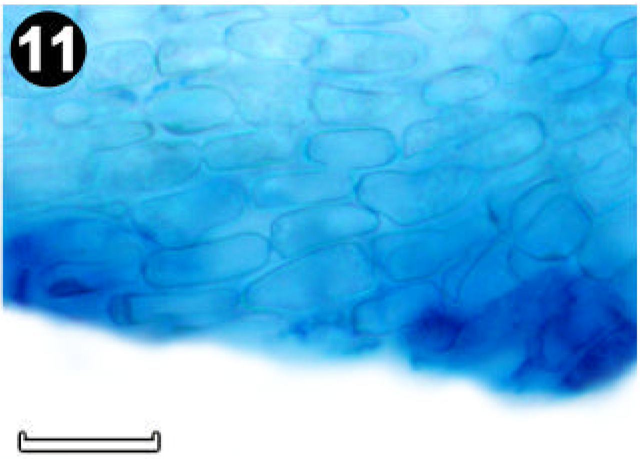
Plate 49











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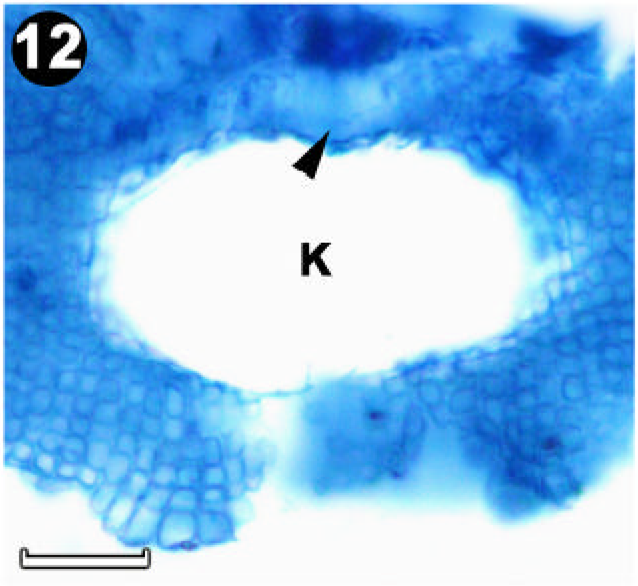

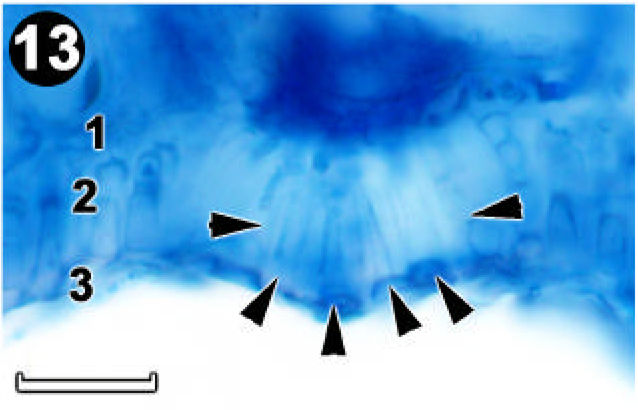

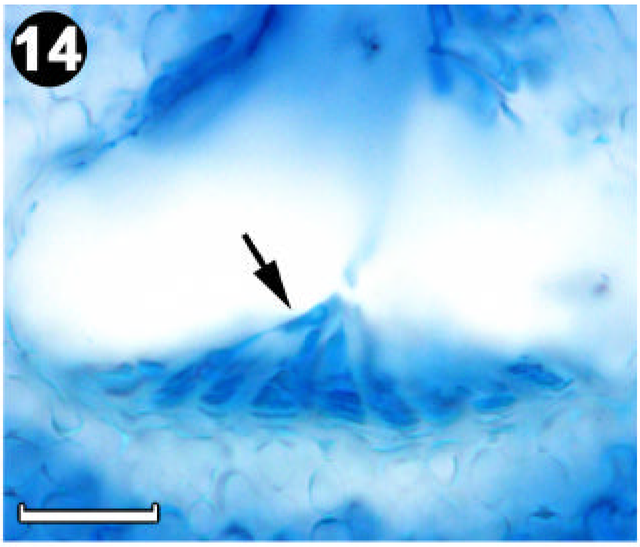

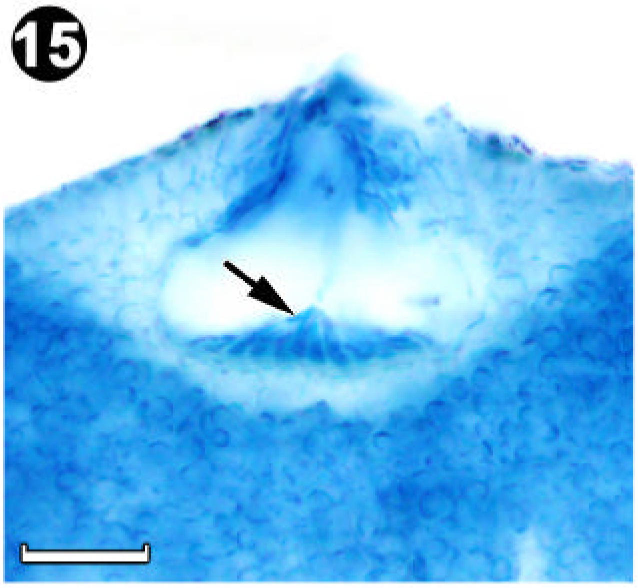

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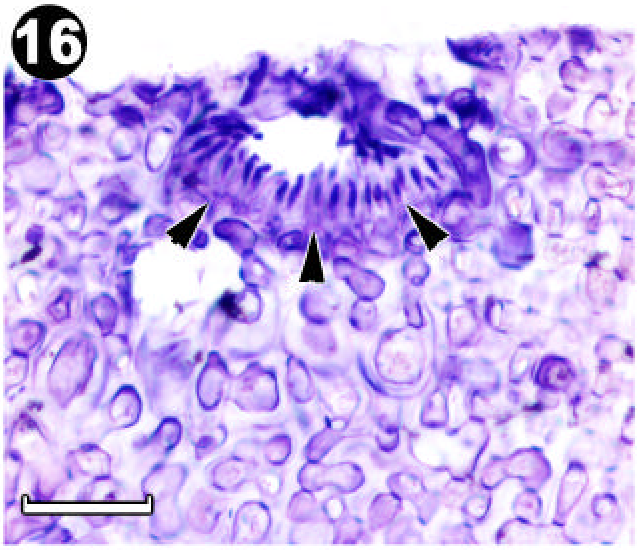

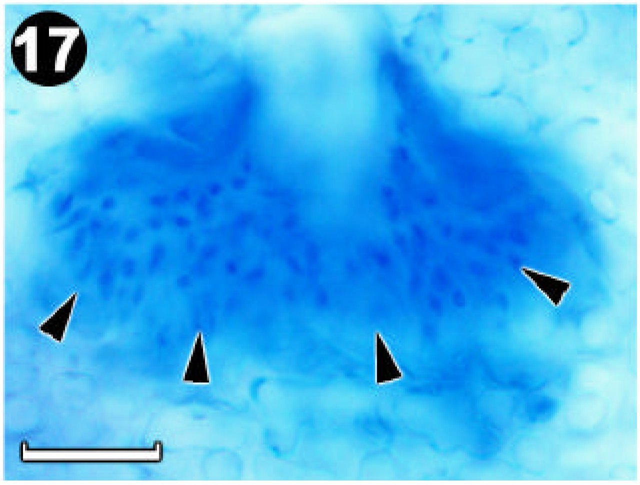

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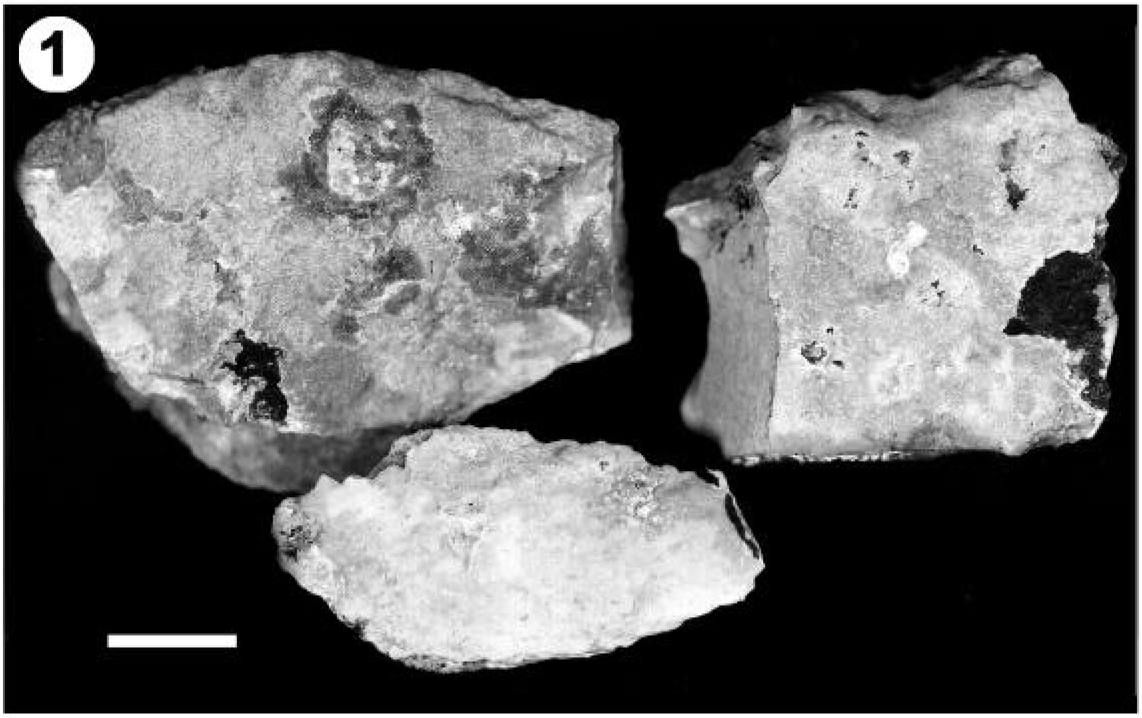

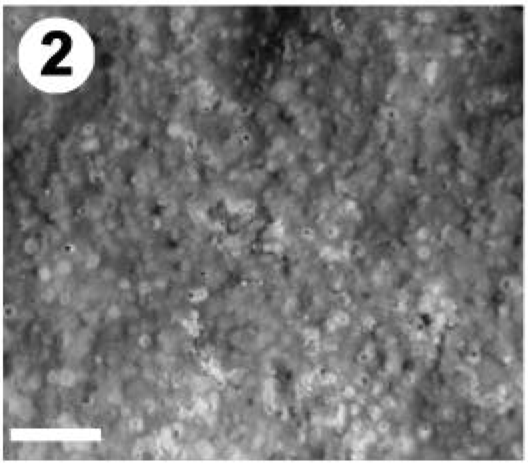

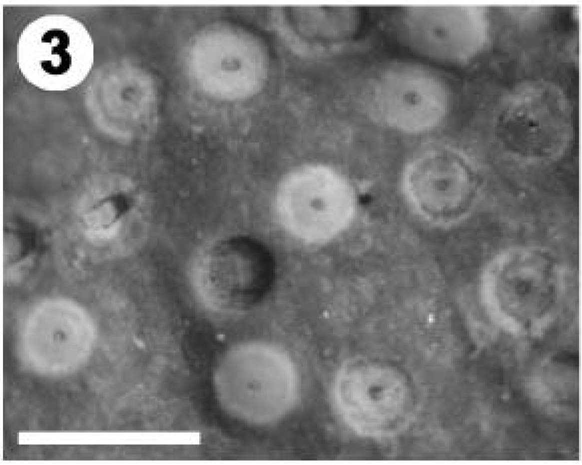

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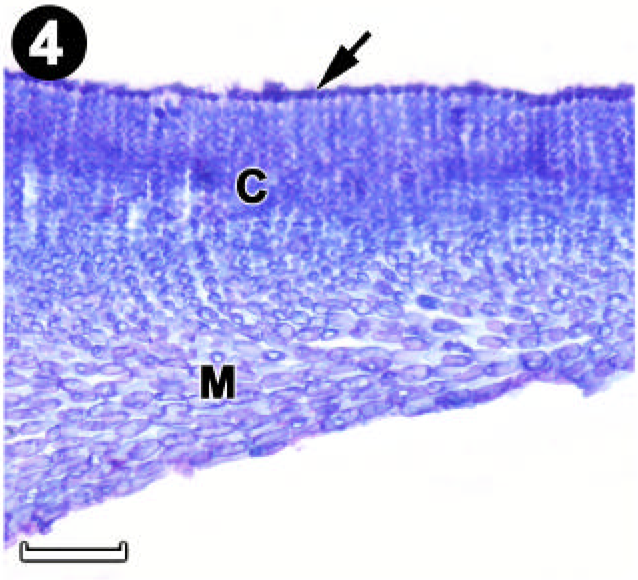

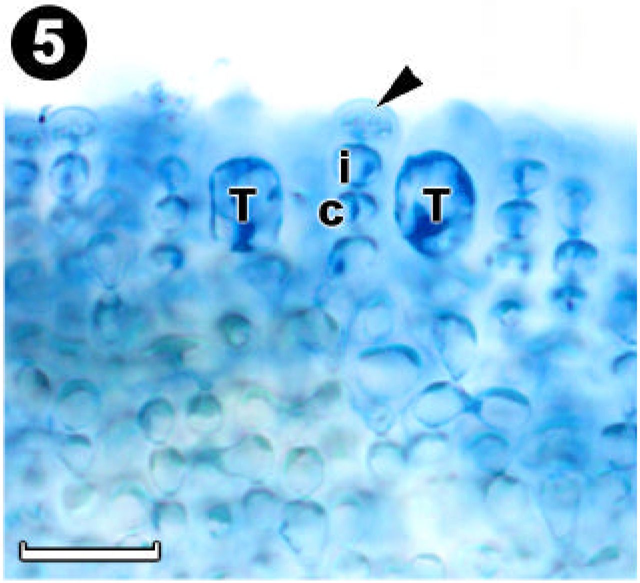

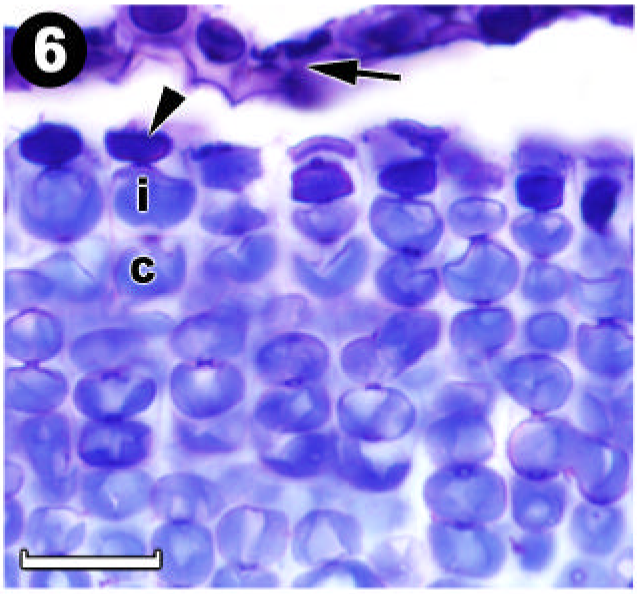

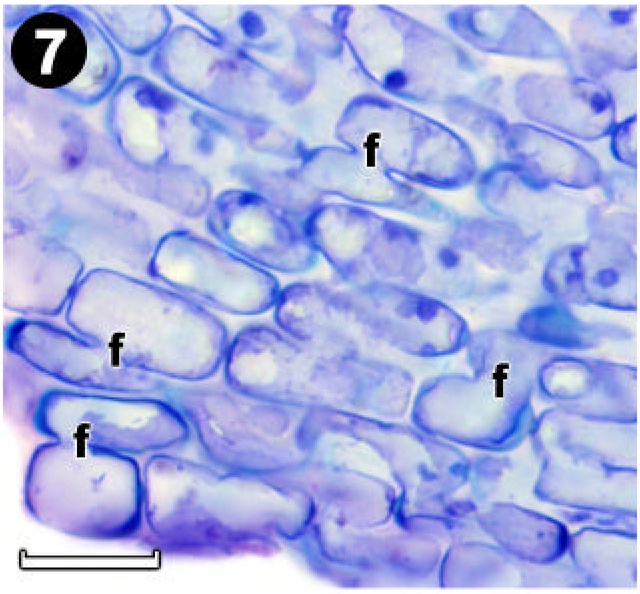

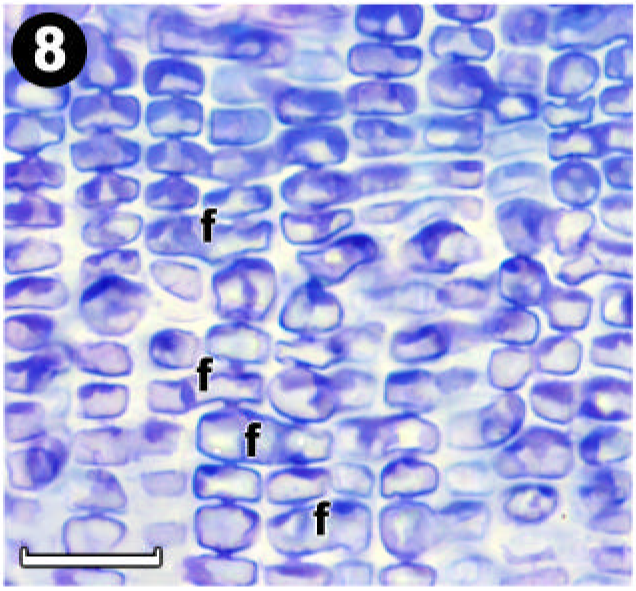

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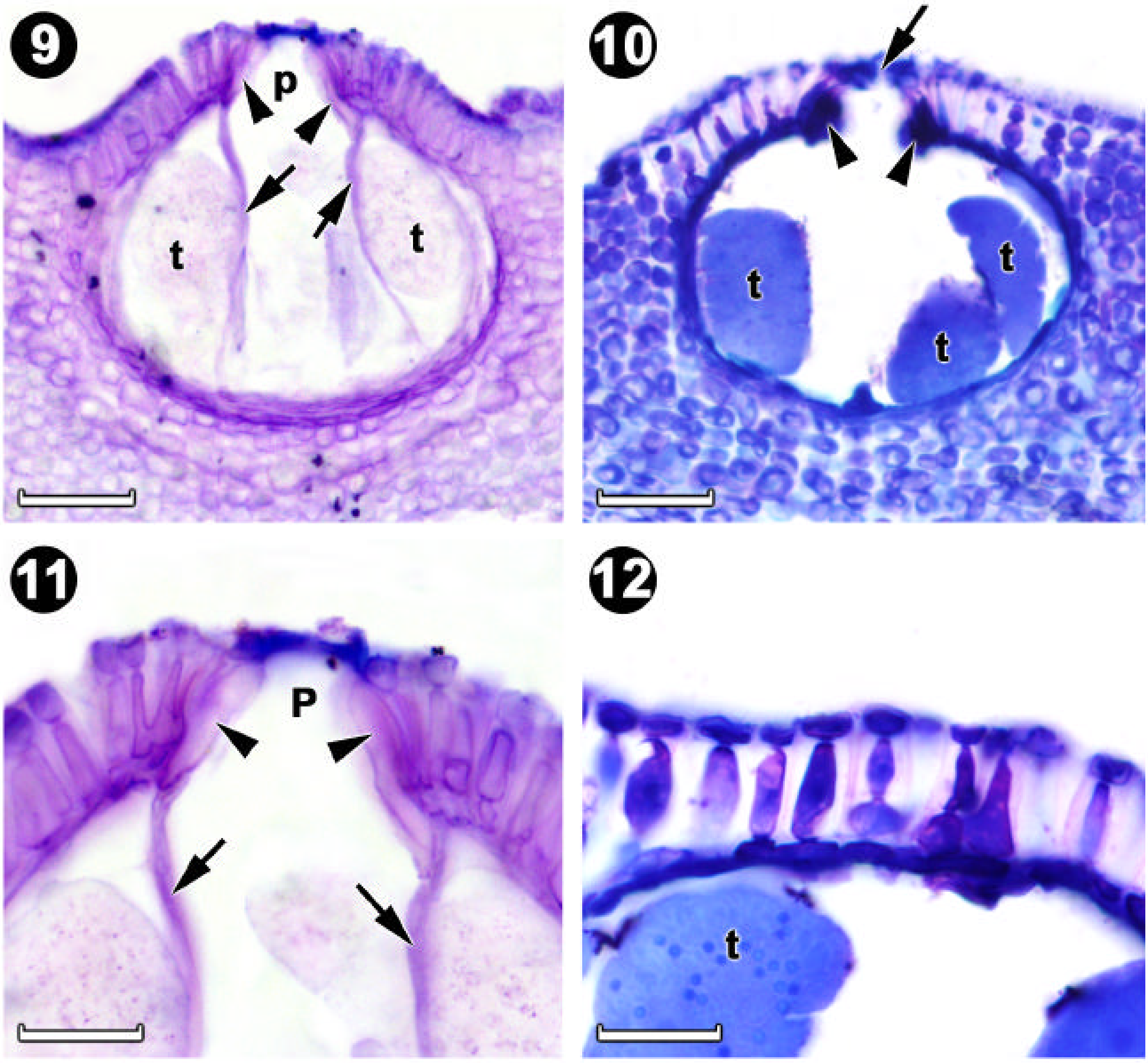
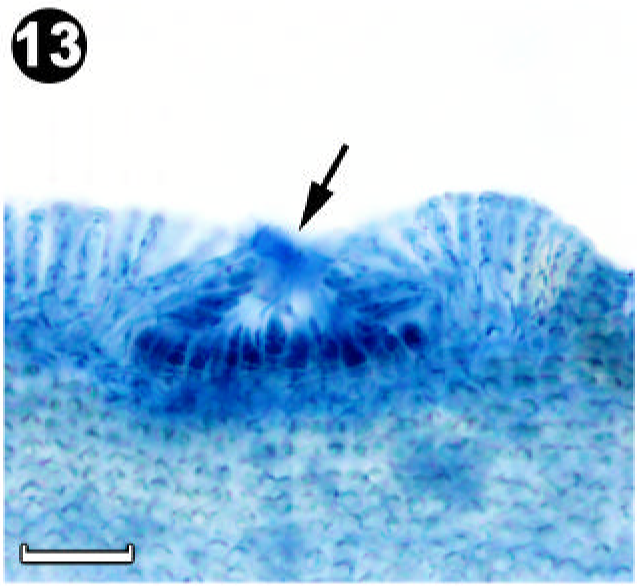
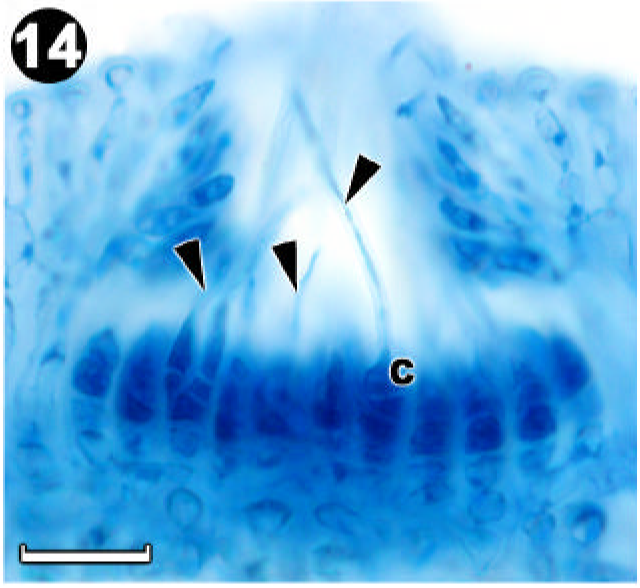
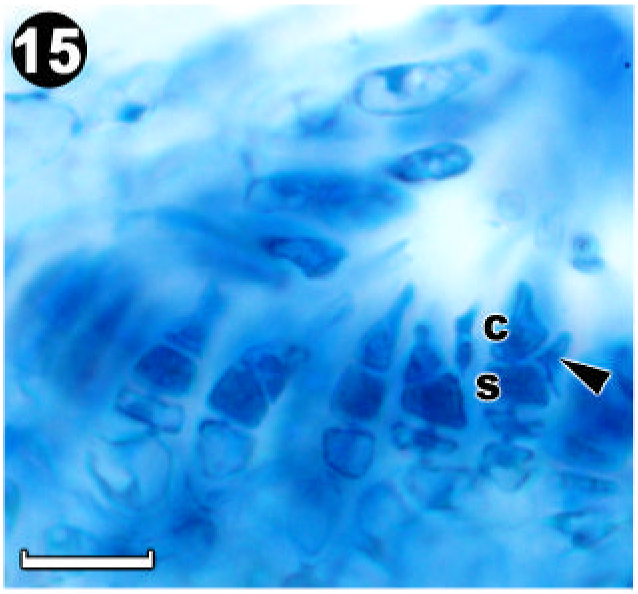
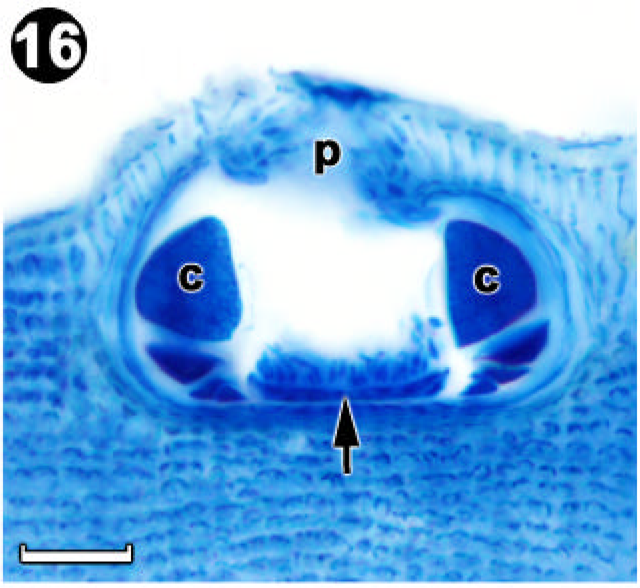


Plate 55









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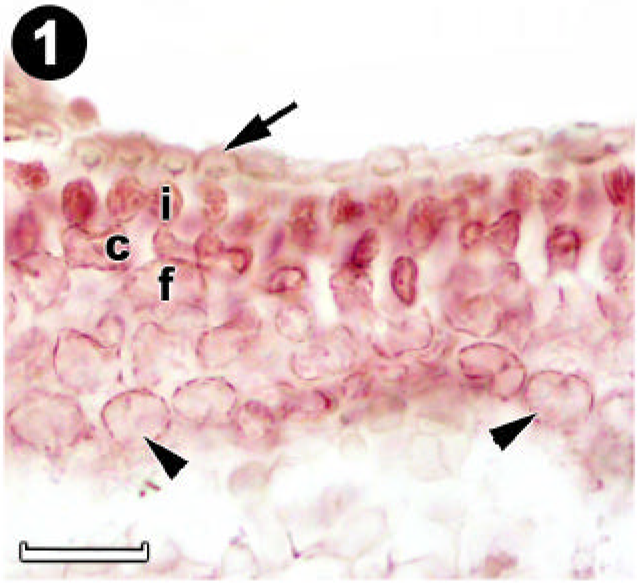

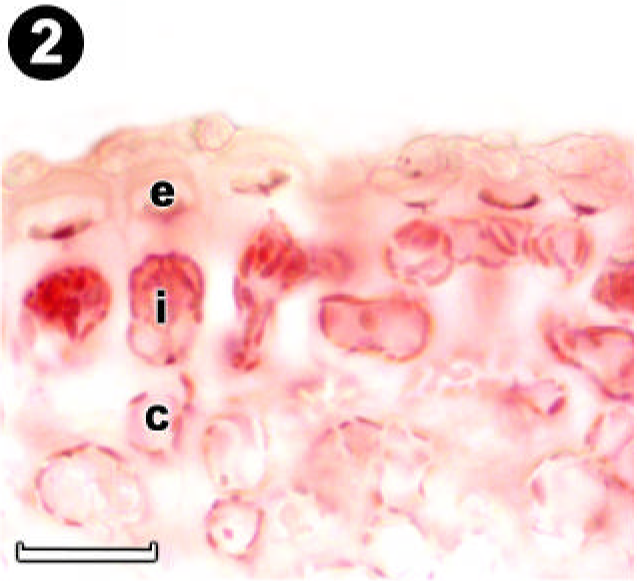

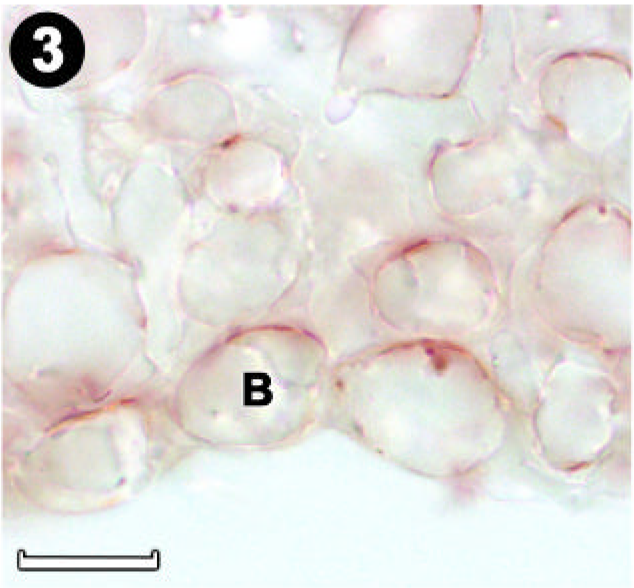

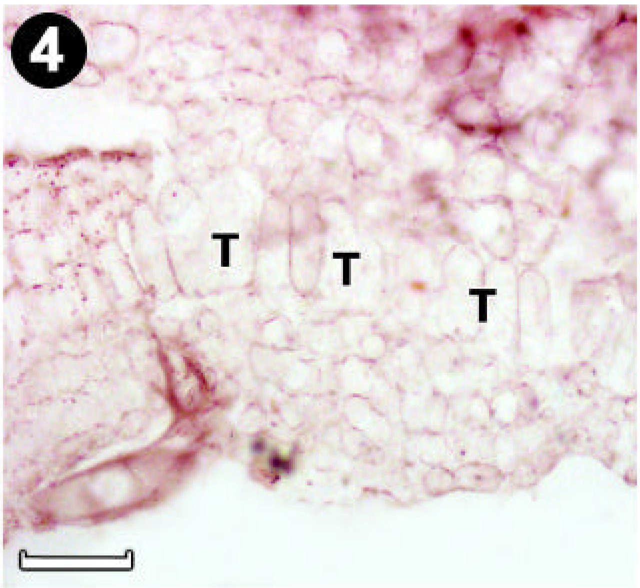

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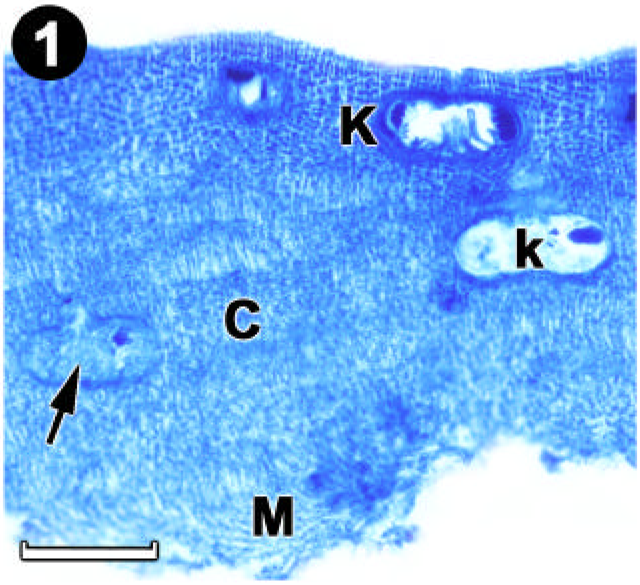
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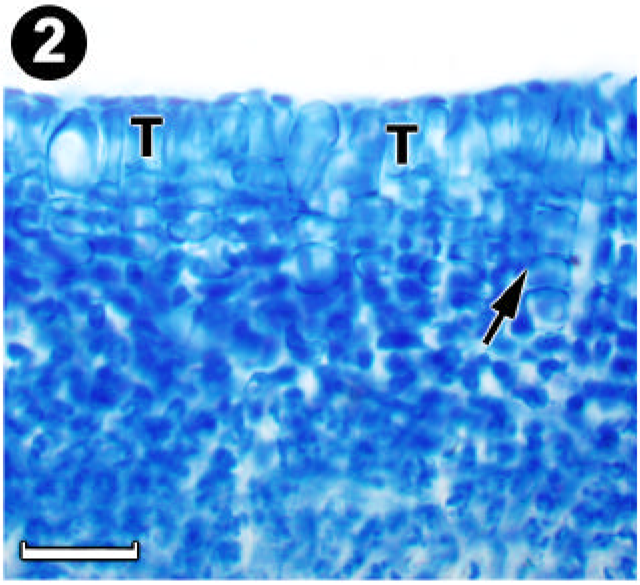
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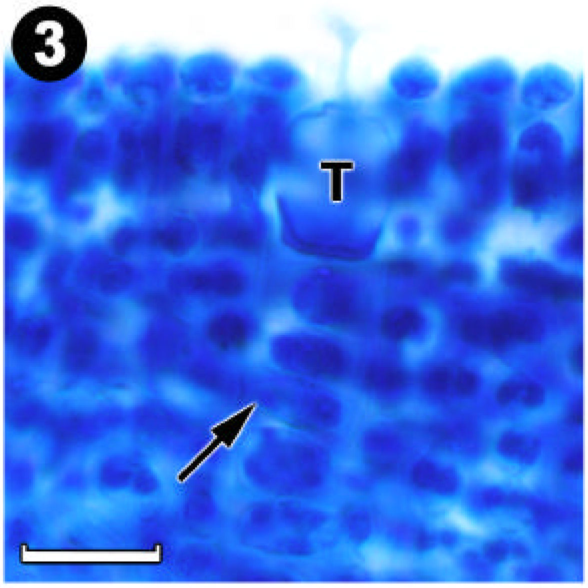
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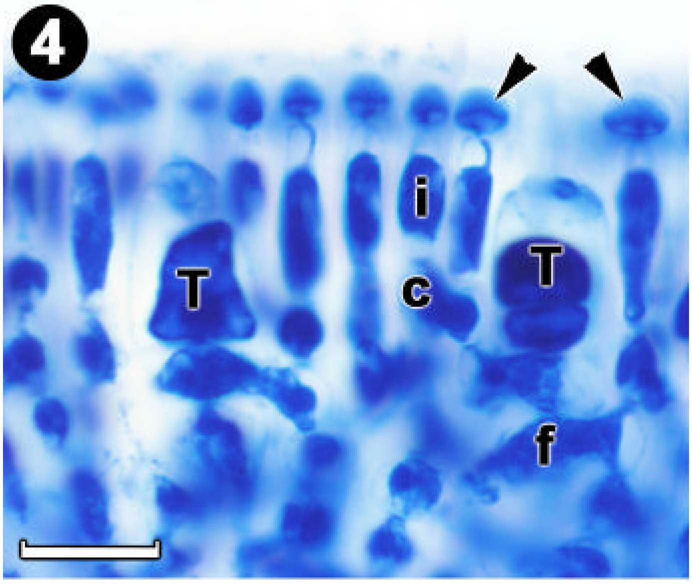
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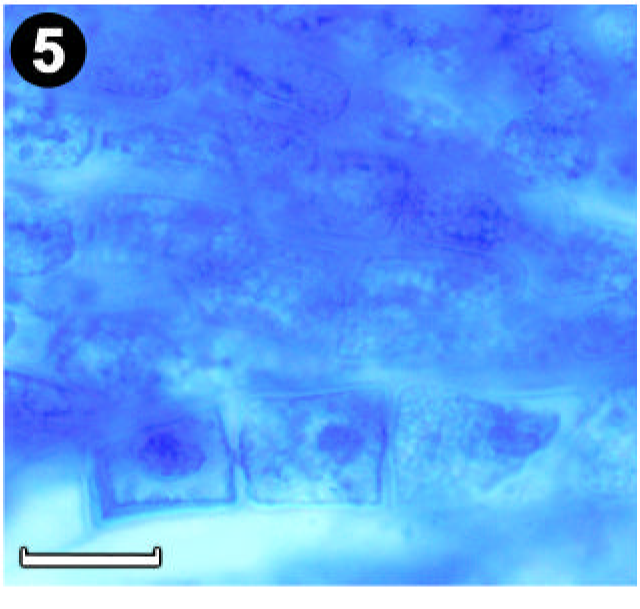
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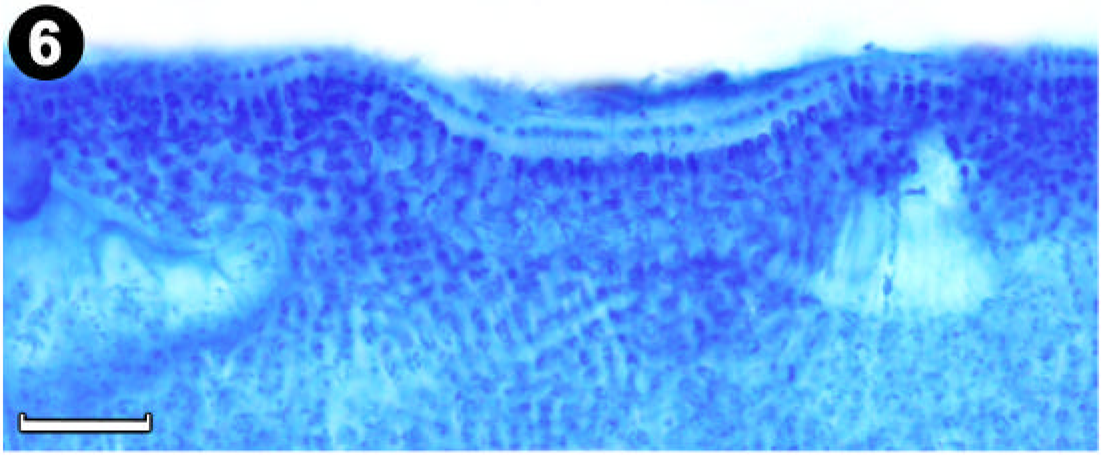
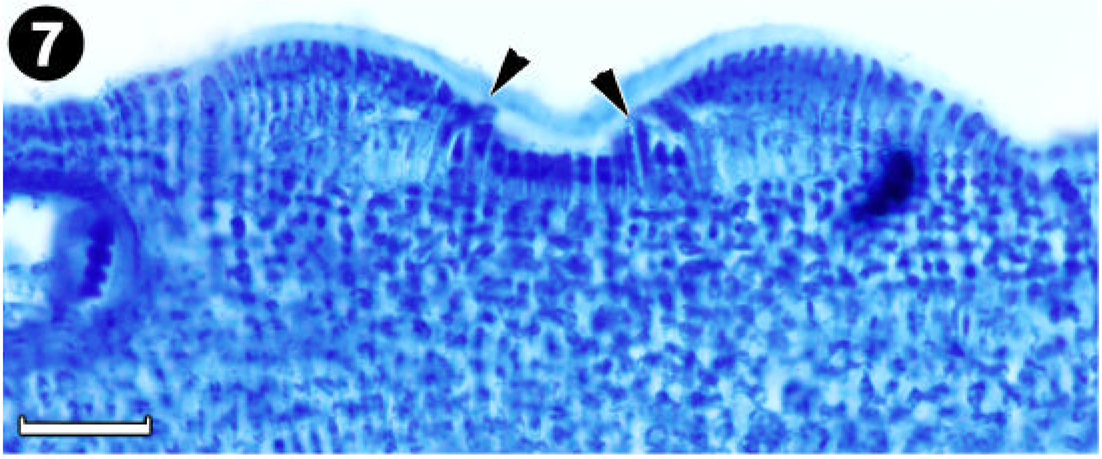
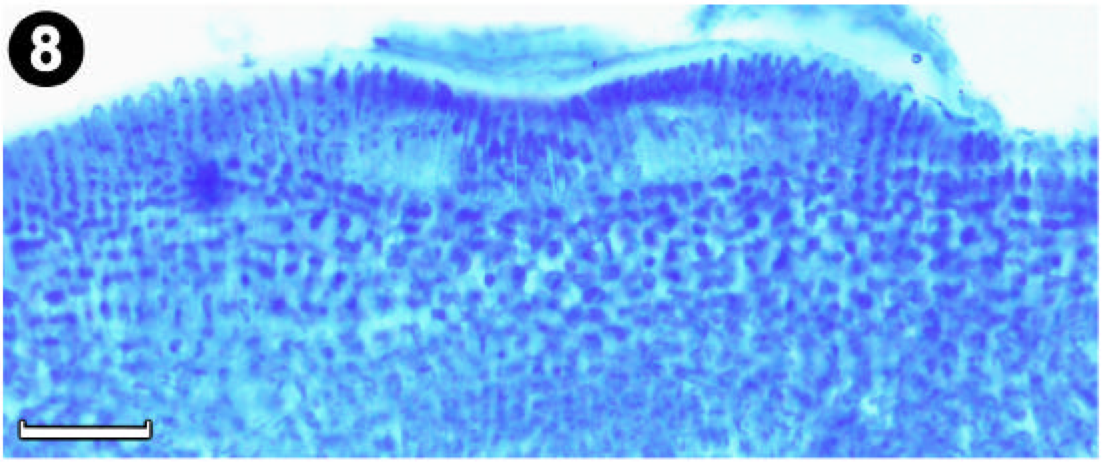
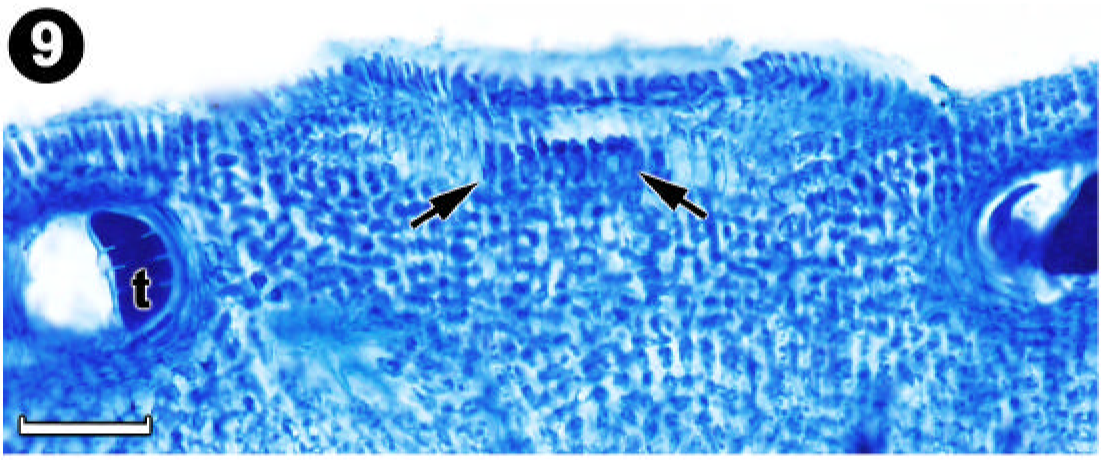
Plate 58









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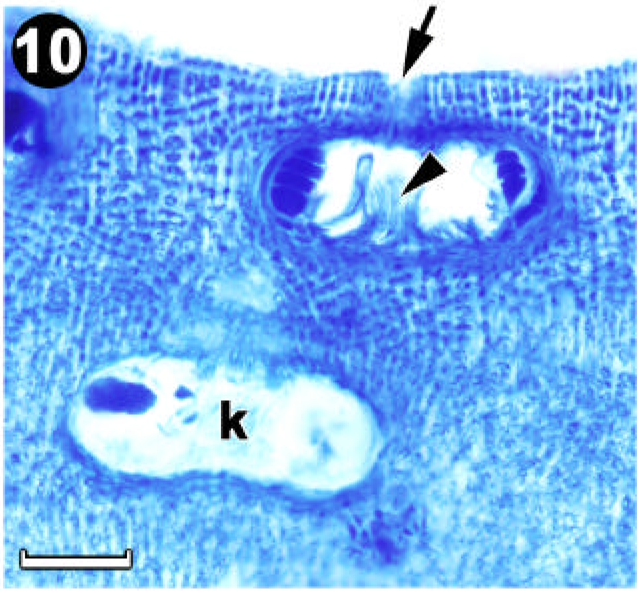

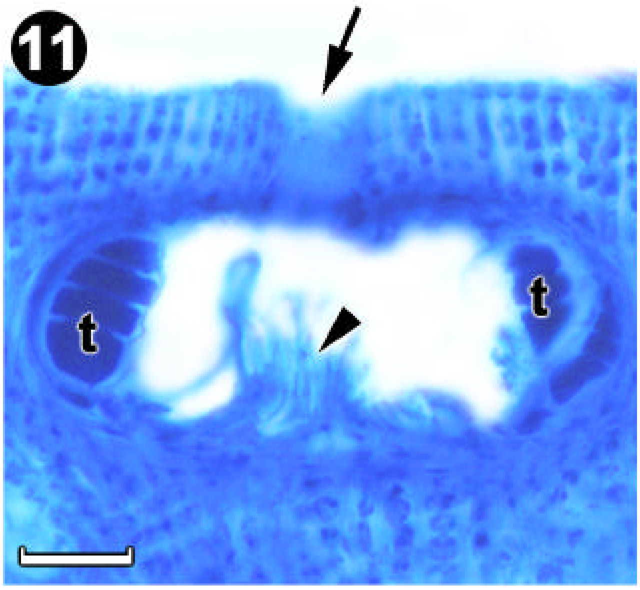

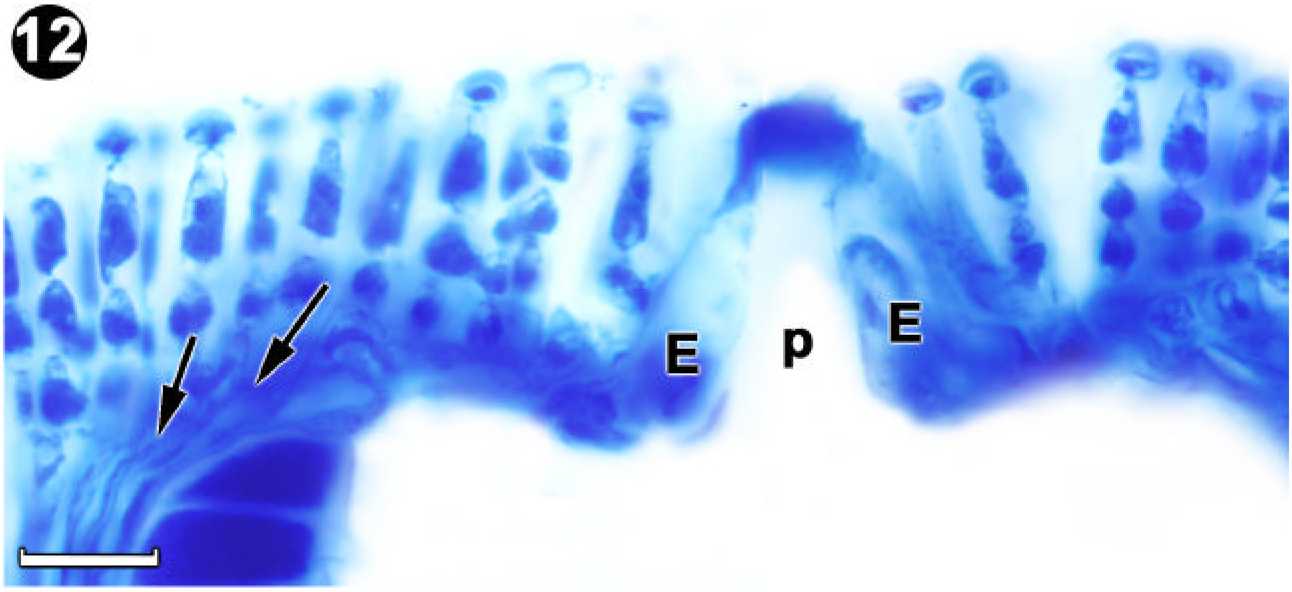

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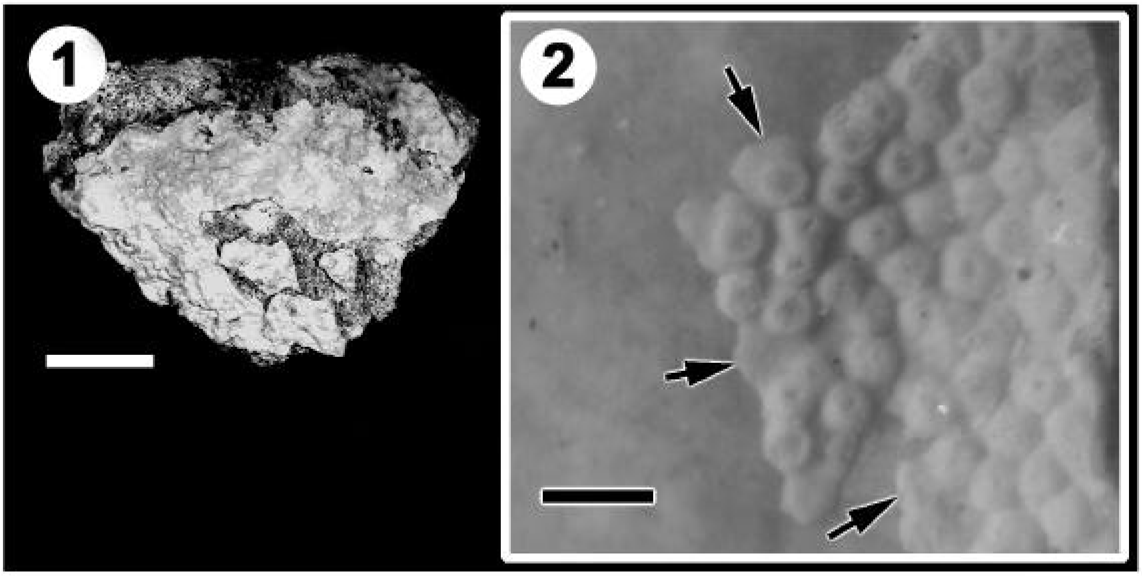

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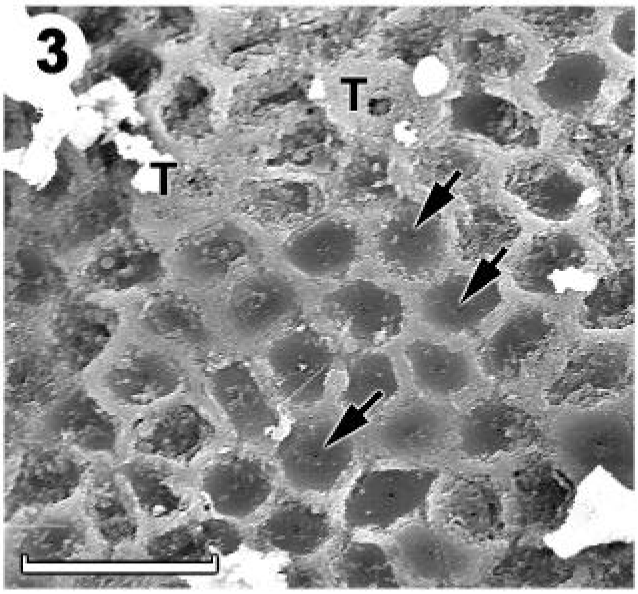

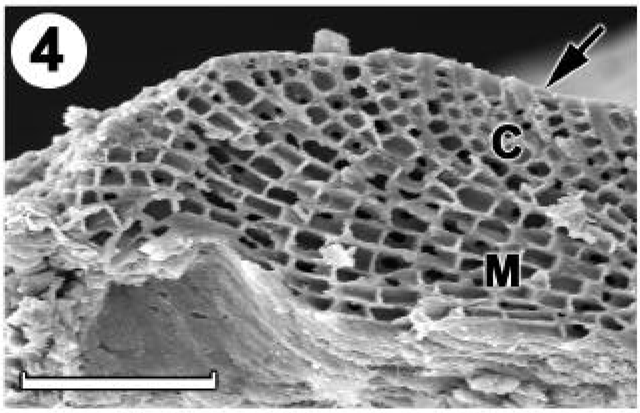

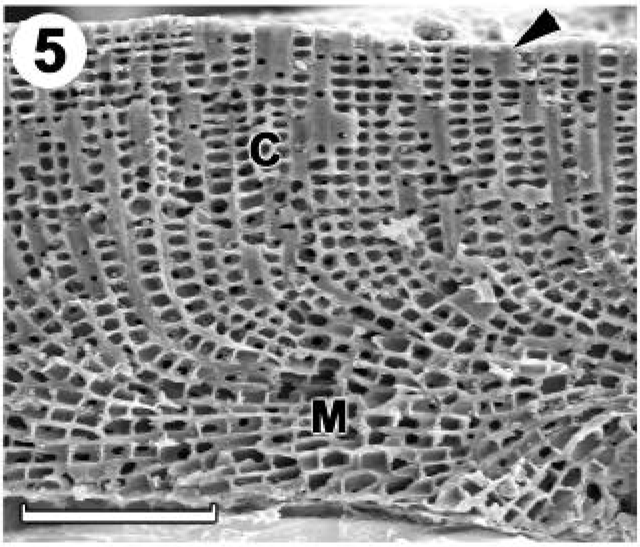

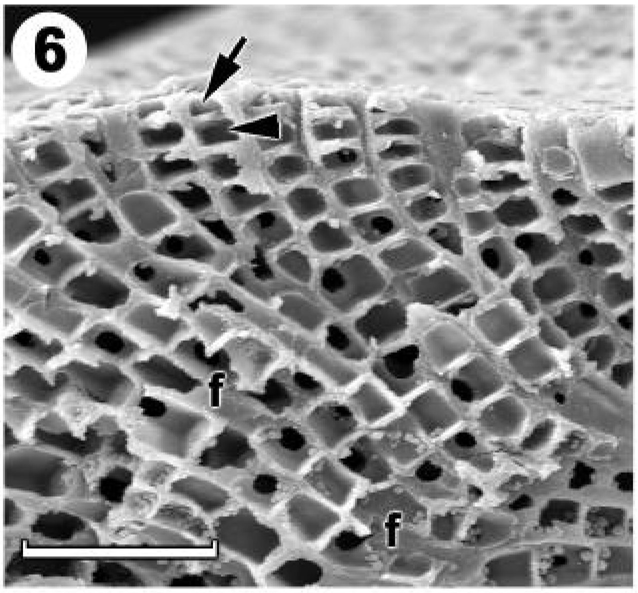

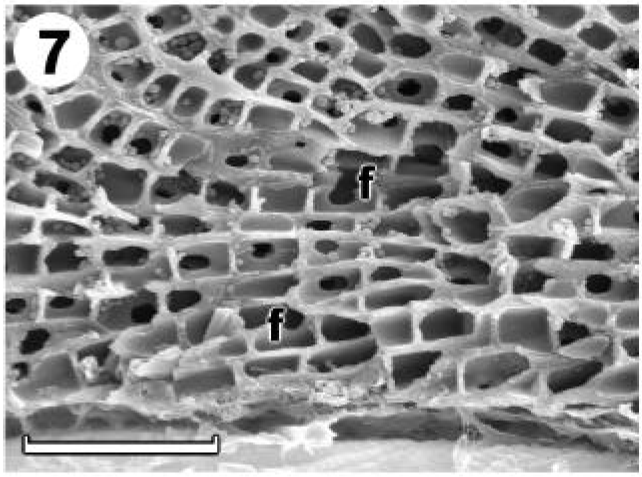

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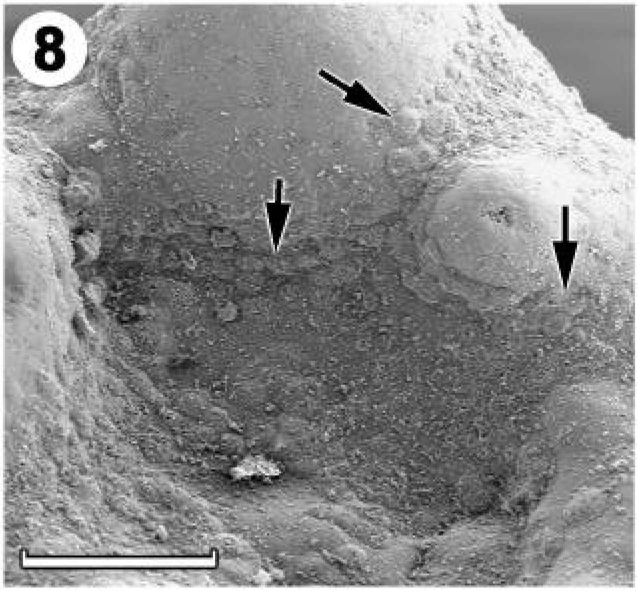

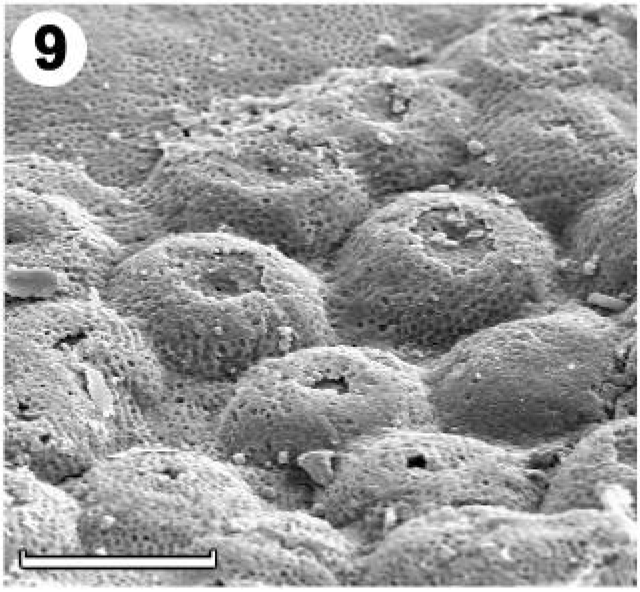

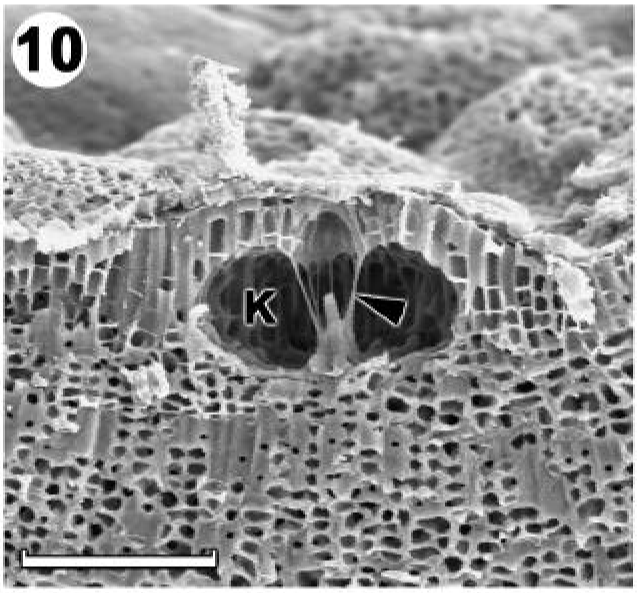

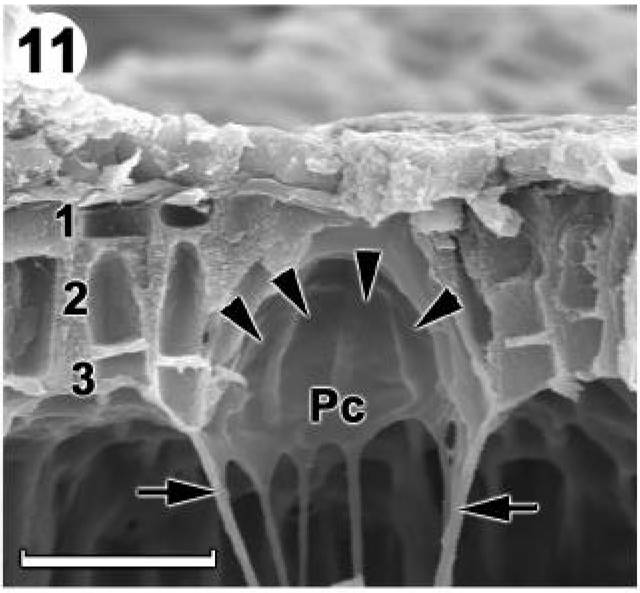

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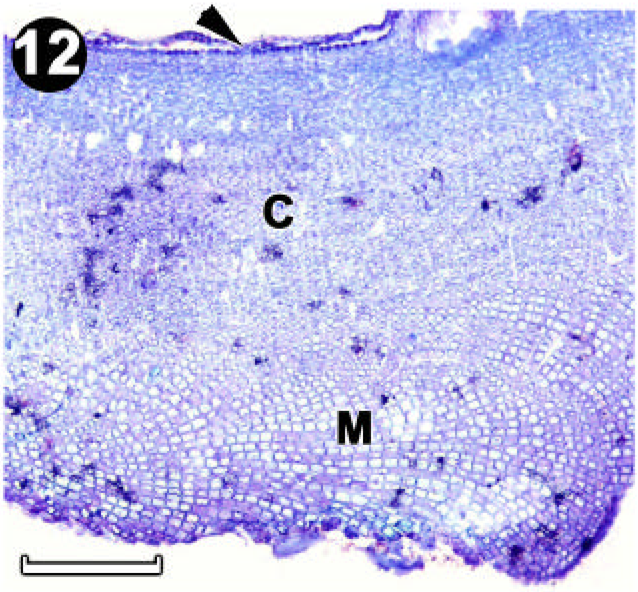

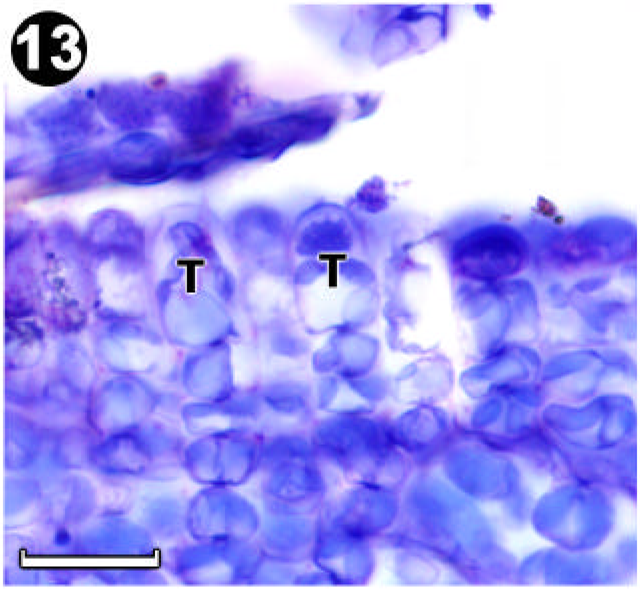

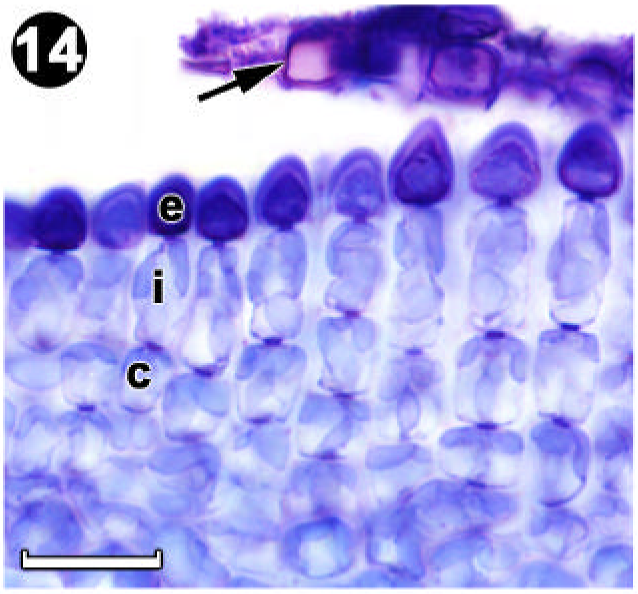

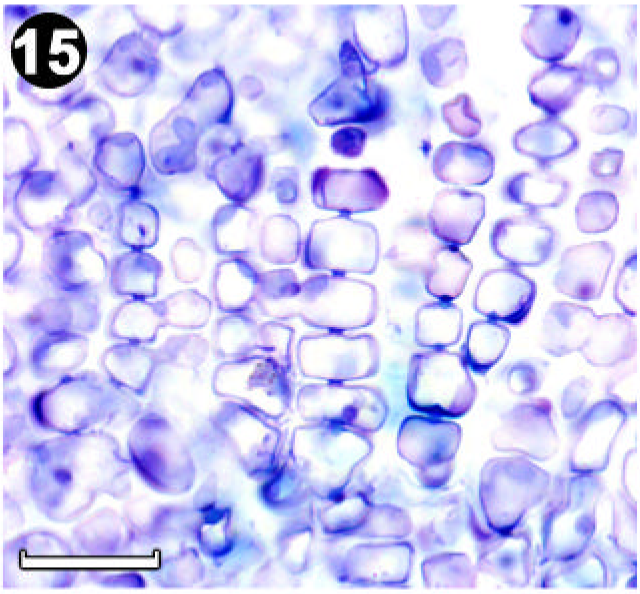

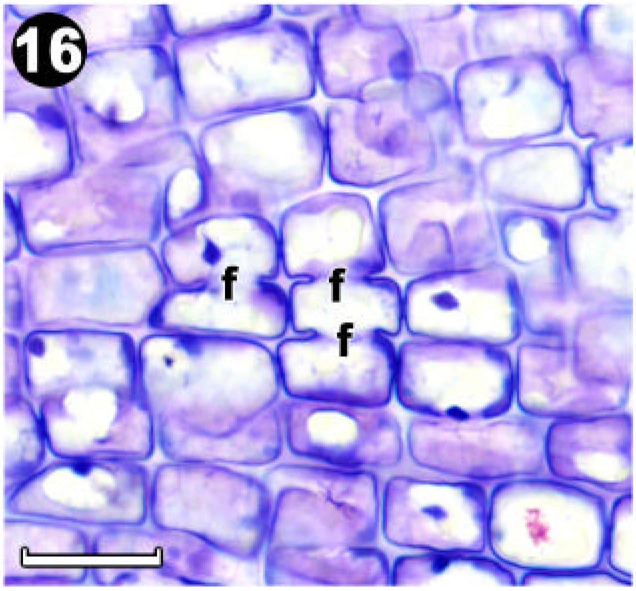

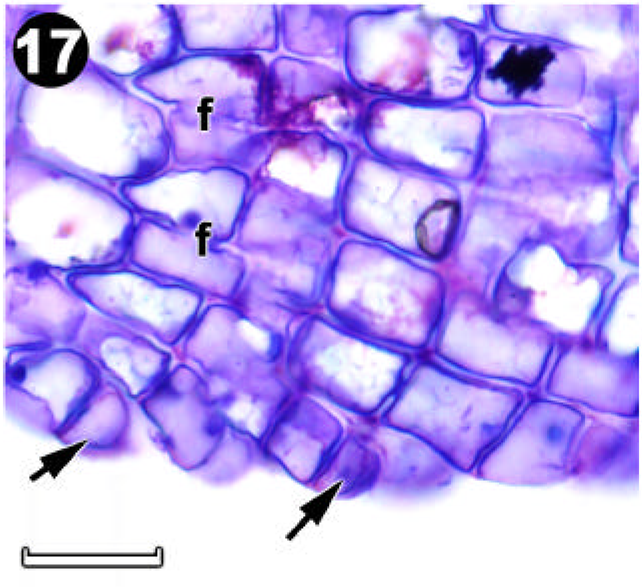

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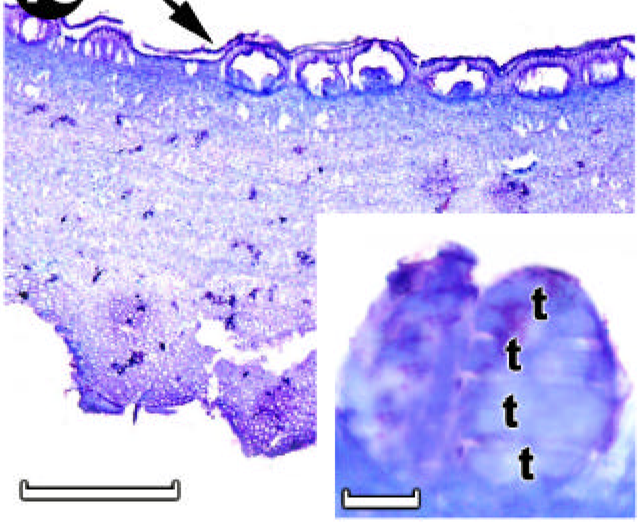

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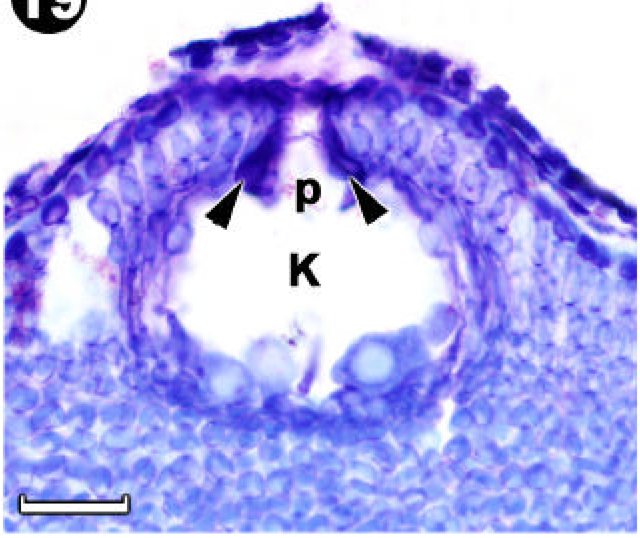

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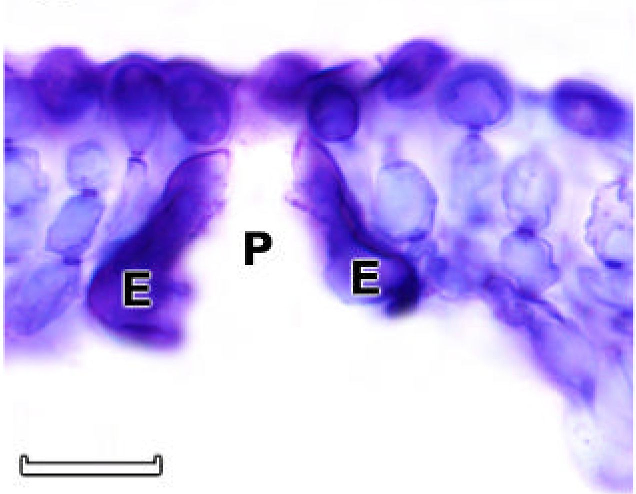

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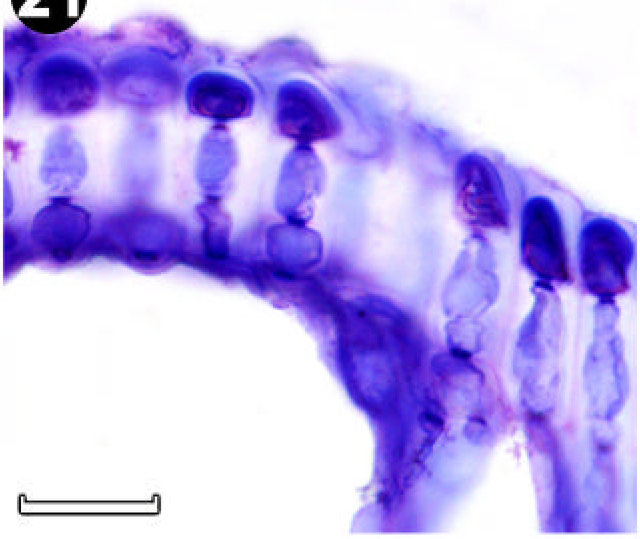

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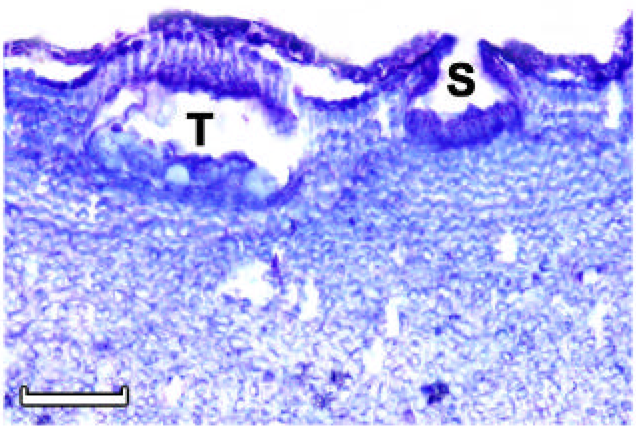

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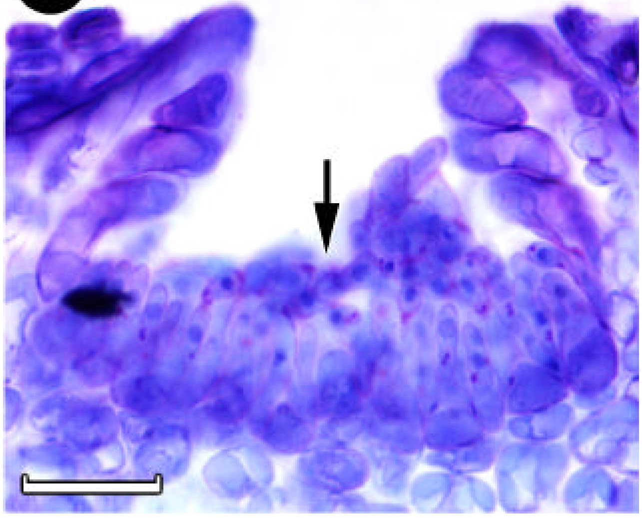


Plate 65

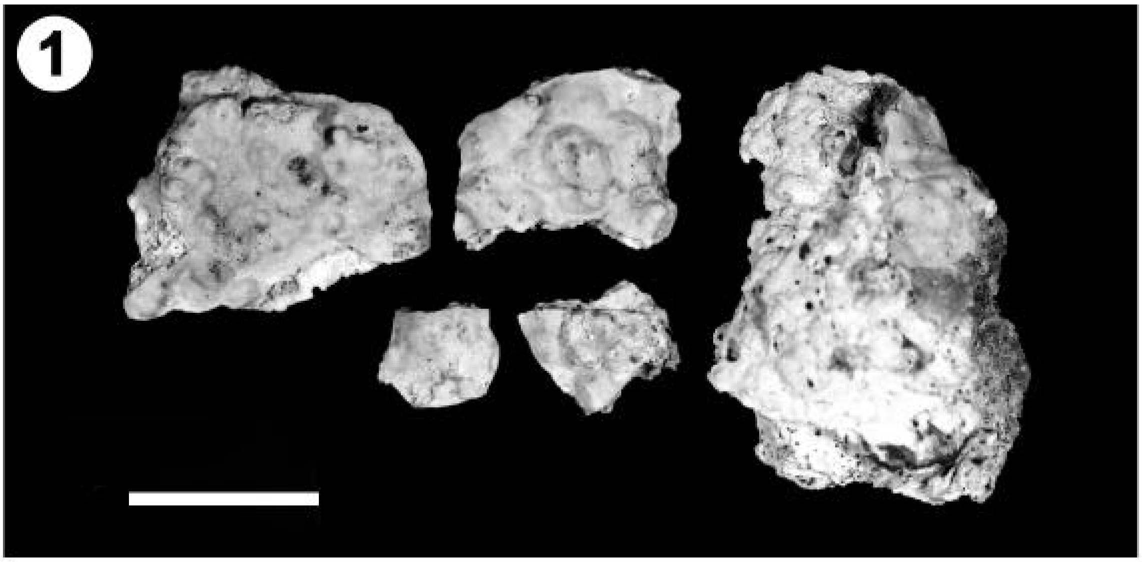
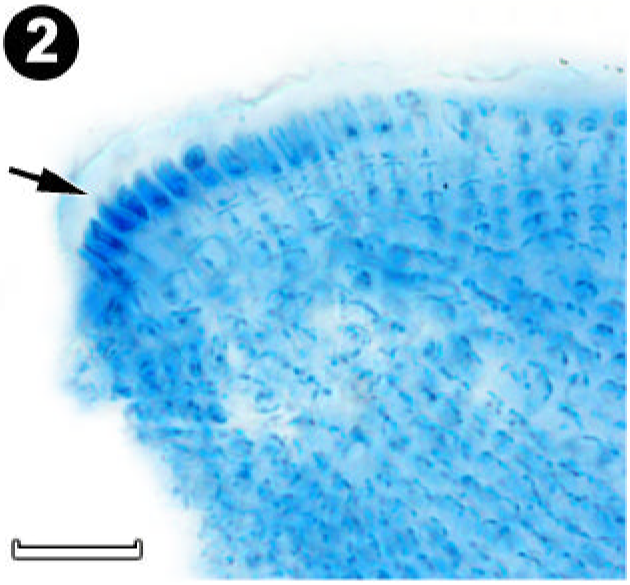
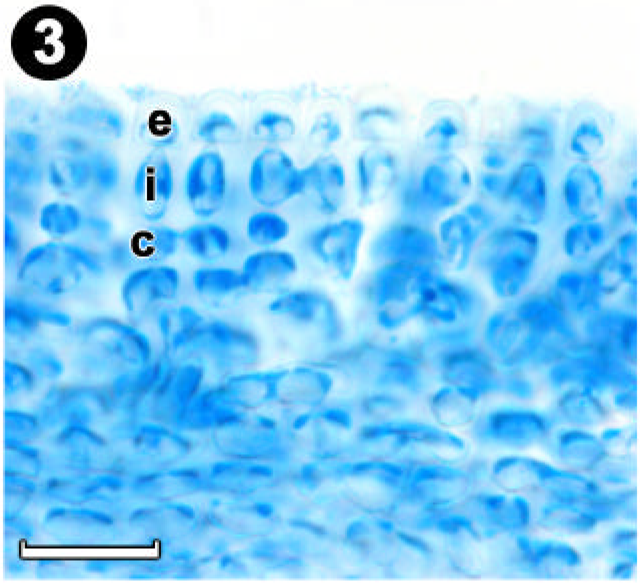


Plate 66





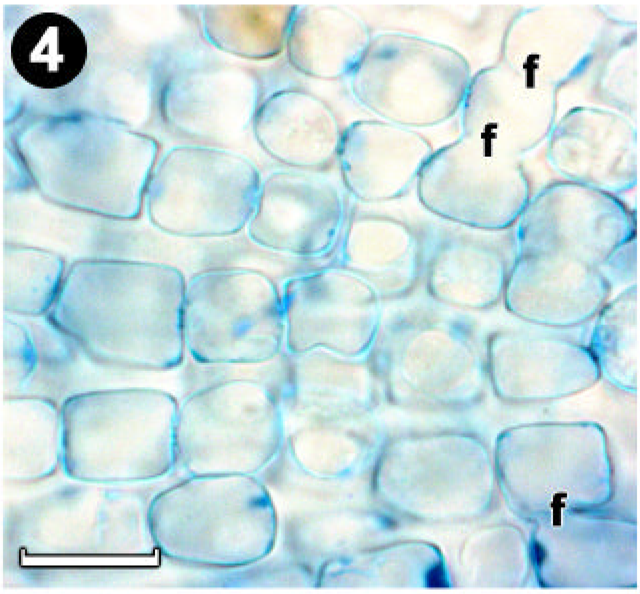


Plate 67

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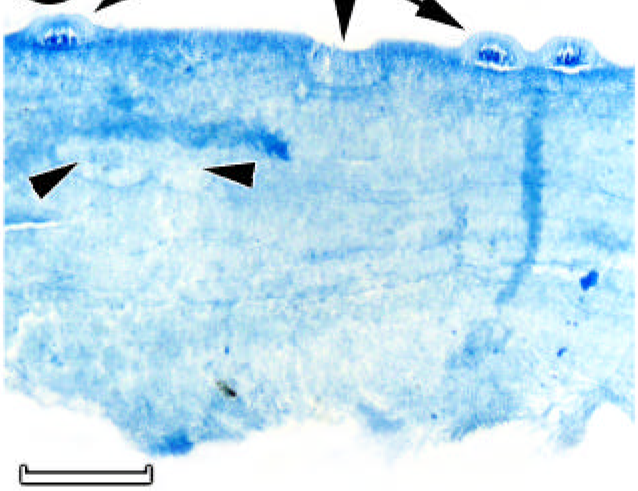

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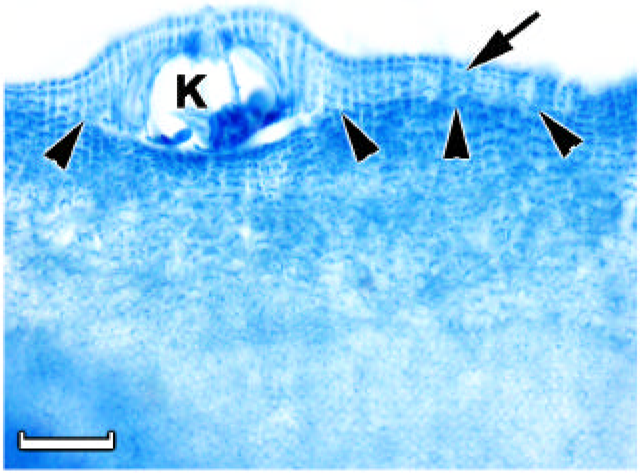

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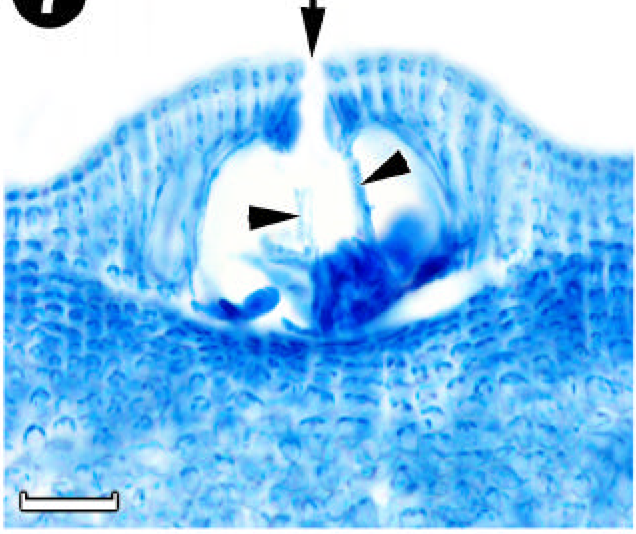

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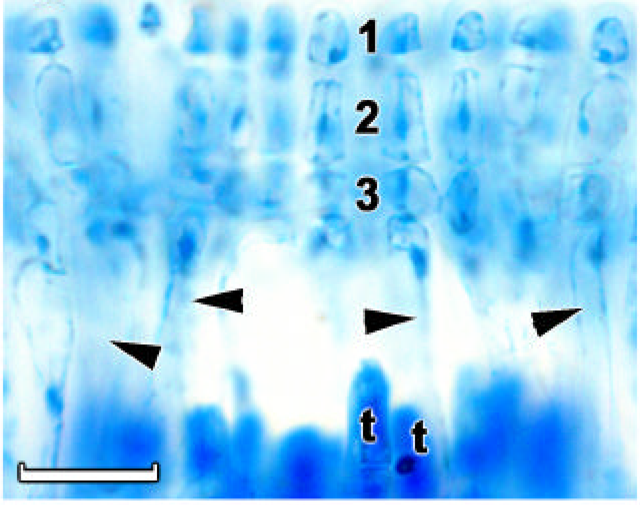

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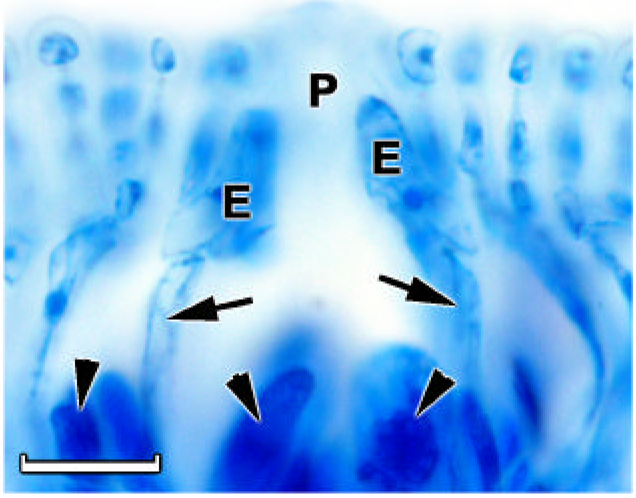

Plate 68

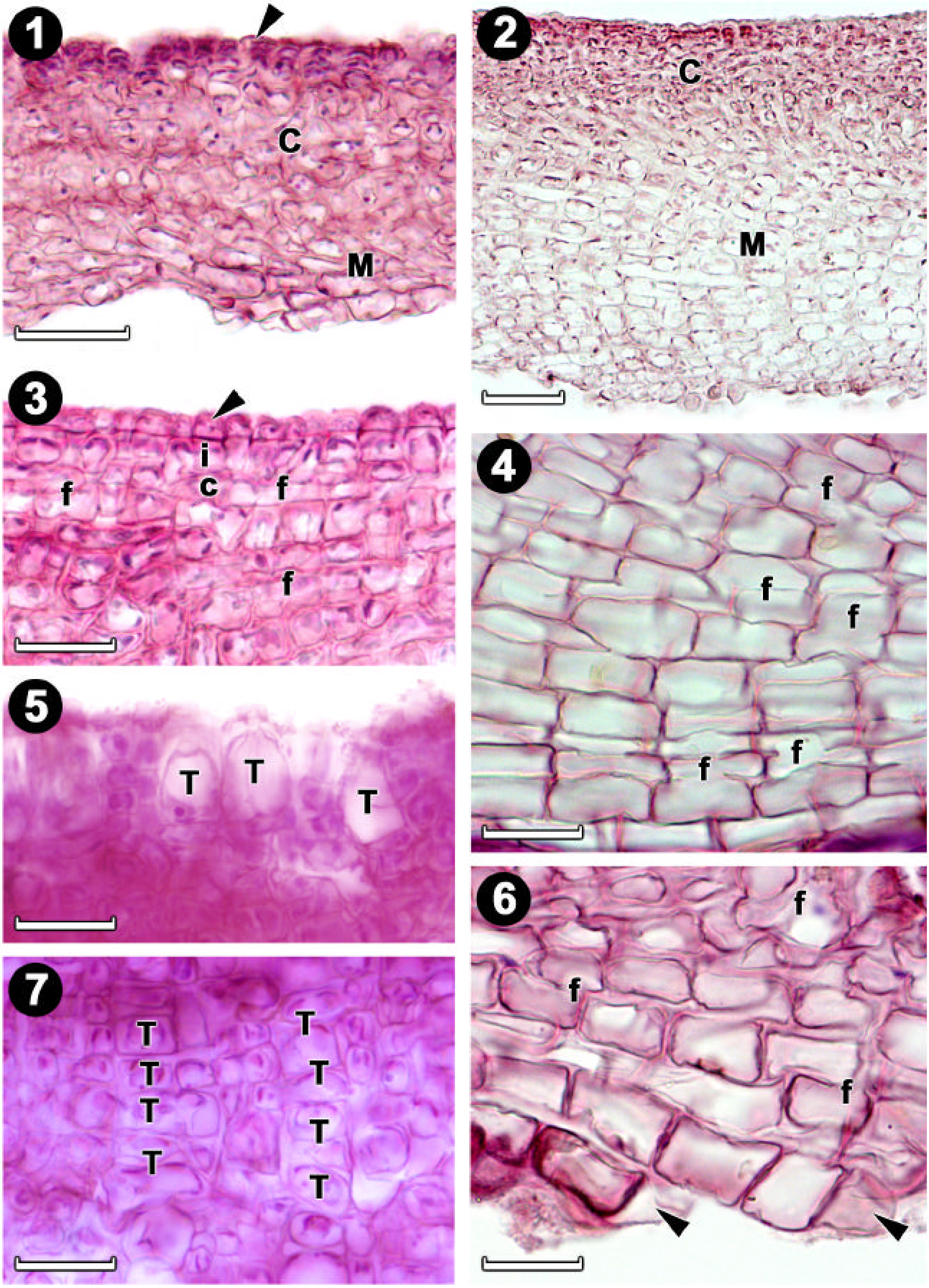

Plate 69

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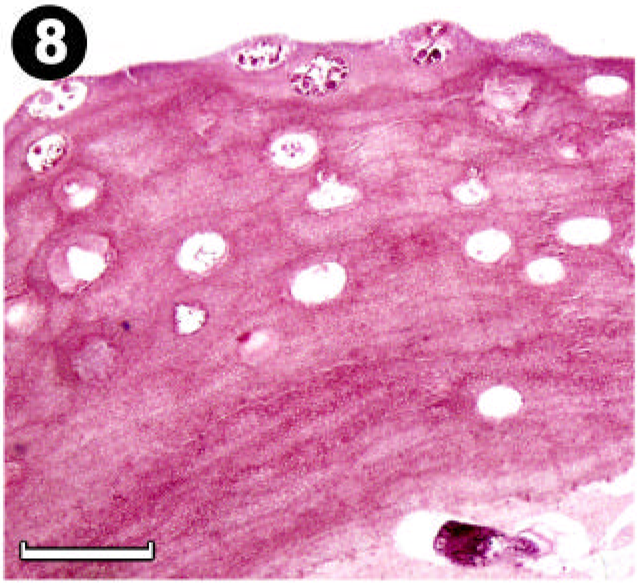

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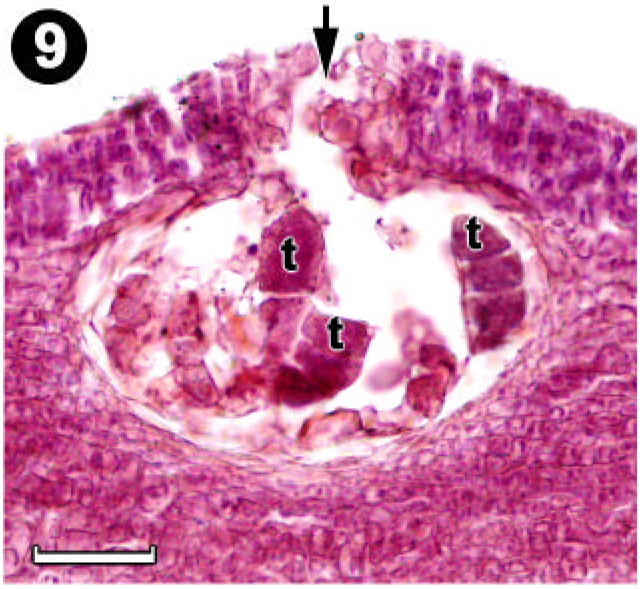

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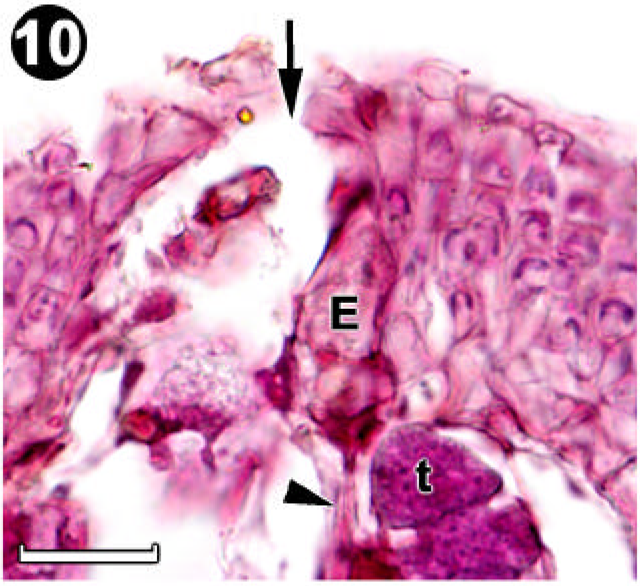

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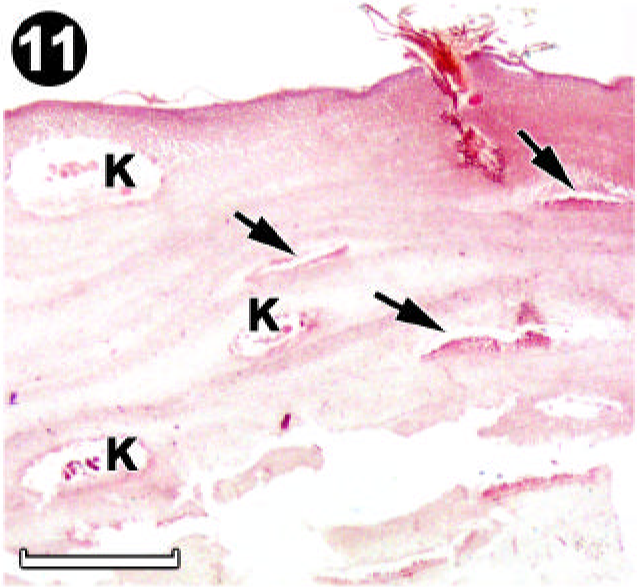

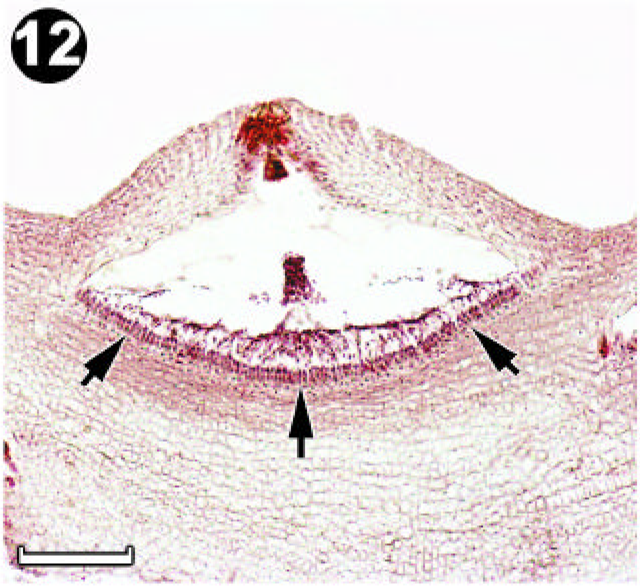

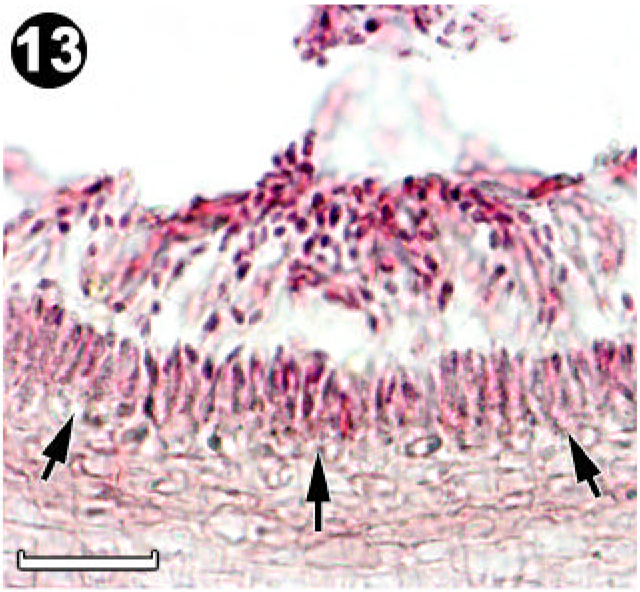

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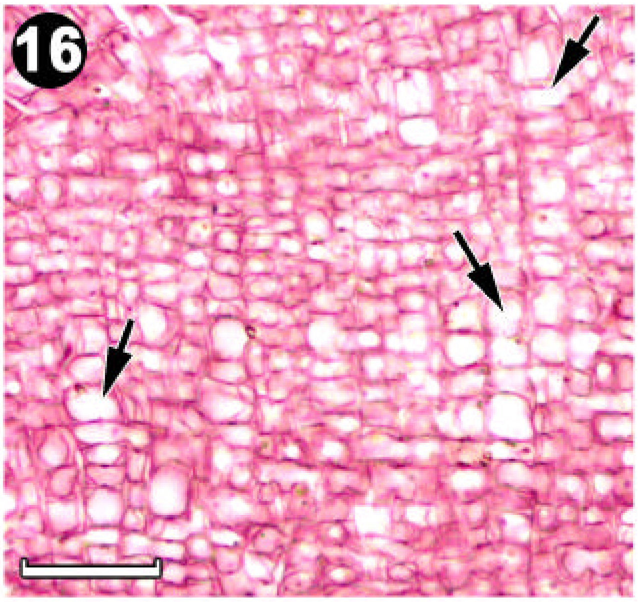

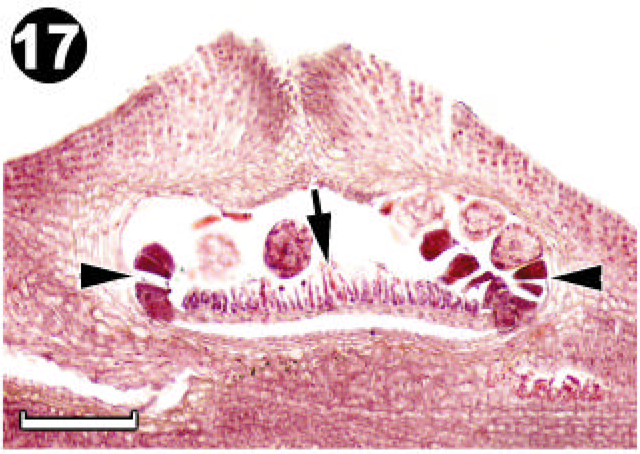

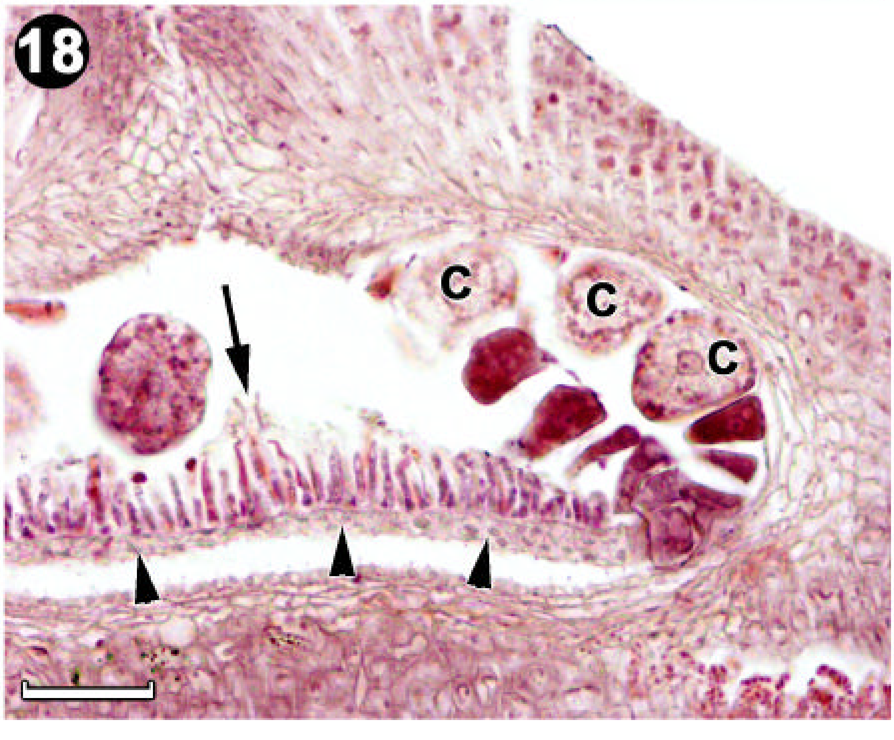

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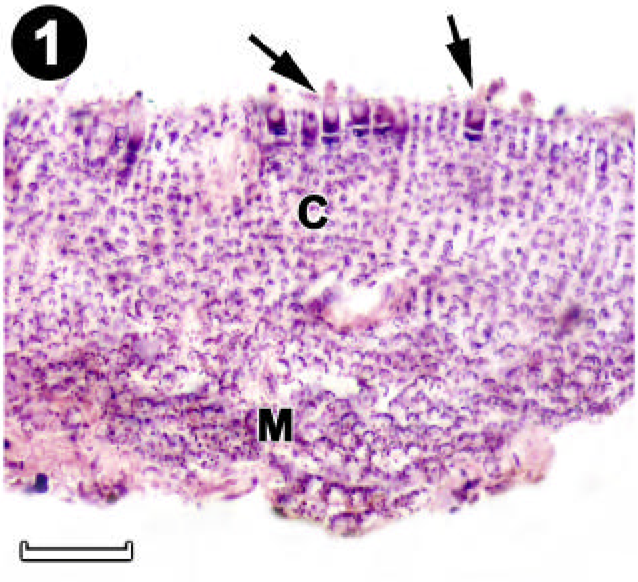

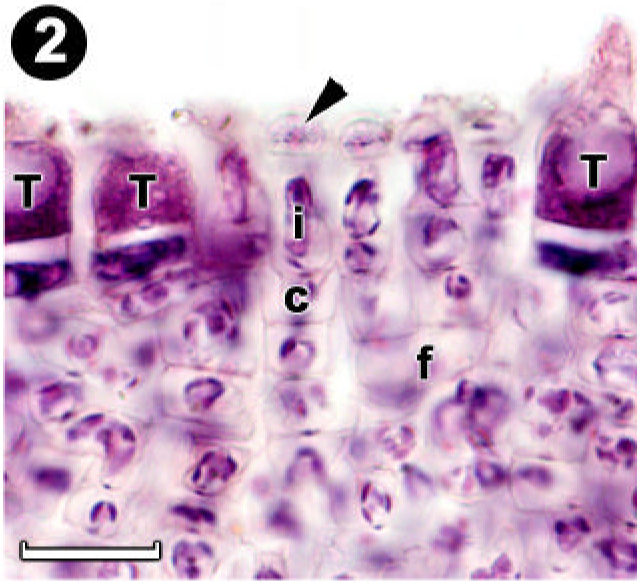

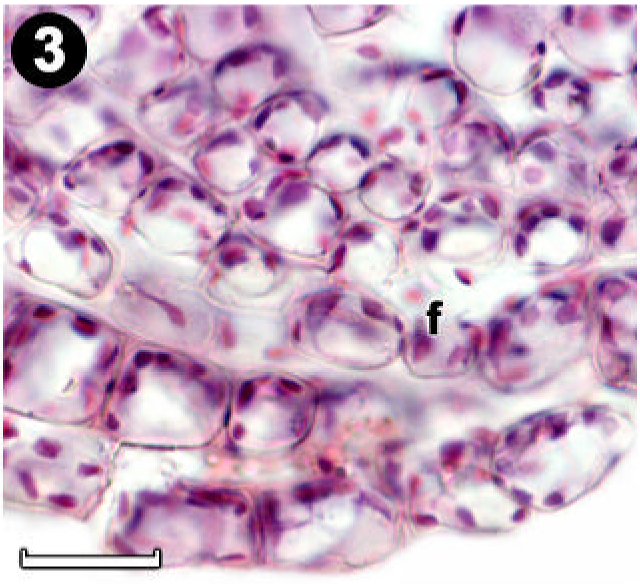

Plate 73

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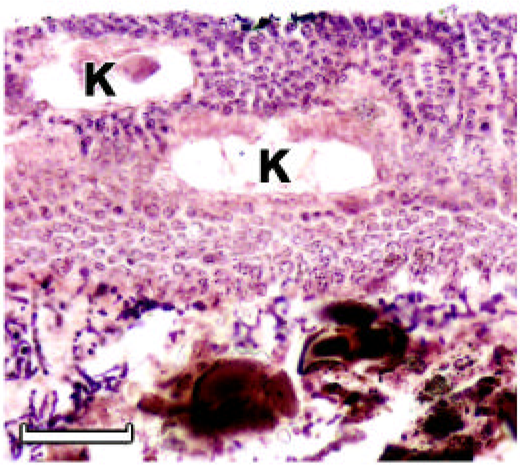

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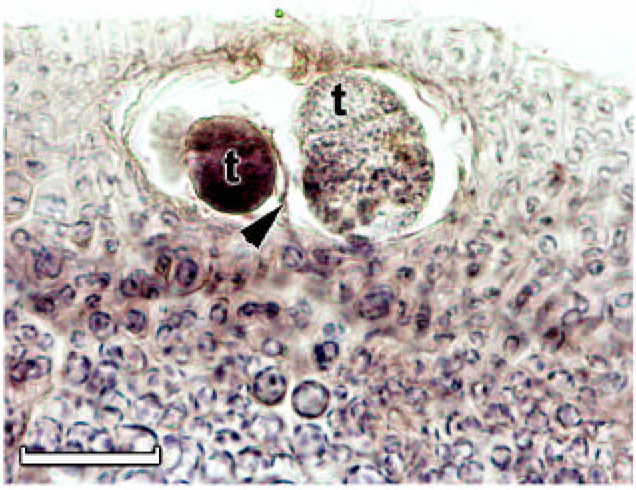

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Paper 3.

A phenetic character analysis of selected taxa belonging to the genus Hydrolithon Foslie (Corallinales, Rhodophyta)

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ABSTRACT

A phenetic character analysis of the taxa ascribed to, and found to conform to the genus Hydrolithon was carried out using both qualitative and quantitative data. The purpose of the research was to determine the affinities between the selected species under study, their relationships represented on a phenogram. This was determined using the Cluster Analysis of the Multivariate Statistical Package of Kovack (MVSP - vs 3.1). In order to determine the most appropriate indices, a series of three Distance and three Similarity indices were first tested on two sets of well-delimited coralline taxa (subfamilies and Mastophoroid genera). The Bray Curtis (Distance) and Percent Similarity (Similarity) indices were found to best resolve the taxa under study. Within the genus Porolithon (defunct) the following taxa were indicated to be conspecific: Porolithon castellum with Hydrolithon craspedium (100%); P. pachydermum (100%) and Porolithon cocosicum (99%) with H. onkodes; P. sandvicense with P. antillarum (99%); P. coarctatum with H. gardineri (98%); and the P. sandvicense / P. antillarum entity with H. onkodes (96%). The data also show a close affinity between Spongites africanum and P. oligocarpum (90%), both taxa conforming well to the generic description of the genus Spongites. Within the genus Hydrolithon the following taxa were found to be conspecific: Neogoniolithon rufum with H. rupestris (99%); N. caribaeum with N. erosum (96%); H. murakoshii with H. munitum (94%); and H. samoënse (93%) and N. rugulosum (91%) with N. erosum; the latter taxon in each of the above combinations possessing nomenclatural priority.

INTRODUCTION

It is highly unlikely that any DNA can be extracted from dried coralline algal material stored for periods in excess of five years, let alone from material that had been stored for decades. This is particularly true for material that had been air dried (Vidal pers. comm.). Although it may be argued that representative material from type localities may be the answer to obtaining DNA for such taxa, many of the original material have been so poorly described that even this becomes problematic. Under such circumstances, morphometric and anatometric analysis of material is probably the only real way to satisfactorily resolve nomenclatural disputes. Many agree (e.g. Keats 1997; Keats et al. 1997) that to make studies on non-geniculate coralline algae useful in the long term, we have to describe as many species characters in sufficient detail so that future researchers will be able to assess species without having to resort to an analysis of type specimens. It is for this very reason that a thorough and detailed account (vegetative and reproductive) of all taxa should be provided.

It has been common practice in systematics to exclude characters in which, for example, polymorphism (continuous or overlapping characters) has been observed, i.e. phylogenetic inferences based on morphological data have often included only discrete characters and character states (Baum 1988; Chappill 1989; Thiele 1993; Wiens 1995). It has been argued that the basis for exclusion of polymorphic characters is because they are less reliable in phylogenetic analyses (e.g. Farris 1966; Klugh & Farris 1969; Pimentel & Riggins 1987; Cranston & Humphries 1988). While some researchers (e.g. Chappill 1989; Wiens, 1995) support the traditional view that polymorphic characters are less reliable in inferring phylogeny, their research did not support their exclusion. Yet others (e.g. Thiele 1993; David & Laurin 1996) have gone on to show that an analysis of polymorphic characters can reflect the phylogeny almost as accurately as more conventional discrete morphological data, arguing that inclusion of polymorphic characters provide total evidence that can only strengthen the systematic analysis.

The generic delimitation within the Mastophoroideae has been well established (Kylin 1956; Woelkerling 1980; Johansen 1981; Chamberlain 1983; Woelkerling 1985, 1987, 1988, 1996a, b; Woelkerling & Ducker 1987; Penrose 1991, 1992; Penrose & Woelkerling 1991, 1992; Chamberlain 1994; Yoshida 1998) and it is only at the species level that much resolution still remains. Based on the development of the sporangial conceptacle roof, *Hydrolithon* and *Porolithon* are considered to be congeneric (Penrose & Woelkerling 1992) and since *Hydrolithon* was described first, *Porolithon* is now considered to be a heterotypic synonym for *Hydrolithon*. In their 1992 reappraisal however, *P. onkodes*, the type species of the former Porolithon, was the only species examined which was formally transferred to *Hydrolithon*. Only a few of the remaining taxa ascribed to *Porolithon* have received varying degrees of taxonomic review in light of these changes; the majority have undergone none. Some have even been transferred without any study e.g. *H. craspedium* (Silva et al. 1996). Yet other, more modern publications (e.g. Littler and Littler 2003), have not even considered the synonymy of *Porolithon* to *Hydrolithon*.

Most of the research investigating the use of polymorphic characters, as well as those objecting to their use, has focused on producing cladograms to reflect phylogenies. The present study is not attempting any such phylogenetic inference in the use of the polymorphic characters, but simply using them as a tool to produce phenotypic trees (phenograms). In other words, the use of the polymorphic characters is solely to determine the associations between taxa already known to be, or suspected of being closely related. The purpose of the present research is therefore to show close affinities and probable synonymies of many of the selected taxa ascribed to the genera *Porolithon* (defunct) and *Hydrolithon* based on both discrete and continuous characters.

MATERIALS AND METHODS

A phenetic character analysis of the taxa ascribed to, and found to conform to the genera Hydrolithon and Porolithon (defunct) was carried out based on both qualitative and quantitative data. In this analysis, individual taxa (subfamilies, Mastophoroid genera, selected species of both Hydrolithon and Porolithon [defunct]) are regarded as the Operational Taxonomic Units (OUT's) (see Sneath & Sokal 1973). Prior to the analysis, characters and character states (attribute values of Thiele 1993) were identified (Tables 1, 3 & 5). Character states identified comprised only those found to exist within the range of taxa examined, rather than an a priori determination of all attributes (or full range of attributes) for any given character. Characters that were (a) difficult to homologize across numerous taxa because of insufficient data, or (b) impossible to discretize into character states (continuously variable quantitative characters) were eliminated. Coding of the characters and states from continuous (overlapping) measurement data follow a modification of Baum (1988); in this study, ranges were ranked by their maximum rather than minimum values and midpoint of their ranges. This was found to be justified since the coralline taxa under study most often differed with respect to their maximum values; there was simply too much overlap with minimum values and midpoint ranges. A data matrix of the codes (discretized range of characters) was then tabulated (Tables 2, 4, 6, & 7) and analysed by means of a Cluster Analyses for construction of a phenogram.

It is not uncommon for different indices to produce different results for the same data set (e.g. Baum 1988; Wiens 1995). For this reason I started using a number of different Distance (Bray Curtis, Euclidean, Mean Character Difference) and Similarity (Gower General Similarity Coefficient, Pearson Coefficient, Percent Similarity) indices to determine the best-suited analysis for the species under study. In order to determine the best-suited measure, the various indices were first tested at the coralline algal subfamily and then

Mastophoroid genera levels. As these two taxonomic levels are well discerned, they would provide a good indication of which indices would provide the most suitable outcome. Following a trial run (Figs 1 & 2), it was found that two Distance (Bray Curtis and Mean Character Difference) and one Similarity (Percent Similarity) index was found to best resolve the taxa under study. Following this, I chose the Distance (Bray Curtis) index which best matched the results obtained with the single Similarity (Percent Similarity) index and ran the species analysis through both indices. Species level phenograms were then constructed by means of a Cluster Analysis and the above two indices using the Multivariate Statistical Package of Kovack (MVSP - vs 3.1).

It should be stressed that in the Cluster Analysis all characters have equal weighting. This means that an outlying taxon, unless it differs in a large number of characters, will not necessarily be depicted as the outgroup in the resulting phenogram. For example, the genera Hydrolithon, Spongites and Pneophyllum differ only with respect to their sporangial conceptacle roof development (Chamberlain 1983, 1994; Penrose & Woelkerling 1992). A Cluster Analysis of taxa from all three genera will not necessarily distribute themselves along three lines in the tree simply because this one character will not be sufficient to separate them. For this reason, multiple trees were constructed. First, all selected taxa ascribed to the two genera under study were included. Second, a series of trees were constructed in which taxa found not to conform to the generic description of either Hydrolithon or Porolithon (results obtained from Papers 1 & 2), as well as those lacking sufficient data, were then removed to provide more clarity to the final phenograms. The final phenograms therefore will only comprise well-delimited taxa for which a full or largely full set of codes was obtained.

RESULTS

The Bray Curtis (Distance) and Percent Similarity (Similarity) indices have consistently shown to provide the most accurate rendering of our present understanding of the coralline algal subfamilies and Mastophoroid genera (Figs 1 & 2). Based on these two indices, it is now possible to obtain phenetic trees for the selected taxa ascribed to the genera Hydrolithon and Porolithon (defunct). While there is an immediate resolution when all taxa are collectively analysed (Figs 3 & 6), the affinities and synonymies are more apparent when we exclude taxa found not to conform to the generic descriptions of Hydrolithon and Porolithon (defunct), as well as those taxa lacking a complete set of codes because of insufficient data (Figs 4 & 7). Ultimately, when we analyze only real taxa (i.e. exclude all conspecific taxa – see Figs 5 & 8) we are able to make an informed assessment as to which characters are important in grouping taxa within Hydrolithon.

Porolithon Foslie (defunct)

Based on percentage similarity, the following taxa are clearly synonymous: Porolithon castellum with Hydrolithon craspedium (100%); P. pachydermum (100%) and Porolithon cocosicum (99%) with H. onkodes; P. sandvicense with P. antillarum (99%); P. coarctatum with H. gardiner (98%); and the P. sandvicense / P. antillarum entity with H. onkodes (96%) (Figs 3 & 4); the latter taxon in each of the above combinations possessing nomenclatural priority (see Paper 1). The data also show a close affinity between Spongites africanum and P. oligocarpum (90%) (Fig. 3). Both taxa conform well to the generic description of the genus Spongites (see Paper 1) so it is not surprising that they cluster together. There is a similarly close affinity between P. aequinoctiale and P. praetextatum (90%). There aren't enough characters for these taxa to adequately determine their position within the phenogram (Table 6, Fig. 3), so they are displayed as outliers in the phenogram. When we remove those taxa that do not conform to the generic description of Porolithon (defunct) as well as those for which we do not have enough characters to code, we find two distinct groupings (Fig. 4). When the data is further filtered, by removing all conspecific taxa, the two sub-groups are more apparent (Fig. 5). The two groups clearly separate out along what I have considered to be two subgenera (Table 6; see also Paper 1), differing in 1) the number of epithallial cell layers, 2) their trichocyte arrangements, and 3) the primary thallus construction.

Hydrolithon Foslie

The following taxa are clearly synonymous: Neogoniolithon rufum with H. rupestris (99%); N. caribaeum with N. erosum (96%); H. murakoshii with H. munitum (94%), and H. samoënse (93%) and N. rugulosum (91%) with N. erosum (Figs 6 & 7); the latter taxon in each of the above combinations possessing nomenclatural priority (see Paper 2). There is a close affinity between H. craspedium and H. gardiner (94%) and these two taxa with H. onkodes (92%). These three taxa are, however, well delimited (see Penrose & Woelkerling 1992; Verheij & Prud'homme van Reine 1993; Silva et al. 1996). The reason for their close affinity is because they are alike in most characters examined (see Tables 6 & 7) except for their general physiognomy and only minor differences in their sporangial conceptacle roof anatomy (see Papers 1 & 2).

There is similarly also a very close affinity between H. boergesenii and H. munitum (& H. murakoshii) (91.5%) (Fig. 7). This affinity was suggested by Walter Adey (pers. comm.). Hydrolithon boergesenii, however, possesses a dimerous thallus construction while H. munitum (& H. murakoshii) possesses a monomerous thallus construction. These two thallus constructions are based on completely different developmental strategies and while primarily dimerous plants may become secondarily monomerous with age, particularly when overgrowing other crusts or during wound repair (Cabioch 1972; Chamberlain & Norris

1994), these appear to be stable characters in germinating spores and young thalli (see Woelkerling & Irvine 1988; Irvine et al. 1994). With this said, it may be premature to suggest that H. boergesenii and H. munitum are conspecific.

Like the genus Porolithon (defunct) (Figs 4 & 5) there are also two groupings (Figs 7 & 8) but these two groups separate out along somewhat different character combinations than in Porolithon. It should be remembered though that not only are there far more real taxa in Hydrolithon, but compared with taxa ascribed to Porolithon, there are far more character differences (see Tables 6 & 7) between the individual taxa. Ultimately, when we analyze only real taxa (i.e. exclude all conspecific taxa), we are able to recognize two broad groupings (Fig. 8 – A & B), one of which can be further subdivided (B1 & B2). At the sub-genus level, the thickness (number of cells) of the sporangial conceptacle roof appears to be of primary importance (A & B). The two sub-groups comprising group B can be separated by 1) their trichocyte arrangement and 2) their number of epithallial cell layers (see also Table 7).

DISCUSSION

According to Chamberlain (1991) it was a widely accepted practice to describe taxa largely or even solely on differences in growth forms. Mikael Foslie, for example, described a large number of taxa in this manner, quite often using only selective morphological and/or vegetative features to delineate taxa (see Woelkerling 1984, 1993). With many researchers following suit (eg. Marie Lemoine) this lead to a substantial increase in the number of described taxa, many of which were poorly delimited (Woelkerling 1984; Chamberlain 1991). Today this problem is being confounded by the fact that many of the characters used to delimit genera are not reliable (see Woelkerling 1985; Penrose & Woelkerling 1988).

It was only recently that the generic delimitation of Hydrolithon was resolved (Penrose 1991, 1992; Penrose & Woelkerling 1991, 1992; Penrose & Chamberlain 1993). The primary character used to delimit Hydrolithon from other Mastophoroid genera concerns those cells lining the base of the tetrasporangial pore canal. In Hydrolithon, the pore canals of the tetrasporangial conceptacles are lined by a ring of conspicuous, enlarged cells that arise from filaments interspersed among the sporangial initials. These cells do not protrude into the pore canal and are oriented more-or-less perpendicularly to the roof surface. Based on these findings, Porolithon was rightly subsumed in Hydrolithon, the latter having nomenclatural priority (Penrose & Woelkerling 1992). A number of taxa that have been ascribed to Hydrolithon (and Porolithon) have been shown to possess characteristics from the closely related genera, Spongites and Pneophyllum (see Papers 1 & 2). Still other taxa ascribed to the genus Neogoniolithon have been recorded which indeed possess the characters that delimit the genus Hydrolithon and these too have been described (see Papers 1 & 2).

From the phenograms above it is evident that a number of taxa are conspecific, the results of the Cluster Analysis supporting the findings from both Papers 1 and 2. It is also clear that Hydrolithon is comprised of at least two (or possibly three) sub-groups. At the sub-genus level, the thickness (number of cells) of the sporangial conceptacle roof appears to be of primary importance. This is followed by the trichocyte arrangement and number of epithallial cell layers, and to a much lesser extent, the thallus construction. It should be stressed though that the Cluster Analysis gives equal weighting to all characters and therefore the relative importance of the above characters may not be clearly expressed. These characters, however, are not presently seen as fundamentally important mostly because their earlier use as diagnostic characters have been at higher taxonomic levels (genus and above) where they have been shown to be inconsistent.

It was reported that Hydrolithon (as Porolithon, see Adey 1970), for example, is characterised by among other features, the existence of horizontal fields of pustulate trichocytes that are not separated by normal cortical cells. Penrose & Woelkerling (1988), however, reported a number of southern Australian taxa, belonging to the genus Spongites, possessing trichocyte fields in horizontal fields and so too have Keats et al. (1997) shown them to occur in Pneophyllum conicum. A number of earlier reports (see Lemoine 1917; Cabioch 1972) had already highlighted the variability in trichocyte arrangements in taxa ascribed to the defunct genus Porolithon. Similarly, differences in thallus construction (dimerous vs. monomerous) have not been viewed as fundamentally important since currently most subfamilies and many genera (and only a few species – see e.g. Cabioch 1972; Chamberlain & Norris 1994) contain examples of both types (Irvine et al. 1994). Dimerous and monomerous thalli constructions are, however, based on completely different developmental strategies and while primarily dimerous plants may become secondarily monomerous with age, particularly when overgrowing other crusts or during wound repair (Cabioch 1972; Chamberlain & Norris 1994), these appear to be stable characters in germinating spores and young thalli (see Woelkerling & Irvine 1988; Irvine et al. 1994). It should be pointed out that only a few studies have examined spore germination and development in young thalli (e.g. Chamberlain 1983, 1984; Chamberlain & Norris 1994), the larger percentage of studies characterizing taxa based on mature material where clearly developmental strategies would not be obvious. Until such time that perhaps DNA analysis can resolve the question around dimerous vs. monomerous thallus constructions, we may never resolve the importance of this particular character. The current research supports the view that trichocyte arrangement (Penrose & Woelkerling 1988) and thallus construction (Woelkerling & Irvine 1988; Irvine et al. 1994) are not diagnostic characters at the level of genus but argues that they may still, however, be useful for distinguishing species and even sub-genera. The data clearly support this idea and suggests that like trichocyte arrangement and thallus construction, the sporangial conceptacle roof thickness (number of cells) and the number of epithallial cell layers may also be useful for distinguishing species and sub-genera.

In conclusion, it is evident that a number of taxa are conspecific. It is not surprising as Chamberlain (1991) had already noted that recent studies would show a considerable reduction in the number of taxa described. This certainly has become true for the genus Hydrolithon Foslie.

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Table 1. The characters and character states used in the construction of the data matrix for Cluster Analysis at the Subfamily level.

	Characters	**Character states**		
		1	**2**	**3**
1	Genicula occurance	present	absent	
2	Genicula cortication	present	absent	both
3	Genicula core	1 tier of cells	1 to several tiers of cells	untiered and several long cells
4	Genicula lateral brances	present	absent	
5	Secondary pit connections	predominant	absent or rare	
6	Cell fusions	predominant	absent or rare	
7	Sporangia borne in	conceptacles	sori	
8	Sporangia produce apical plugs	yes	no	
9	Sporangial conceptacle/sori roof poration	uniporate	multiporate	

Table 2. Data matrix for Cluster Analysis at the Subfamily level.

Characters	*Amphiroideae*	*Austrolithoideae*	*Choreonematoideae*	*Corallinoideae*	*Lithophylloideae*	*Mastophoroideae*	*Melobesioideae*	*Metagoniolithoideae*	*Sporolithoideae*
1	1	2	2	1	2	2	2	1	2
2	3			2				1	
3	2			1				3	
4	2			2				1	
5	1	2	2	2	1	2	2	2	2
6	2	2	2	1	2	1	1	1	1
7	1	1	1	1	1	1	1	1	2
8	2	1	1	2	2	2	1	2	2
9	1	2	1	1	1	1	2	1	1

Information obtained from Womersley (1996) and Woelkerling (1988).

Table 3. The characters and character states used in the construction of the data matrix for Cluster Analysis at the genus level.

	Characters	Character states			
		1	2	3	4
1	Habit endophytic	yes	no	both	
2	Haustoria	present	absent		
3	Growth form	encrusting	aborescent	neither	
4	Secondary pit connections	absent or rare	common		
5	cell fusion	absent or rare	common		
6	Thallus construction	monomerous	dimerous	both	diffuse
7	Basal layer comprised of predominantly palisade cells	yes	no		
8	Thickness of individual crusts (no. of cells)	≤ 5	> 5	variable	
9	Sporangial concept. basal pore canal cell shape	pappilate	enlarged	both	
10	Sporangial concept. pore canal cell projection	into pore	not into pore		
11	Sporangial concept. pore canal cell orientation	parallel to roof	perpendicular to roof		
12	Sporangial concept. roof development	peripheral	from filaments interspersed	both	
13	Sporangial concept. sporangia distribution	peripheral	across	both	
14	Sporangial concept. columella (present/absent)	present	absent	both	
15	Spermatangial type	simple	not simple		
16	Distribution of spermatangia	floor only	floor, walls and roof		
17	Distribution of gonimoblast filaments	periperal	across		

Table 4. Data matrix for Cluster Analysis at the genus level (Mastophoroideae).

Characters	*Hydrolithon*	*Lesueuria*	*Lithoporella*	*Mastophora*	*Metamastophora*	*Neogoniolithon*	*Spongites*	*Pneophyllum*
1	2	1	2	2	2	2	2	2
2	2	1	2	2	2	2	2	2
3	1	3	1	1	2	1	1	1
4	1	1	1	1	1	1	1	1
5	2	2	2	2	2	2	2	2
6	3	4	2	2	2	1	3	3
7	2	2	1	1	1	2	2	2
8	2	3	1	1	2	2	2	2
9	2	1	2	1	1	1	1	1
10	2	1	2	1	1	1	1	1
11	2	1	2	1	1	1	1	1
12	2	1	2	1	1	1	1	3
13	3	1	2	1	1	3	3	3
14	3	1	2	1	1	3	3	3
15	1	1	1	1	1	1	1	1
16	1	1	1	1	1	2	1	1
17	1	1	1	1	1	2	1	1

Information obtained from Kylin (1956), Woelkerling (1980), Johansen (1981), Chamberlain (1983, 1994), Woelkerling (1985, 1987, 1988, 1996a, b), Woelkerling & Ducker (1987), Penrose (1991, 1992), Penrose & Woelkerling (1991, 1992) and Yoshida (1998).

Table 5. The characters and character states used in the construction of the data matrix for Cluster Analysis at the species level.

	Characters	**Character states**					
		1	**2**	**3**	**4**	**5**	**6**
1	General thallus form	smooth	smooth to warty or lumpy	lobed	fruticose	massive, mountain-like	
2	Protuberance diameter (mm)	absent	≤ 3	> 3			
3	Protuberance height (mm)	absent	≤ 3	> 3	> 30		
4	Thallus construction (primarily)	monomerous	dimerous				
5	Dominant contiguous vegetative filament connections	cell fusions	pit connections				
6	Number of epithallial cells (excluding cells being shed)	1	>1				
7	Trichocyte arrangement	single and/or paired	single, paired & vertical rows	single & small horizontal groups and/or single & vertical rows	horizontal fields		
8	Trichocytes in pustulate fields	yes	no				
9	Trichocytes seperated by normal cortical cells	yes	no	both			
10	Trichocytes buried	yes	no/none seen				
11	Medulla (coaxial/plumose)	predominatly coaxial	predominatly plumose	N/A			
12	Sporangial concept. (raised/flush/sunken)	slightly raised	flush to slightly raised to slightly sunken	markedly raised			
13	Sporangial concept. diameter	≤ 200	≤ 300	≤ 550	< 700	≤ 900	> 900
14	Sporangial concept. chamber height	≤ 125	< 200	> 200			

	Characters	Character states					
		1	**2**	**3**	**4**	**5**	**6**
15	Sporangial concept. chamber diameter	< 130	< 200	< 375	≤ 500	> 500	
16	Sporangial concept. depth of floor (cells)	+4 - 0	0 - 4	≤ 12	≤ 21		
17	Sporangial concept. roof cell number	≤ 4	4-6	≤12	≤ 15		
18	Sporangial concept. basal pore canal cell shape	regular pappilate	enlarged				
19	Sporangial concept. pore canal cell projection	into pore	not into pore				
20	Sporangial concept. pore canal cell orientation	parallel to roof	perpendicular to roof				
21	Sporangial concept. roof development	peripheral	from filaments interspersed	both			
22	Sporangial conceptacles buried or shed	buried	shed/none seen	both			
23	Sporangial conceptacle sporangia distribution	peripheral	across				
24	Sporangial conceptacle columella	present	absent/none seen				

Table 6. Data matrix for Cluster Analysis for the defunct genus *Porolithon*.

Characters	*P. aequinoctiale*	*S. africanum*	*P. antillarum*	*H. boergesenii*	*P. castellum*	*P. cocosicum*	*P. coarctatum*	*H. craspedium*	*H. improcerum*	*H. gardineri*	*P. oligocarpum*
1	4	4	3	2	5	2	4	5	1	4	1
2	2	3	1	2	3	2	2	3	1	3	1
3	3	3	1	2	4	2	3	4	1	3	1
4	1	1	1	2	1	1	1	1	2	1	1
5	1	1	1	1	1	1	1	1	1	1	1
6	2	2	2	1	2	2	2	2	1	2	2
7	4	4	4	3	4	4	4	4	3	4	4
8	1	1	1	2	1	1	1	1	2	1	1
9	2	2	2	3	2	2	2	2	3	2	2
10	1	1	1	1	1	1	1	1	1	1	1
11	2	1	2	3	2	2	2	2	3	2	2
12		2	2	2	2	2	1	2	3	1	2
13		4	3	3	3	3	3	3	3	4	3
14		1	2	2	1	2	1	1	1	1	1
15		3	3	3	3	3	3	3	3	3	3
16		4	4	3	4	4	4	4	2	4	4
17		3	3	2	3	3	2	3	1	2	3
18		1	2	2	2	2	2	2	2	2	1
19		1	2	2	2	2	2	2	2	2	1
20		1	2	2	2	2	2	2	2	2	1
21		1	2	2	2	2	2	2	2	2	1
22		1	1	1	1	1	1	1	1	1	1
23		1	1		1	1	1	1	1	1	1
24		1	1	2	1	2	2	1	2	2	1

Table 6 continued(Additional Information obtained from Penrose (1996)).

Characters	*H. onkodes*	*P. marshallense*	*P. pachydermum*	*P. praetextatum*	*H. reinboldii*	*P. sandvicense*
1	2	4	2	4	2	3
2	2	3	2	2	3	1
3	2	3	2	3	3	1
4	1	1	1	1	2	1
5	1	1	1	1	1	1
6	2	2	2	2	1	2
7	4	4	4	4	1	4
8	1	1	1	1	2	1
9	2	2	2	2	1	2
10	1	1	1	1	1	1
11	2	2	2	2	3	2
12	2	2	2	2	1	2
13	3	3	3	3	5	3
14	2	2	2		2	1
15	3	2	3		4	3
16	4	4	4		3	4
17	3	2	3		2	3
18	2	2	2		2	2
19	2	2	2		2	2
20	2	2	2		2	2
21	2	2	2		2	2
22	1	1	1		1	1
23	1	1	1		2	1
24	1	1	1		2	1

Table 7. Data matrix for Cluster Analysis for the genus *Hydrolithon*.

Characters	*H. boergesenii*	*H. breviclavium*	*N. caribaeum*	*L. consociatum*	*H. craspedium*	*N. erosum*	*L. falklandicum*	*H. improcerum*	*H. gardineri*	*H. megacystum*
1	2	2	1	2	5	1	2	1	4	2
2	2	3	1	3	3	1	3	1	3	3
3	2	3	1	3	4	1	3	1	3	3
4	2	2	1	2	1	1	2	2	1	2
5	1	1	1	1	1	1	1	1	1	1
6	1	1	1	2	2	1	2	1	2	1
7	3	3	1	1	4	1	1	3	4	1
8	2	2	2	2	1	2	2	2	1	2
9	3	3	1	1	2	1	1	3	2	1
10	1	1	2	2	1	2	2	1	1	
11	3	3	2	3	2	2	3	3	2	3
12	2	3	2	2	2	2		3	1	1
13	3	6	1	3	3	2		3	4	5
14	2	3	1	1	1	1		1	1	3
15	3	5	1	3	3	2		3	3	4
16	3	2	4	4	4	4		2	4	
17	2	4	1	3	3	1		1	2	
18	2	1	2	1	2	2		2	2	
19	2	1	2	1	2	2		2	2	
20	2	1	2	1	2	2		2	2	
21	2	1	2	3	2	2		2	2	
22	1	1	3	1	1	2		1	1	
23		1	1	1	1	1		1	1	2
24	2	1	2	1	1	2		2	2	1

Table 7 continued (Additional information obtained from Adey et al. (1982), Mendoza & Cabioch (1986) and Iryu & Matsuda (1996)).

Characters	*H. munitum*	*H. murakoshii*	*H. onkodes*	*H. reinboldii*	*N. rufum*	*N. rugulosum*	*H. rupestris*	*H. samoënse*	*L. subantarcticum*	*H. superficiale*
1	2	1	2	2	2	2	2	1	1	1
2	3	1	2	3	1	1	1	1	1	1
3	3	1	2	3	1	1	1	1	1	1
4	1	1	1	2	1	1	1	1	2	1
5	1	1	1	1	1	1	1	1	1	1
6	1	1	2	1	1	1	1	1	2	1
7	3	3	4	1	2	1	3	2	1	1
8	2	2	1	2	2	2	2	2	2	2
9	3	3	2	1	1	3	1	3	1	1
10	2	1	1	1	1	2	1	1	2	1
11	2	2	2	3	2	2	2	2	3	2
12	2	2	2	1	2	2	2	2		1
13	3	3	3	5	3	1	3	1		2
14	2	2	2	2	1	1	1	1		1
15	3	3	3	4	2	1	2	1		1
16	3	3	4	3	4	3	4	4		1
17	3	2	3	2	3	1	3	1		1
18	2	2	2	2	2	2	2	2		2
19	2	2	2	2	2	2	2	2		2
20	2	2	2	2	2	2	2	2		2
21	2	2	2	2	2	2	2	2		2
22	1	1	1	1	1	1	1	3		2
23	1	1	1	2	2	2	2	1		2
24	1	1	1	2	2	2	2	2		2

FIGURE CAPTIONS

Figure 1. The phenotypic trees obtained when analyzing the coralline algal subfamilies using the six different Distance and Similarity indices.

Figure 2. The phenotypic trees obtained when analyzing the coralline algal Mastophoroid genera using the six different Distance and Similarity indices.

Figure 3. The phenotypic trees obtained using the Bray Curtis (Distance) and Percent Similarity (Similarity) indices for all the selected taxa ascribed to the genus Porolithon (defunct).

Figure 4. The phenotypic trees obtained using the Bray Curtis (Distance) and Percent Similarity (Similarity) indices for the selected taxa ascribed to the genus Porolithon (defunct). Taxa analysed are only those that conform to the generic description of Porolithon (defunct) as well as those taxa for which a complete set of codes was obtained. Two distinct groups (1 & 2) emerge separated by their number of epithallial cell layers, their trichocyte arrangements, and their primary thallus construction.

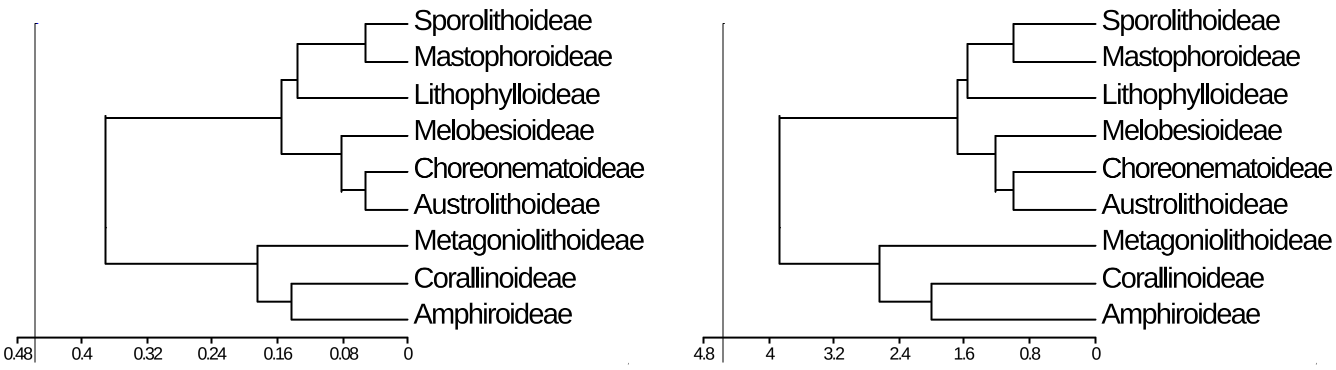
Figure 5. The phenotypic trees obtained using the Bray Curtis (Distance) and Percent Similarity (Similarity) indices for all real taxa ascribed to the defunct genus Porolithon. The two distinct groups (1 & 2) that emerge are more evident once conspecific taxa are excluded.

Figure 6. The phenotypic trees obtained using the Bray Curtis (Distance) and Percent Similarity (Similarity) indices when analyzing all the selected taxa ascribed to the genus Hydrolithon.

Figure 7. The phenotypic trees obtained using the Bray Curtis (Distance) and Percent Similarity (Similarity) indices for the selected taxa ascribed to the genus

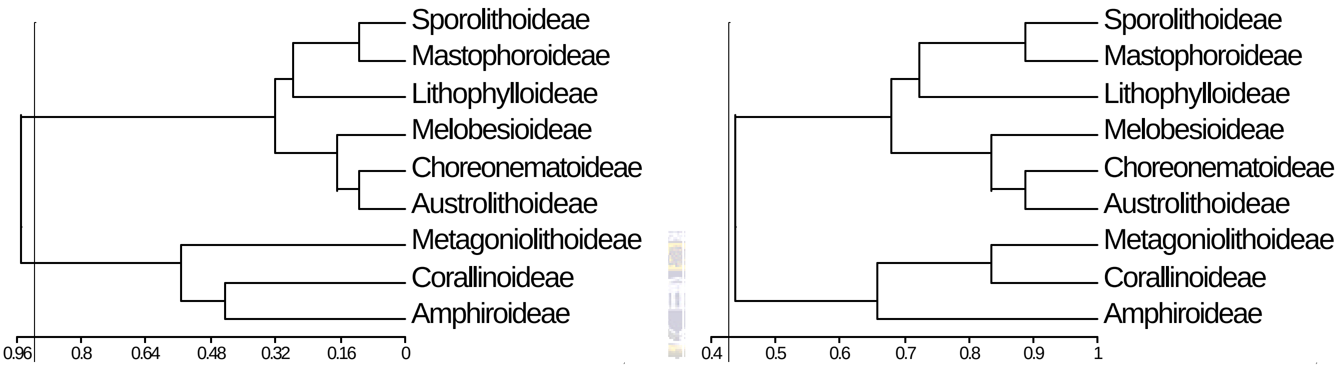
Hydrolithon. Taxa analysed are only those that conform to the generic description of Hydrolithon as well as those taxa for which a complete set of codes was obtained. Two distinct groups (A & B) emerge separated by the number of cell layers in their sporangial conceptacle roofs. Probable synonymies are labeled 1-3.

Figure 8. The phenotypic trees obtained using the Bray Curtis (Distance) and Percent Similarity (Similarity) indices for all real taxa found to conform to Hydrolithon. The distinct groups that emerge are more evident once conspecific taxa are excluded. Groups A and B are separated by the number of cells in their sporangial conceptacle roofs. Sub-groups B1 and B2 are separated by their trichocyte arrangements and number of epithallial cell layers.



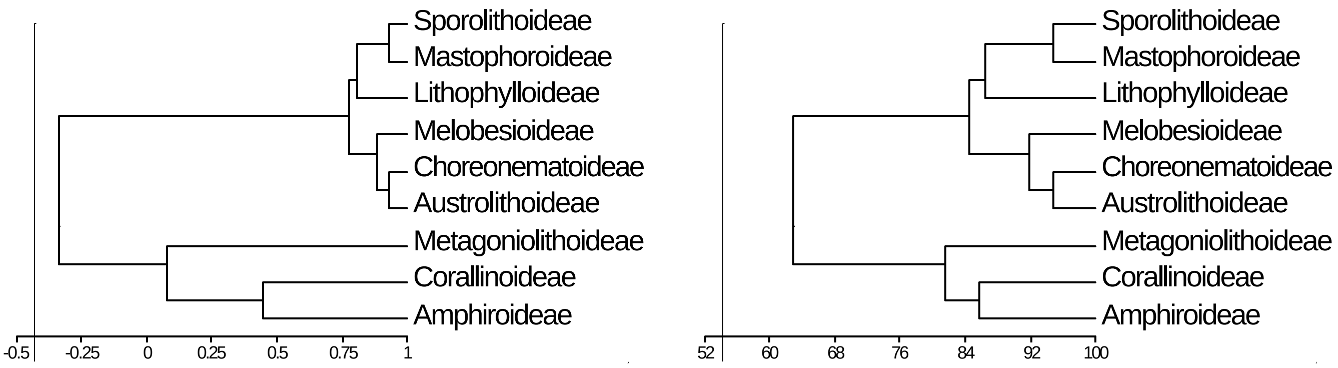
Bray Curtis

Euclidean



Mean Character Difference

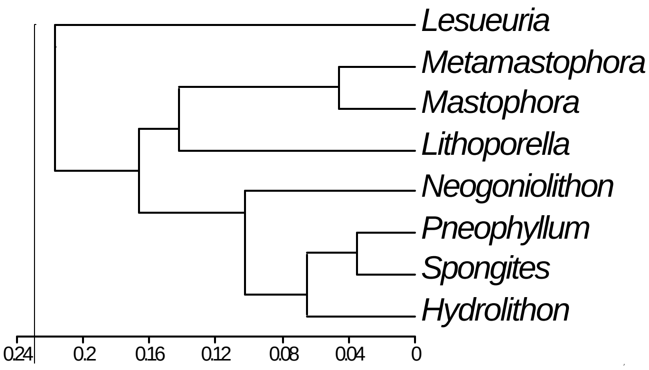
Gower General Similarity Coefficient



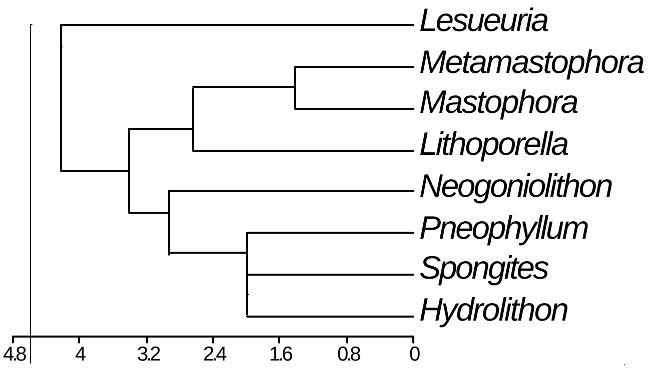
Pearson Coefficient

Percent Similarity

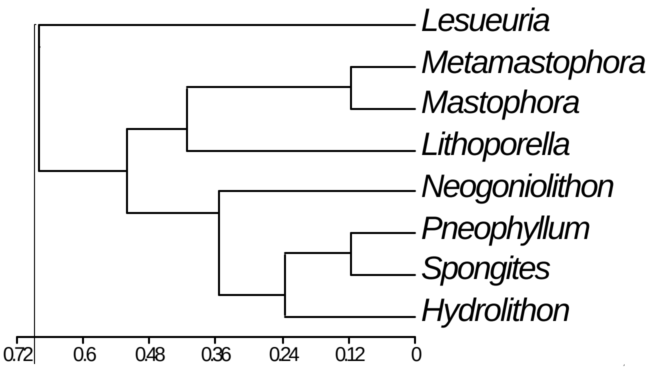
Figure 1.



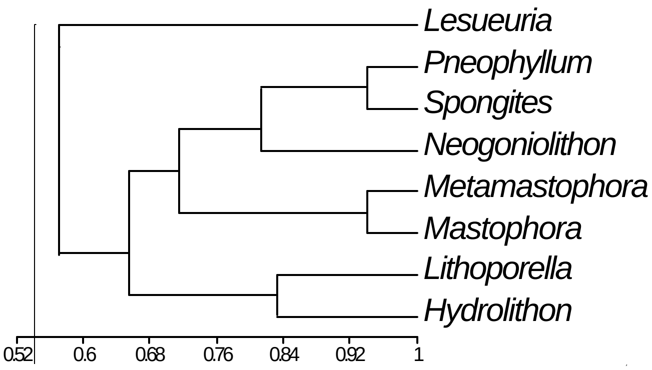
Bray Curtis



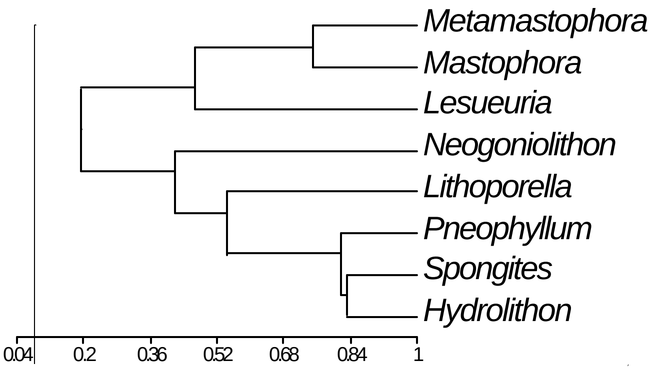
Euclidean



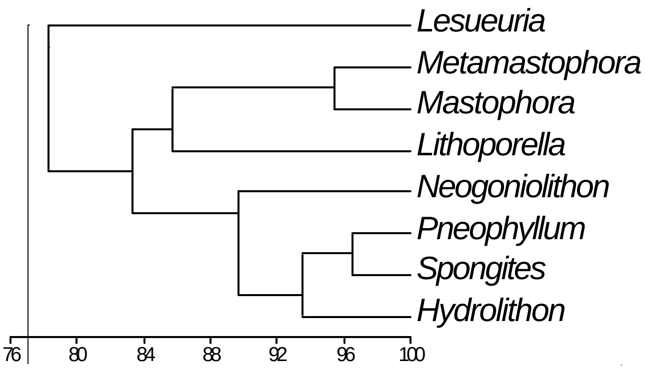
Mean Character Difference



Gower General Similarity Coefficient



Pearson Coefficient



Percent Similarity

Figure 2.

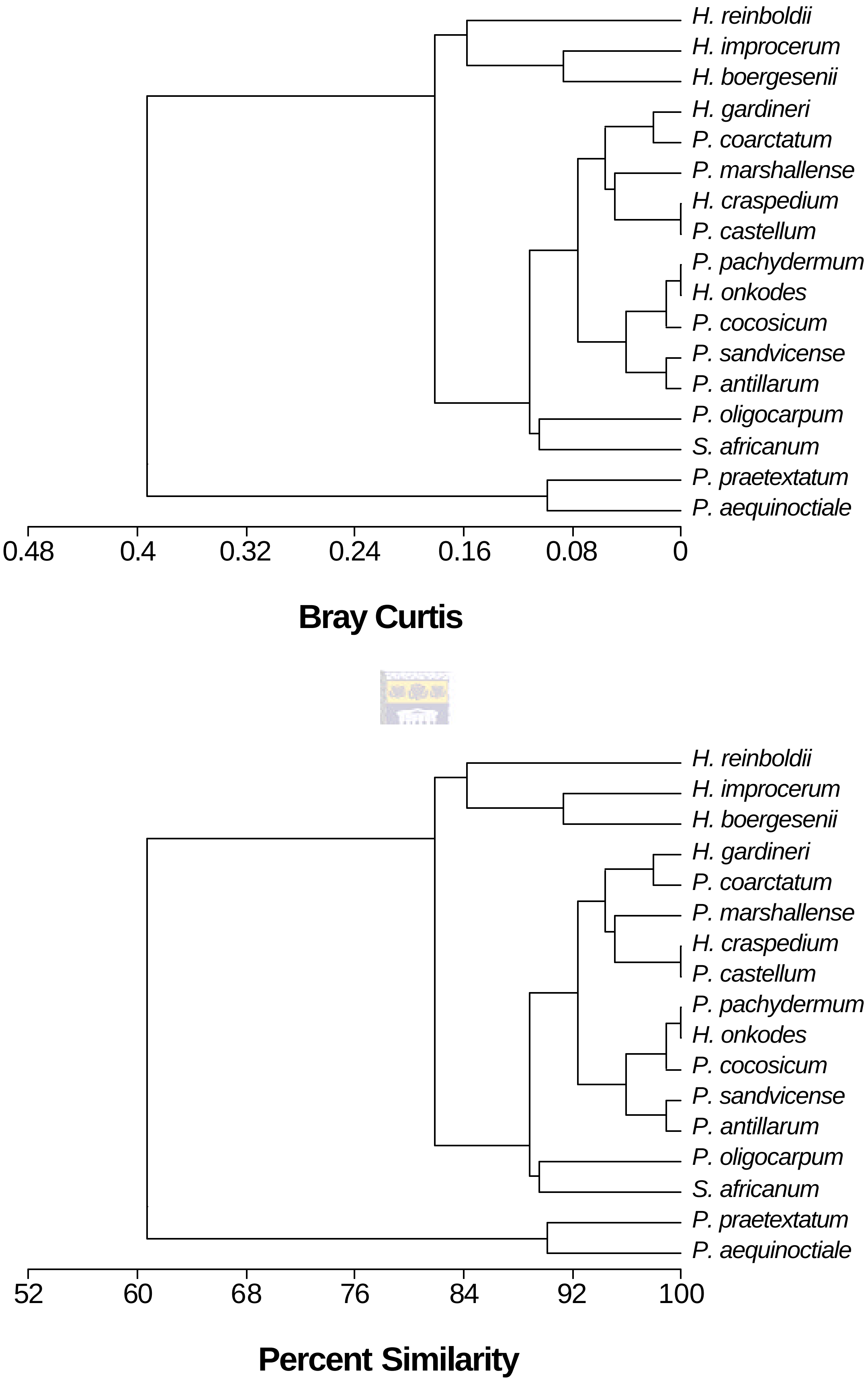
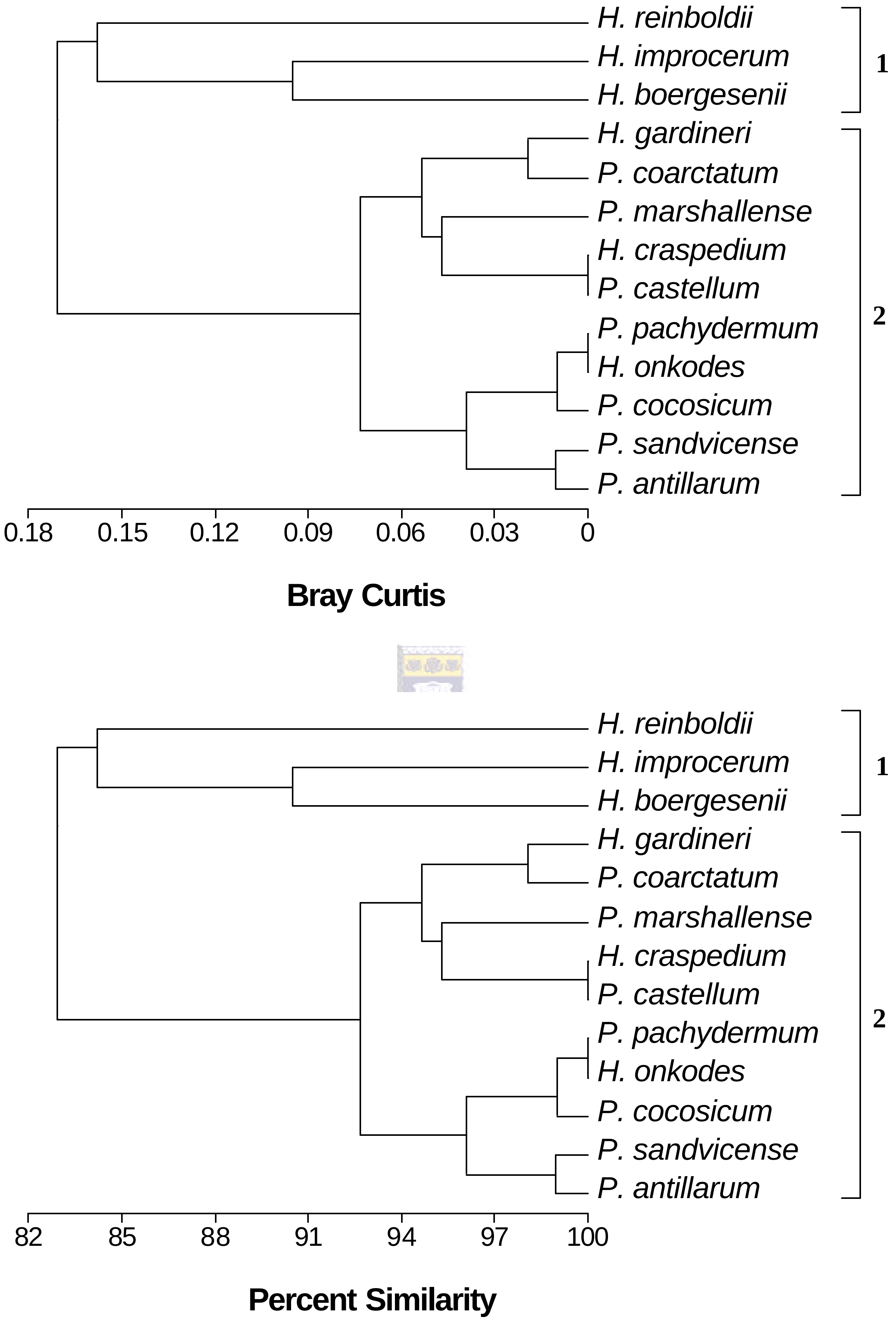

H. reinboldii
H. improcerum
H. boergesenii
H. gardineri
P. coarctatum
P. marshallense
H. craspedium
P. castellum
P. pachydermum
H. onkodes
P. cocosicum
P. sandvicense
P. antillarum
P. oligocarpum
S. africanum
P. praetextatum
P. aequinoctiale
0.48
0.4
0.32
0.24
0.16
0.08
0
Bray Curtis
H. reinboldii
H. improcerum
H. boergesenii
H. gardineri
P. coarctatum
P. marshallense
H. craspedium
P. castellum
P. pachydermum
H. onkodes
P. cocosicum
P. sandvicense
P. antillarum
P. oligocarpum
S. africanum
P. praetextatum
P. aequinoctiale
52
60
68
76
84
92
100
Percent Similarity

Figure 3.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H. improcerum
H. boergesenii
H. gardineri
P. coarctatum
P. marshallense
H. craspedium
P. castellum
P. pachydermum
H. onkodes
P. cocosicum
P. sandvicense
P. antillarum
1
2
0.18
0.15
0.12
0.09
0.06
0.03
0
Bray Curtis
H. reinboldii
H. improcerum
H. boergesenii
H. gardineri
P. coarctatum
P. marshallense
H. craspedium
P. castellum
P. pachydermum
H. onkodes
P. cocosicum
P. sandvicense
P. antillarum
1
2
82
85
88
91
94
97
100
Percent Similarity

Figure 4.

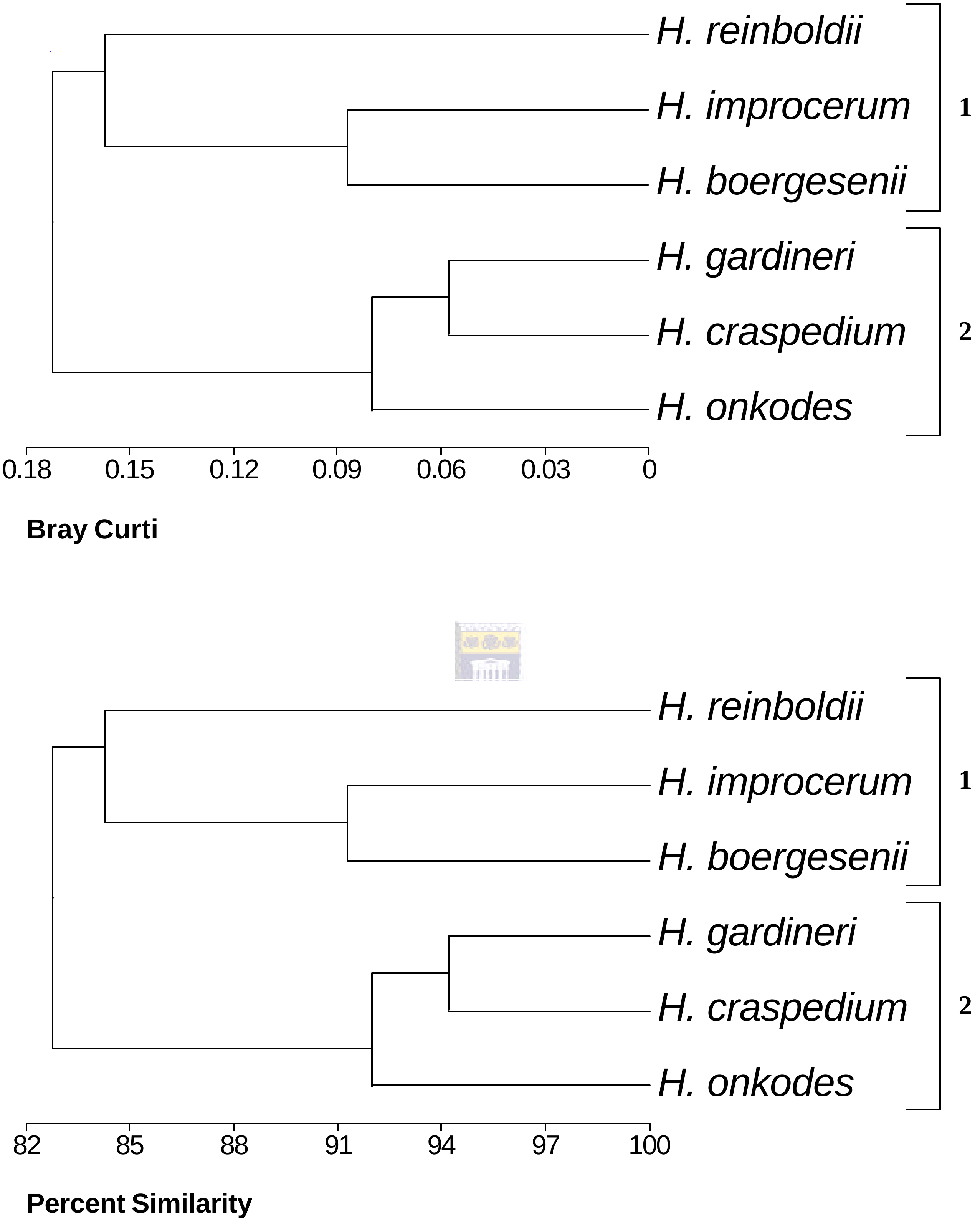
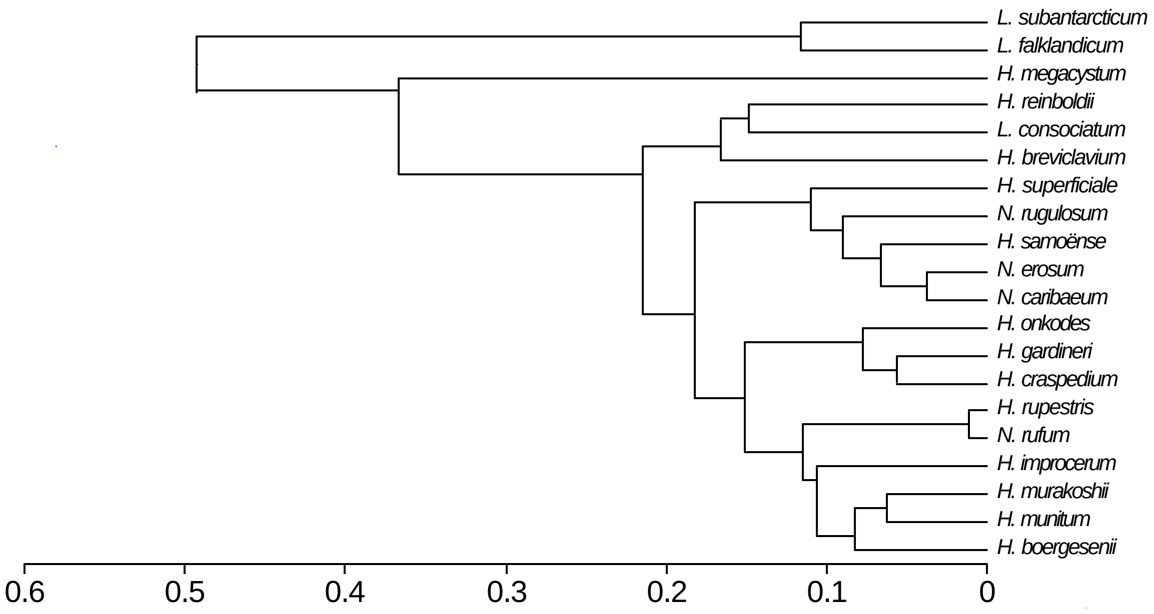
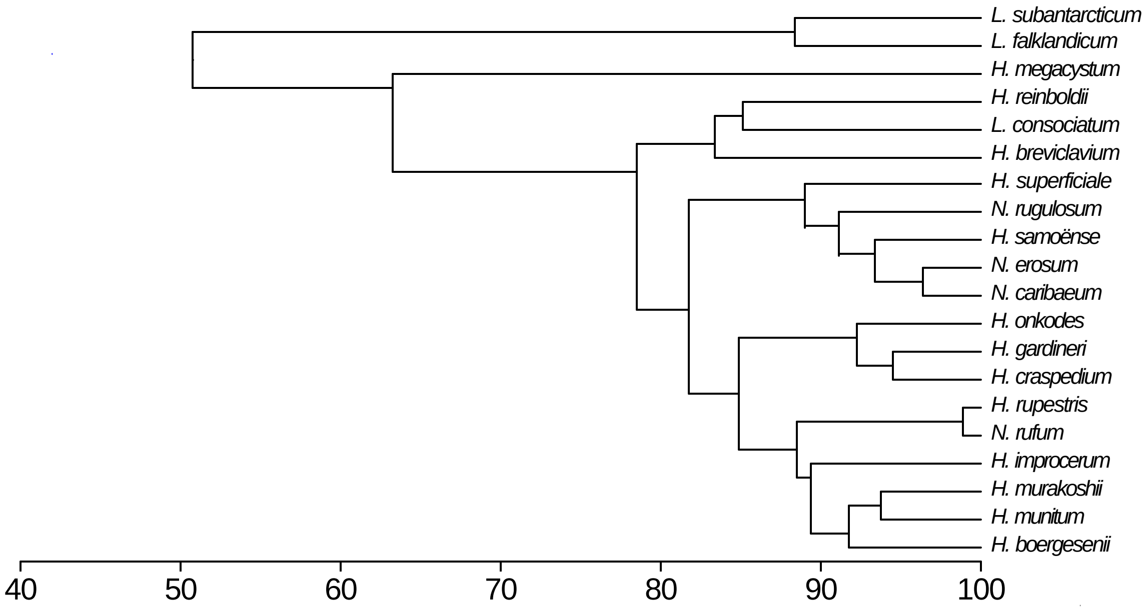

H. reinboldii
H. improcerum
H. boergesenii
H. gardineri
H. craspedium
H. onkodes
1
2
0.18
0.15
0.12
0.09
0.06
0.03
0
Bray Curti
H. reinboldii
H. improcerum
H. boergesenii
H. gardineri
H. craspedium
H. onkodes
1
2
82
85
88
91
94
97
100
Percent Similarity

Figure 5.

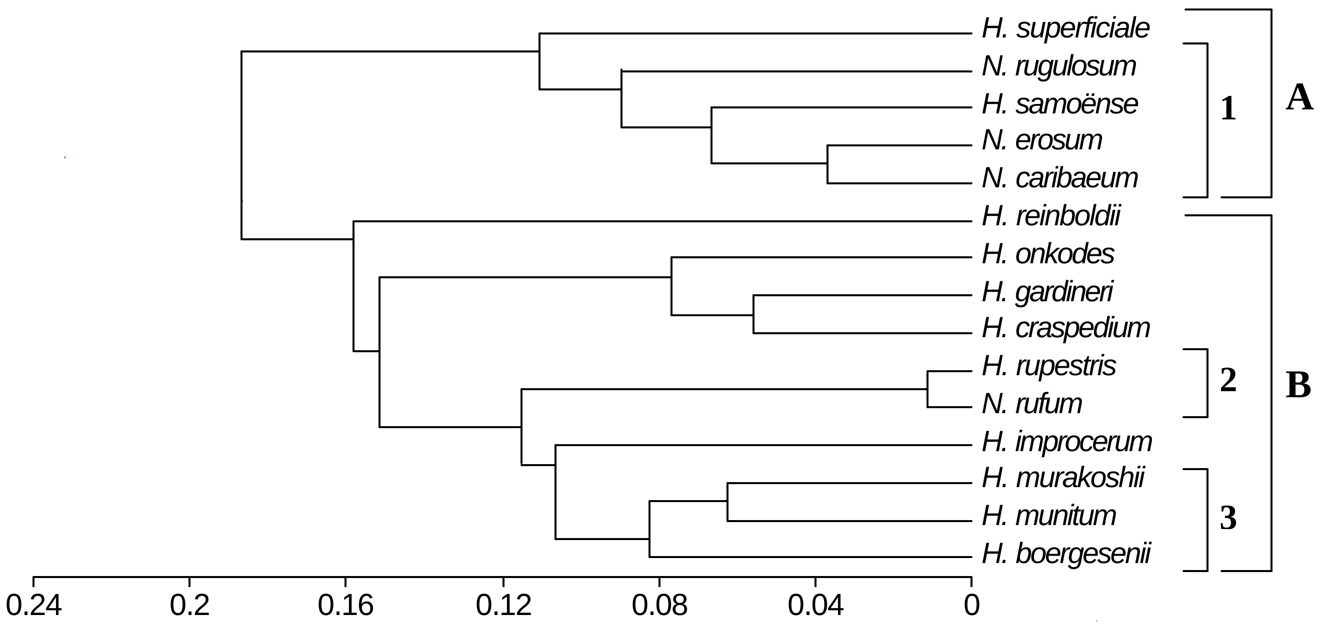


Bray Curtis

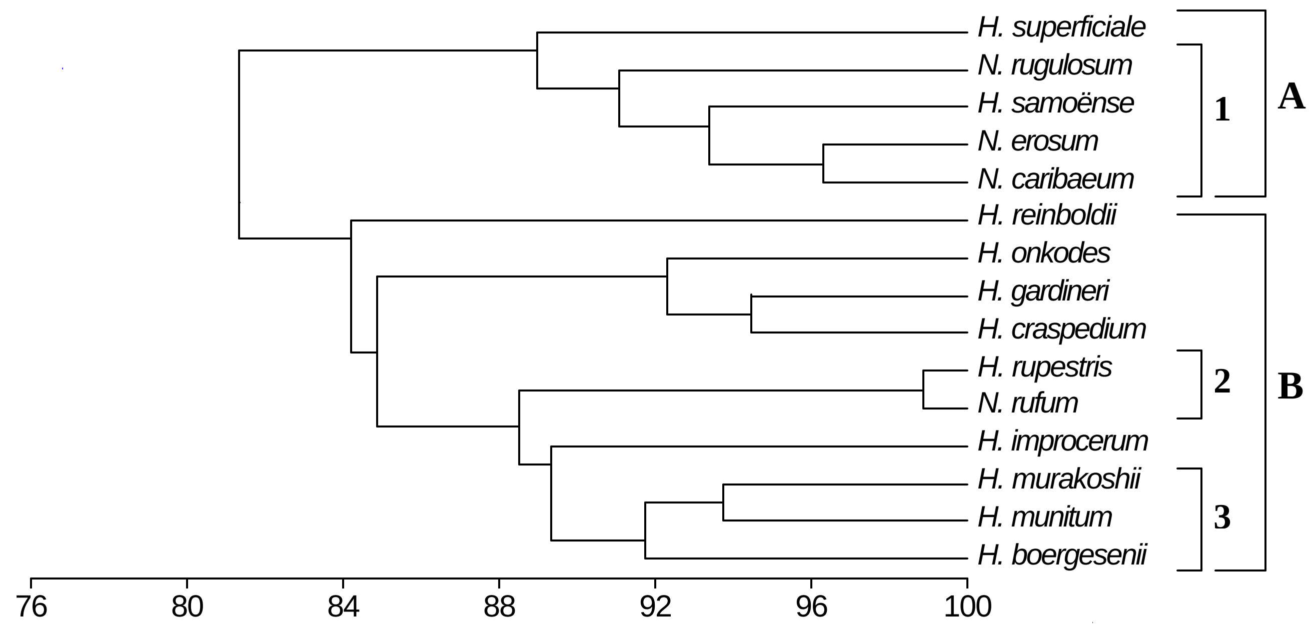


Percent Similarity

Figure 6.



Bray Curtis



Percent Similarity

Figure 7.

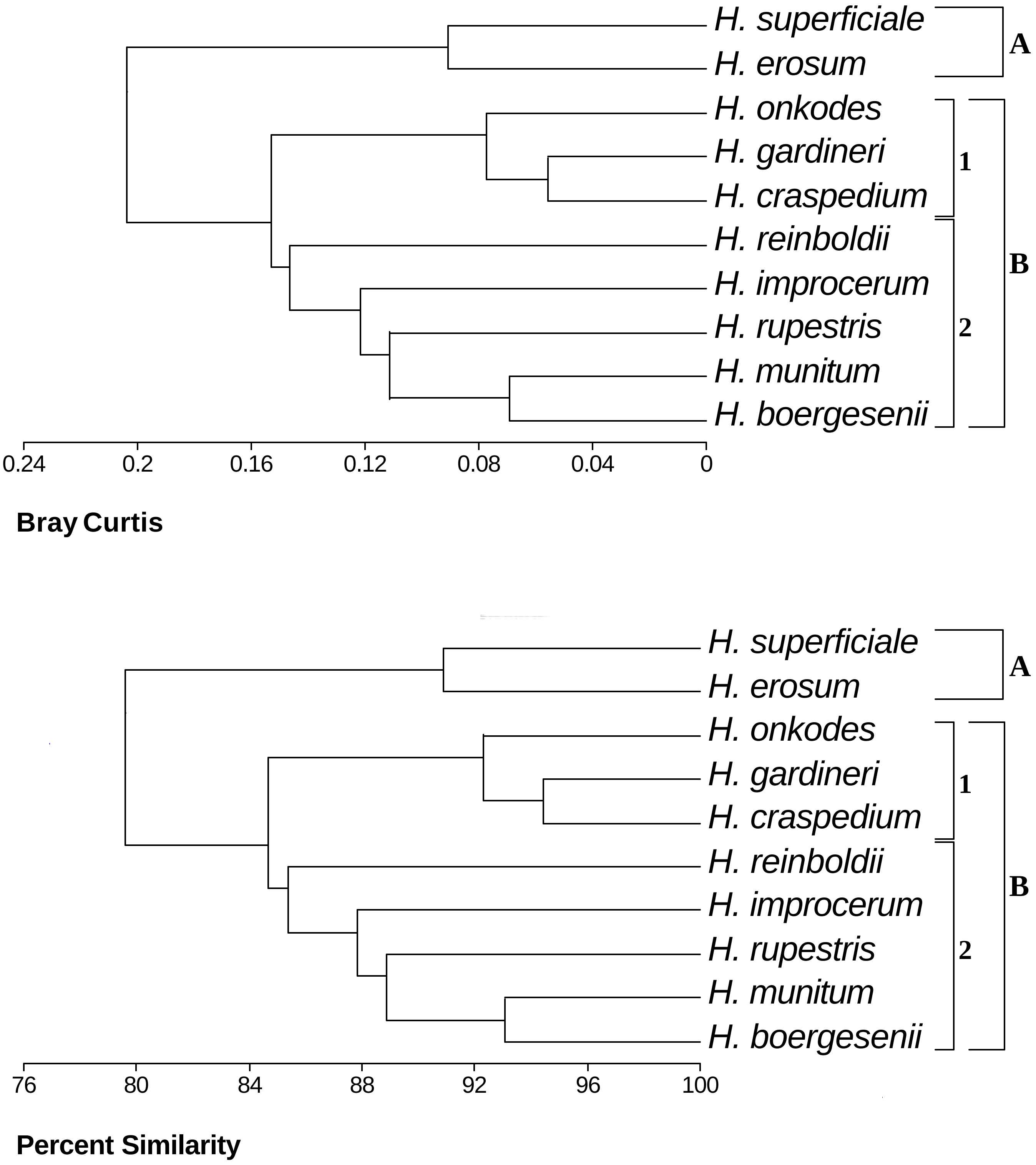

H. superficiale
H. erosum
H. onkodes
H. gardineri
H. craspedium
H. reinboldii
H. improcerum
H. rupestris
H. munitum
H. boergesenii
A
1
B
2
0.24
0.2
0.16
0.12
0.08
0.04
0
Bray Curtis
H. superficiale
H. erosum
H. onkodes
H. gardineri
H. craspedium
H. reinboldii
H. improcerum
H. rupestris
H. munitum
H. boergesenii
A
1
B
2
76
80
84
88
92
96
100
Percent Similarity

Figure 8.

APPENDICES

Appendix 1.1. Subfamilies – Bray Curtis, Distance matrix

	Amphiroideae	**Austrolithoideae**	**Choreonematoideae**	**Corallinoideae**	**Lithophylloideae**	**Mastophoroideae**	**Melobesioideae**	**Metagoniolithoideae**	**Sporolithoideae**
Amphiroideae	0								
Austrolithoideae	0.44	0							
Choreonematoideae	0.417	0.053	0						
Corallinoideae	0.143	0.391	0.364	0					
Lithophylloideae	0.333	0.158	0.111	0.364	0				
Mastophoroideae	0.417	0.158	0.111	0.273	0.111	0			
Melobesioideae	0.5	0.053	0.111	0.364	0.222	0.111	0		
Metagoniolithoideae	0.214	0.391	0.364	0.154	0.364	0.273	0.364	0	
Sporolithoideae	0.44	0.2	0.158	0.304	0.158	0.053	0.158	0.304	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	Austrolithoideae	Choreonematoideae	0.053	2
2	Mastophoroideae	Sporolithoideae	0.053	2
3	Node 1	Melobesioideae	0.082	3
4	Lithophylloideae	Node 2	0.135	3
5	Amphiroideae	Corallinoideae	0.143	2
6	Node 3	Node 4	0.154	6
7	Node 5	Metagoniolithoideae	0.184	3
8	Node 7	Node 6	0.37	9

Appendix 1.2. Subfamilies – Euclidean, Distance matrix

	Amphiroideae	**Austrolithoideae**	**Choreonematoideae**	**Corallinoideae**	**Lithophylloideae**	**Mastophoroideae**	**Melobesioideae**	**Metagoniolithoideae**	**Sporolithoideae**
Amphiroideae	0								
Austrolithoideae	4.583	0							
Choreonematoideae	4.472	1	0						
Corallinoideae	2	3.606	3.464	0					
Lithophylloideae	4.243	1.732	1.414	3.464	0				
Mastophoroideae	4.472	1.732	1.414	3.162	1.414	0			
Melobesioideae	4.69	1	1.414	3.464	2	1.414	0		
Metagoniolithoideae	2.828	3.873	3.742	2.449	3.742	3.464	3.742	0	
Sporolithoideae	4.583	2	1.732	3.317	1.732	1	1.732	3.606	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	Austrolithoideae	Choreonematoideae	1	2
2	Mastophoroideae	Sporolithoideae	1	2
3	Node 1	Melobesioideae	1.207	3
4	Lithophylloideae	Node 2	1.573	3
5	Node 3	Node 4	1.686	6
6	Amphiroideae	Corallinoideae	2	2
7	Node 6	Metagoniolithoideae	2.639	3
8	Node 7	Node 5	3.871	9

Appendix 1.3. Subfamilies – Mean Character Difference, Distance matrix

	Amphiroideae	**Austrolithoideae**	**Choreonematoideae**	**Corallinoideae**	**Lithophylloideae**	**Mastophoroideae**	**Melobesioideae**	**Metagoniolithoideae**	**Sporolithoideae**
Amphiroideae	0								
Austrolithoideae	1.222	0							
Choreonematoideae	1.111	0.111	0						
Corallinoideae	0.444	1	0.889	0					
Lithophylloideae	0.889	0.333	0.222	0.889	0				
Mastophoroideae	1.111	0.333	0.222	0.667	0.222	0			
Melobesioideae	1.333	0.111	0.222	0.889	0.444	0.222	0		
Metagoniolithoideae	0.667	1	0.889	0.444	0.889	0.667	0.889	0	
Sporolithoideae	1.222	0.444	0.333	0.778	0.333	0.111	0.333	0.778	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	Austrolithoideae	Choreonematoideae	0.111	2
2	Mastophoroideae	Sporolithoideae	0.111	2
3	Node 1	Melobesioideae	0.167	3
4	Lithophylloideae	Node 2	0.278	3
5	Node 3	Node 4	0.321	6
6	Amphiroideae	Corallinoideae	0.444	2
7	Node 6	Metagoniolithoideae	0.556	3
8	Node 7	Node 5	0.951	9

Appendix 1.4. Subfamilies – Gower general Similarity Coefficient, Similarity matrix

	Amphiroideae	**Austrolithoideae**	**Choreonematoideae**	**Corallinoideae**	**Lithophylloideae**	**Mastophoroideae**	**Melobesioideae**	**Metagoniolithoideae**	**Sporolithoideae**
Amphiroideae	1								
Austrolithoideae	0.259	1							
Choreonematoideae	0.37	0.889	1						
Corallinoideae	0.704	0.333	0.444	1					
Lithophylloideae	0.593	0.667	0.778	0.444	1				
Mastophoroideae	0.37	0.667	0.778	0.667	0.778	1			
Melobesioideae	0.148	0.889	0.778	0.444	0.556	0.778	1		
Metagoniolithoideae	0.611	0.352	0.463	0.833	0.463	0.685	0.463	1	
Sporolithoideae	0.259	0.556	0.667	0.556	0.667	0.889	0.667	0.574	1

Node	Group 1	Group 2	Simil.	Objects in group
1	Austrolithoideae	Choreonematoideae	0.889	2
2	Mastophoroideae	Sporolithoideae	0.889	2
3	Corallinoideae	Metagoniolithoideae	0.833	2
4	Node 1	Melobesioideae	0.833	3
5	Lithophylloideae	Node 2	0.722	3
6	Node 4	Node 5	0.679	6
7	Amphiroideae	Node 3	0.657	3
8	Node 7	Node 6	0.438	9

Appendix 1.5. Subfamilies – Pearson coefficient, Similarity matrix

	Amphiroideae	Austrolithoideae	Choreonematoideae	Corallinoideae	Lithophylloideae	Mastophoroideae	Melobesioideae	Metagoniolithoideae	Sporolithoideae
Amphiroideae	1								
Austrolithoideae	-0.699	1							
Choreonematoideae	-0.612	0.933	1						
Corallinoideae	0.447	-0.369	-0.274	1					
Lithophylloideae	-0.408	0.778	0.833	-0.274	1				
Mastophoroideae	-0.612	0.778	0.833	0	0.833	1			
Melobesioideae	-0.816	0.933	0.833	-0.274	0.667	0.833	1		
Metagoniolithoideae	0.081	-0.268	-0.199	0.073	-0.199	0	-0.199	1	
Sporolithoideae	-0.699	0.71	0.778	-0.114	0.778	0.933	0.778	-0.082	1

Node	Group 1	Group 2	Simil.	Objects in group
1	Mastophoroideae	Sporolithoideae	0.933	2
2	Austrolithoideae	Choreonematoideae	0.933	2
3	Node 2	Melobesioideae	0.883	3
4	Lithophylloideae	Node 1	0.806	3
5	Node 3	Node 4	0.776	6
6	Amphiroideae	Corallinoideae	0.447	2
7	Node 6	Metagoniolithoideae	0.077	3
8	Node 7	Node 5	-0.339	9

Appendix 1.6. Subfamilies – Percent Similarity, Similarity matrix

	Amphiroideae	Austrolithoideae	Choreonematoideae	Corallinoideae	Lithophylloideae	Mastophoroideae	Melobesioideae	Metagoniolithoideae	Sporolithoideae
Amphiroideae	100								
Austrolithoideae	56	100							
Choreonematoideae	58.333	94.737	100						
Corallinoideae	85.714	60.87	63.636	100					
Lithophylloideae	66.667	84.211	88.889	63.636	100				
Mastophoroideae	58.333	84.211	88.889	72.727	88.889	100			
Melobesioideae	50	94.737	88.889	63.636	77.778	88.889	100		
Metagoniolithoideae	78.571	60.87	63.636	84.615	63.636	72.727	63.636	100	
Sporolithoideae	56	80	84.211	69.565	84.211	94.737	84.211	69.565	100

Node	Group 1	Group 2	Simil.	Objects in group
1	Austrolithoideae	Choreonematoideae	94.737	2
2	Mastophoroideae	Sporolithoideae	94.737	2
3	Node 1	Melobesioideae	91.813	3
4	Lithophylloideae	Node 2	86.55	3
5	Amphiroideae	Corallinoideae	85.714	2
6	Node 3	Node 4	84.587	6
7	Node 5	Metagoniolithoideae	81.593	3
8	Node 7	Node 6	62.971	9

Appendix 2.1. Mastophoroid genera – Bray Curtis, Distance matrix

	Hydrolithon	***Lesueuria***	***Lithoporella***	***Mastophora***	***Metamastophora***	***Neogoniolithon***	***Spongites***	***Pneophyllum***
Hydrolithon	0							
Lesueuria	0.241	0						
Lithoporella	0.085	0.283	0					
Mastophora	0.208	0.191	0.125	0				
Metamastophora	0.2	0.143	0.16	0.045	0			
Neogoniolithon	0.133	0.259	0.2	0.184	0.176	0		
Spongites	0.067	0.185	0.164	0.143	0.137	0.071	0	
Pneophyllum	0.065	0.214	0.158	0.176	0.17	0.103	0.034	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	*Spongites*	*Pneophyllum*	0.034	2
2	*Mastophora*	*Metamastophora*	0.045	2
3	*Hydrolithon*	Node 1	0.066	3
4	Node 3	*Neogoniolithon*	0.103	4
5	*Lithoporella*	Node 2	0.143	3
6	Node 4	Node 5	0.167	7
7	Node 6	*Lesueuria*	0.217	8

Appendix 2.2. Mastophoroid genera – Euclidean, Distance matrix

	Hydrolithon	***Lesueuria***	***Lithoporella***	***Mastophora***	***Metamastophora***	***Neogoniolithon***	***Spongites***	***Pneophyllum***
Hydrolithon	0							
Lesueuria	4.472	0						
Lithoporella	2.236	4.583	0					
Mastophora	3.873	3.873	2.449	0				
Metamastophora	3.873	3	2.828	1.414	0			
Neogoniolithon	3.162	5.099	3.317	3.606	3.606	0		
Spongites	2	4	3	3.317	3.317	2.449	0	
Pneophyllum	2	4.472	3	3.873	3.873	3.162	2	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	*Mastophora*	*Metamastophora*	1.414	2
2	*Hydrolithon*	*Spongites*	2	2
3	Node 2	*Pneophyllum*	2	3
4	*Lithoporella*	Node 1	2.639	3
5	Node 3	*Neogoniolithon*	2.925	4
6	Node 5	Node 4	3.407	7
7	Node 6	*Lesueuria*	4.214	8

Appendix 2.3. Mastophoroid genera – Mean Character Difference, Distance matrix

	Hydrolithon	***Lesueuria***	***Lithoporella***	***Mastophora***	***Metamastophora***	***Neogoniolithon***	***Spongites***	***Pneophyllum***
Hydrolithon	0							
Lesueuria	0.824	0						
Lithoporella	0.294	0.882	0					
Mastophora	0.647	0.529	0.353	0				
Metamastophora	0.647	0.412	0.471	0.118	0			
Neogoniolithon	0.471	0.824	0.647	0.529	0.529	0		
Spongites	0.235	0.588	0.529	0.412	0.412	0.235	0	
Pneophyllum	0.235	0.706	0.529	0.529	0.529	0.353	0.118	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	*Mastophora*	*Metamastophora*	0.118	2
2	*Spongites*	*Pneophyllum*	0.118	2
3	*Hydrolithon*	Node 2	0.235	3
4	Node 3	*Neogoniolithon*	0.353	4
5	*Lithoporella*	Node 1	0.412	3
6	Node 4	Node 5	0.52	7
7	Node 6	*Lesueuria*	0.681	8

Appendix 2.4. Mastophoroid genera – Gower general Similarity Coefficient, Similarity matrix

	Hydrolithon	***Lesueuria***	***Lithoporella***	***Mastophora***	***Metamastophora***	***Neogoniolithon***	***Spongites***	***Pneophyllum***
Hydrolithon	1							
Lesueuria	0.451	1						
Lithoporella	0.833	0.402	1					
Mastophora	0.569	0.667	0.735	1				
Metamastophora	0.569	0.725	0.676	0.941	1			
Neogoniolithon	0.637	0.5	0.51	0.657	0.657	1		
Spongites	0.794	0.657	0.627	0.775	0.775	0.843	1	
Pneophyllum	0.794	0.598	0.627	0.716	0.716	0.784	0.941	1

Node	Group 1	Group 2	Simil.	Objects in group
1	*Mastophora*	*Metamastophora*	0.941	2
2	*Spongites*	*Pneophyllum*	0.941	2
3	*Hydrolithon*	*Lithoporella*	0.833	2
4	*Neogoniolithon*	Node 2	0.814	3
5	Node 1	Node 4	0.716	5
6	Node 3	Node 5	0.654	7
7	Node 6	*Lesueuria*	0.571	8

Appendix 2.5. Mastophoroid genera – Pearson coefficient, Similarity matrix

	Hydrolithon	***Lesueuria***	***Lithoporella***	***Mastophora***	***Metamastophora***	***Neogoniolithon***	***Spongites***	***Pneophyllum***
Hydrolithon	1							
Lesueuria	0.196	1						
Lithoporella	0.739	-0.169	1					
Mastophora	0.302	0.285	0.464	1				
Metamastophora	0.129	0.649	0.118	0.751	1			
Neogoniolithon	0.421	-0.172	0.093	0.084	0.021	1		
Spongites	0.833	0.352	0.397	0.439	0.342	0.666	1	
Pneophyllum	0.813	0.248	0.497	0.334	0.215	0.491	0.822	1

Node	Group 1	Group 2	Simil.	Objects in group
1	*Hydrolithon*	*Spongites*	0.833	2
2	Node 1	*Pneophyllum*	0.817	3
3	*Mastophora*	*Metamastophora*	0.751	2
4	Node 2	*Lithoporella*	0.544	4
5	*Lesueuria*	Node 3	0.467	3
6	Node 4	*Neogoniolithon*	0.418	5
7	Node 6	Node 5	0.193	8

Appendix 2.6. Mastophoroid genera – Percent Similarity - Similarity matrix

	Hydrolithon	***Lesueuria***	***Lithoporella***	***Mastophora***	***Metamastophora***	***Neogoniolithon***	***Spongites***	***Pneophyllum***
Hydrolithon	100							
Lesueuria	75.862	100						
Lithoporella	91.525	71.698	100					
Mastophora	79.245	80.851	87.5	100				
Metamastophora	80	85.714	84	95.455	100			
Neogoniolithon	86.667	74.074	80	81.633	82.353	100		
Spongites	93.333	81.481	83.636	85.714	86.275	92.857	100	
Pneophyllum	93.548	78.571	84.211	82.353	83.019	89.655	96.552	100

Node	Group 1	Group 2	Simil.	Objects in group
1	*Spongites*	*Pneophyllum*	96.552	2
2	*Mastophora*	*Metamastophora*	95.455	2
3	*Hydrolithon*	Node 1	93.441	3
4	Node 3	*Neogoniolithon*	89.726	4
5	*Lithoporella*	Node 2	85.75	3
6	Node 4	Node 5	83.33	7
7	Node 6	*Lesueuria*	78.322	8

Appendix 3.1. *Porolithon* – Bray Curtis, Distance matrix (all taxa)

	P. aequinoctiale	***S. africanum***	***P. antillarum***	***H. boergesenii***	***P. castellum***	***P. cocosicum***	***P. coarctatum***	***H. craspedium***	***H. improcerum***	***H. gardineri***	***P. oligocarpum***	***H. onkodes***	***P. marshallense***	***P. pachydermum***	***P. praetextatum***	***H. reinboldii***	***P. sandvicense***
P. aequinoctiale	0																
S. africanum	0.204	0															
P. antillarum	0.281	0.121	0														
H. boergesenii	0.319	0.193	0.16	0													
P. castellum	0.216	0.05	0.135	0.204	0												
P. cocosicum	0.253	0.101	0.06	0.098	0.115	0											
P. coarctatum	0.174	0.073	0.129	0.165	0.088	0.107	0										
H. craspedium	0.24	0.068	0.156	0.207	0.016	0.135	0.071	0									
H. improcerum	0.45	0.327	0.236	0.143	0.333	0.253	0.283	0.32	0								
H. gardineri	0.2	0.044	0.154	0.189	0.077	0.132	0.028	0.061	0.305	0							
P. oligocarpum	0.333	0.157	0.054	0.179	0.17	0.074	0.167	0.192	0.19	0.192	0						
H. onkodes	0.253	0.101	0.06	0.098	0.115	0	0.107	0.135	0.253	0.132	0.074	0					
P. marshallense	0.175	0.043	0.113	0.167	0.059	0.093	0.064	0.077	0.32	0.054	0.168	0.093	0				
P. pachydermum	0.253	0.101	0.06	0.098	0.115	0	0.107	0.135	0.253	0.132	0.074	0	0.093	0			
P. praetextatum	0.059	0.146	0.213	0.25	0.159	0.188	0.134	0.181	0.365	0.16	0.258	0.188	0.118	0.188	0		
H. reinboldii	0.355	0.189	0.255	0.115	0.217	0.192	0.2	0.221	0.269	0.167	0.278	0.192	0.182	0.192	0.306	0	
P. sandvicense	0.273	0.113	0.01	0.172	0.127	0.071	0.12	0.148	0.227	0.146	0.043	0.071	0.124	0.071	0.204	0.267	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	*P. cocosicum*	*H. onkodes*	0	2
2	Node 1	*P. pachydermum*	0	3
3	*P. antillarum*	*P. sandvicense*	0.01	2
4	*P. castellum*	*H. craspedium*	0.016	2

Node	Group 1	Group 2	Dissimil.	Objects in group
5	*P. coarctatum*	*H. gardineri*	0.028	2
6	*S. africanum*	*P. marshallense*	0.043	2
7	Node 3	*P. oligocarpum*	0.049	3
8	Node 6	Node 5	0.059	4
9	*P. aequinoctiale*	*P. praetextatum*	0.059	2
10	Node 7	Node 2	0.068	6
11	Node 8	Node 4	0.069	6
12	*H. boergesenii*	*H. reinboldii*	0.115	2
13	Node 11	Node 10	0.13	12
14	Node 13	Node 12	0.187	14
15	Node 9	Node 14	0.222	16
16	Node 15	*H. improcerum*	0.283	17

Appendix 3.2. ***Porolithon*** **– Percent Similarity, Similarity matrix (all taxa)**

	P. aequinoctiale	***S. africanum***	***P. antillarum***	***H. boergesenii***	***P. castellum***	***P. cocosicum***	***P. coarctatum***	***H. craspedium***	***H. improcerum***	***H. gardineri***	***P. oligocarpum***	***H. onkodes***	***P. marshallense***	***P. pachydermum***	***P. praetextatum***	***H. reinboldii***	***P. sandvicense***
P. aequinoctiale	100																
S. africanum	79.592	100															
P. antillarum	71.91	87.85	100														
H. boergesenii	68.132	80.734	84	100													
P. castellum	78.431	95	86.486	79.646	100												
P. cocosicum	74.725	89.908	94	90.196	88.496	100											
P. coarctatum	82.609	92.727	87.129	83.495	91.228	89.32	100										
H. craspedium	76	93.22	84.404	79.279	98.361	86.486	92.857	100									
H. improcerum	55	67.347	76.404	85.714	66.667	74.725	71.739	68	100								
H. gardineri	80	95.575	84.615	81.132	92.308	86.792	97.196	93.913	69.474	100							
P. oligocarpum	66.667	84.314	94.624	82.105	83.019	92.632	83.333	80.769	80.952	80.808	100						
H. onkodes	74.725	89.908	94	90.196	88.496	100	89.32	86.486	74.725	86.792	92.632	100					
P. marshallense	82.474	95.652	88.679	83.333	94.118	90.741	93.578	92.308	68.041	94.643	83.168	90.741	100				
P. pachydermum	74.725	89.908	94	90.196	88.496	100	89.32	86.486	74.725	86.792	92.632	100	90.741	100			
P. praetextatum	94.118	85.437	78.723	75	84.112	81.25	86.598	81.905	63.529	84	74.157	81.25	88.235	81.25	100		
H. reinboldii	64.516	81.081	74.51	88.462	78.261	80.769	80	77.876	73.118	83.333	72.165	80.769	81.818	80.769	69.388	100	
P. sandvicense	72.727	88.679	98.969	82.828	87.273	92.929	88	85.185	77.273	85.437	95.652	92.929	87.619	92.929	79.57	73.267	100

Node	Group 1	Group 2	Simil.	Objects in group
1	*P. cocosicum*	*H. onkodes*	100	2
2	Node 1	*P. pachydermum*	100	3
3	*P. antillarum*	*P. sandvicense*	98.969	2
4	*P. castellum*	*H. craspedium*	98.361	2

Node	Group 1	Group 2	Simil.	Objects in group
5	*P. coarctatum*	*H. gardineri*	97.196	2
6	*S. africanum*	*P. marshallense*	95.652	2
7	Node 3	*P. oligocarpum*	95.138	3
8	Node 6	Node 5	94.131	4
9	*P. aequinoctiale*	*P. praetextatum*	94.118	2
10	Node 7	Node 2	93.187	6
11	Node 8	Node 4	93.119	6
12	*H. boergesenii*	*H. reinboldii*	88.462	2
13	Node 11	Node 10	87	12
14	Node 13	Node 12	81.323	14
15	Node 9	Node 14	77.79	16
16	Node 15	*H. improcerum*	71.715	17

Appendix 33. ***Porolithon*** **– Bray Curtis, Distance matrix (excluding non-*Porolithon* taxa and taxa for which data was largely lacking)**

	P. antillarum	***H. boergesenii***	***P. castellum***	***P. cocosicum***	***P. coarctatum***	***H. craspedium***	***H. improcerum***	***H. gardineri***	***H. onkodes***	***P. marshallense***	***P. pachydermum***	***H. reinboldii***	***P. sandvicense***
P. antillarum	0												
H. boergesenii	0.16	0											
P. castellum	0.135	0.204	0										
P. cocosicum	0.06	0.098	0.115	0									
P. coarctatum	0.129	0.165	0.088	0.107	0								
H. craspedium	0.156	0.207	0.016	0.135	0.071	0							
H. improcerum	0.236	0.143	0.333	0.253	0.283	0.32	0						
H. gardineri	0.154	0.189	0.077	0.132	0.028	0.061	0.305	0					
H. onkodes	0.06	0.098	0.115	0	0.107	0.135	0.253	0.132	0				
P. marshallense	0.113	0.167	0.059	0.093	0.064	0.077	0.32	0.054	0.093	0			
P. pachydermum	0.06	0.098	0.115	0	0.107	0.135	0.253	0.132	0	0.093	0		
H. reinboldii	0.255	0.115	0.217	0.192	0.2	0.221	0.269	0.167	0.192	0.182	0.192	0	
P. sandvicense	0.01	0.172	0.127	0.071	0.12	0.148	0.227	0.146	0.071	0.124	0.071	0.267	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	*P. cocosicum*	*H. onkodes*	0	2
2	Node 1	*P. pachydermum*	0	3
3	*P. antillarum*	*P. sandvicense*	0.01	2
4	*P. castellum*	*H. craspedium*	0.016	2
5	*P. coarctatum*	*H. gardineri*	0.028	2
6	Node 5	*P. marshallense*	0.059	3
7	Node 3	Node 2	0.065	5
8	Node 4	Node 6	0.072	5

Node	Group 1	Group 2	Dissimil.	Objects in group
9	*H. boergesenii*	*H. reinboldii*	0.115	2
10	Node 7	Node 8	0.124	10
11	Node 10	Node 9	0.182	12
12	Node 11	*H. improcerum*	0.266	13

Appendix 34. ***Porolithon*** **– Percent Similarity, Similarity matrix (excluding non-*Porolithon* taxa and taxa for which data was largely lacking)**

	P. antillarum	***H. boergesenii***	***P. castellum***	***P. cocosicum***	***P. coarctatum***	***H. craspedium***	***H. improcerum***	***H. gardineri***	***H. onkodes***	***P. marshallense***	***P. pachydermum***	***H. reinboldii***	***P. sandvicense***
P. antillarum	100												
H. boergesenii	84	100											
P. castellum	86.486	79.646	100										
P. cocosicum	94	90.196	88.496	100									
P. coarctatum	87.129	83.495	91.228	89.32	100								
H. craspedium	84.404	79.279	98.361	86.486	92.857	100							
H. improcerum	76.404	85.714	66.667	74.725	71.739	68	100						
H. gardineri	84.615	81.132	92.308	86.792	97.196	93.913	69.474	100					
H. onkodes	94	90.196	88.496	100	89.32	86.486	74.725	86.792	100				
P. marshallense	88.679	83.333	94.118	90.741	93.578	92.308	68.041	94.643	90.741	100			
P. pachydermum	94	90.196	88.496	100	89.32	86.486	74.725	86.792	100	90.741	100		
H. reinboldii	74.51	88.462	78.261	80.769	80	77.876	73.118	83.333	80.769	81.818	80.769	100	
P. sandvicense	98.969	82.828	87.273	92.929	88	85.185	77.273	85.437	92.929	87.619	92.929	73.267	100

Node	Group 1	Group 2	Simil.	Objects in group
1	*P. cocosicum*	*H. onkodes*	100	2
2	Node 1	*P. pachydermum*	100	3
3	*P. antillarum*	*P. sandvicense*	98.969	2
4	*P. castellum*	*H. craspedium*	98.361	2
5	*P. coarctatum*	*H. gardineri*	97.196	2
6	Node 5	*P. marshallense*	94.11	3
7	Node 3	Node 2	93.465	5

Node	Group 1	Group 2	Simil.	Objects in group
8	Node 4	Node 6	92.789	5
9	*H. boergesenii*	*H. reinboldii*	88.462	2
10	Node 7	Node 8	87.613	10
11	Node 10	Node 9	81.784	12
12	Node 11	*H. improcerum*	73.384	13

Appendix 35. Real taxa ascribed to *Porolithon* – Bray Curtis, Distance matrix

	H. onkodes	***H. boergesenii***	***H. craspedium***	***H. improcerum***	***H. gardineri***	***H. reinboldii***
H. onkodes	0					
H. boergesenii	0.104	0				
H. craspedium	0.069	0.168	0			
H. improcerum	0.174	0.087	0.216	0		
H. gardineri	0.091	0.152	0.058	0.2	0	
H. reinboldii	0.184	0.122	0.204	0.191	0.149	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	*H. craspedium*	*H. gardineri*	0.058	2
2	*H. onkodes*	Node 1	0.08	3
3	*H. boergesenii*	*H. improcerum*	0.087	2
4	Node 3	*H. reinboldii*	0.157	3
5	Node 2	Node 4	0.172	6

Appendix 3.6. Real taxa ascribed to *Porolithon* – Percent Similarity, Similarity matrix

	H. onkodes	***H. boergesenii***	***H. craspedium***	***H. improcerum***	***H. gardineri***	***H. reinboldii***
H. onkodes	100					
H. boergesenii	89.583	100				
H. craspedium	93.069	83.168	100			
H. improcerum	82.609	91.304	78.351	100		
H. gardineri	90.909	84.848	94.231	80	100	
H. reinboldii	81.633	87.755	79.612	80.851	85.149	100

Node	Group 1	Group 2	Simil.	Objects in group
1	*H. craspedium*	*H. gardineri*	94.231	2
2	*H. onkodes*	Node 1	91.989	3
3	*H. boergesenii*	*H. improcerum*	91.304	2
4	Node 3	*H. reinboldii*	84.303	3
5	Node 2	Node 4	82.772	6

Appendix 4.1. ***Hydrolithon*** **– Bray Curtis, Distance matrix (all taxa)**

	H. boergesenii	***H. breviclavium***	***N. caribaeum***	***L. consociatum***	***H. craspedium***	***N. erosum***	***L. falklandicum***	***H. improcerum***	***H. gardineri***	***H. megacystum***	***H. munitum***	***H. murakoshii***	***H. onkodes***	***H. reinboldii***	***N. rufum***	***N. rugulosum***	***H. rupestris***	***H. samoënse***	***L. subantarcticum***	***H. superficiale***
H. boergesenii	0																			
H. breviclavium	0.173	0																		
N. caribaeum	0.213	0.368	0																	
L. consociatum	0.184	0.173	0.236	0																
H. craspedium	0.173	0.218	0.263	0.154	0															
N. erosum	0.178	0.333	0.037	0.2	0.229	0														
L. falklandicum	0.452	0.443	0.5	0.342	0.494	0.508	0													
H. improcerum	0.085	0.2	0.2	0.234	0.22	0.163	0.536	0												
H. gardineri	0.157	0.222	0.247	0.176	0.056	0.213	0.481	0.204	0											
H. megacystum	0.326	0.217	0.481	0.279	0.391	0.436	0.311	0.39	0.356	0										
H. munitum	0.08	0.151	0.209	0.14	0.113	0.174	0.44	0.146	0.115	0.318	0									
H. murakoshii	0.085	0.2	0.176	0.213	0.16	0.14	0.565	0.089	0.163	0.39	0.063	0								
H. onkodes	0.111	0.2	0.222	0.152	0.067	0.187	0.514	0.179	0.087	0.379	0.089	0.095	0							
H. reinboldii	0.129	0.159	0.239	0.149	0.196	0.204	0.421	0.196	0.143	0.191	0.126	0.175	0.176	0						
N. rufum	0.13	0.265	0.133	0.196	0.184	0.095	0.522	0.136	0.167	0.375	0.128	0.091	0.14	0.137	0					
N. rugulosum	0.156	0.313	0.086	0.244	0.25	0.098	0.477	0.163	0.234	0.436	0.152	0.14	0.209	0.204	0.095	0				
H. rupestris	0.118	0.253	0.143	0.204	0.172	0.106	0.529	0.124	0.155	0.383	0.116	0.079	0.128	0.146	0.011	0.106	0			
H. samoënse	0.165	0.32	0.049	0.275	0.237	0.084	0.545	0.149	0.221	0.494	0.183	0.126	0.196	0.255	0.129	0.084	0.14	0		
L. subantarcticum	0.5	0.541	0.458	0.441	0.595	0.467	0.116	0.5	0.583	0.429	0.543	0.531	0.565	0.521	0.516	0.467	0.524	0.508	0	
H. superficiale	0.224	0.363	0.105	0.294	0.297	0.091	0.5	0.185	0.258	0.397	0.241	0.185	0.256	0.205	0.114	0.117	0.125	0.128	0.455	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	*N. rufum*	*H. rupestris*	0.011	2
2	*N. caribaeum*	*N. erosum*	0.037	2
3	*H. craspedium*	*H. gardineri*	0.056	2
4	*H. munitum*	*H. murakoshii*	0.063	2
5	Node 2	*H. samoënse*	0.067	3
6	Node 3	*H. onkodes*	0.077	3
7	*H. boergesenii*	Node 4	0.083	3
8	Node 5	*N. rugulosum*	0.089	4
9	Node 7	*H. improcerum*	0.107	4
10	Node 8	*H. superficiale*	0.11	5
11	Node 9	Node 1	0.115	6
12	*L. falklandicum*	*L. subantarcticum*	0.116	2
13	*L. consociatum*	*H. reinboldii*	0.149	2
14	Node 11	Node 6	0.151	9
15	*H. breviclavium*	Node 13	0.166	3
16	Node 14	Node 10	0.183	14
17	Node 16	Node 15	0.215	17
18	Node 17	*H. megacystum*	0.367	18
19	Node 18	Node 12	0.492	20

Appendix 4.2. *Hydrolithon* – Percent Similarity, Similarity matrix (all taxa)

	H. boergesenii	***H. breviclavium***	***N. caribaeum***	***L. consociatum***	***H. craspedium***	***N. erosum***	***L. falklandicum***	***H. improcerum***	***H. gardineri***	***H. megacystum***	***H. munitum***	***H. murakoshii***	***H. onkodes***	***H. reinboldii***	***N. rufum***	***N. rugulosum***	***H. rupestris***	***H. samoënse***	***L. subantarcticum***	***H. superficiale***
H. boergesenii	100																			
H. breviclavium	82.692	100																		
N. caribaeum	78.652	63.158	100																	
L. consociatum	81.633	82.692	76.404	100																
H. craspedium	82.692	78.182	73.684	84.615	100															
N. erosum	82.222	66.667	96.296	80	77.083	100														
L. falklandicum	54.795	55.696	50	65.753	50.633	49.231	100													
H. improcerum	91.489	80	80	76.596	78	83.721	46.377	100												
H. gardineri	84.314	77.778	75.269	82.353	94.444	78.723	51.948	79.592	100											
H. megacystum	67.442	78.261	51.948	72.093	60.87	56.41	68.852	60.976	64.444	100										
H. munitum	92	84.906	79.121	86	88.679	82.609	56	85.417	88.462	68.182	100									
H. murakoshii	91.489	80	82.353	78.723	84	86.047	43.478	91.111	83.673	60.976	93.75	100								
H. onkodes	88.889	80	77.778	84.848	93.333	81.319	48.649	82.105	91.262	62.069	91.089	90.526	100							
H. reinboldii	87.129	84.112	76.087	85.149	80.374	79.57	57.895	80.412	85.714	80.899	87.379	82.474	82.353	100						
N. rufum	86.957	73.469	86.747	80.435	81.633	90.476	47.761	86.364	83.333	62.5	87.234	90.909	86.022	86.316	100					
N. rugulosum	84.444	68.75	91.358	75.556	75	90.244	52.308	83.721	76.596	56.41	84.783	86.047	79.121	79.57	90.476	100				
H. rupestris	88.172	74.747	85.714	79.57	82.828	89.412	47.059	87.64	84.536	61.728	88.421	92.135	87.234	85.417	98.851	89.412	100			
H. samoënse	83.516	68.041	95.122	72.527	76.289	91.566	45.455	85.057	77.895	50.633	81.72	87.356	80.435	74.468	87.059	91.566	86.047	100		
L. subantarcticum	50	45.946	54.237	55.882	40.541	53.333	88.372	50	41.667	57.143	45.714	46.875	43.478	47.887	48.387	53.333	47.619	49.18	100	
H. superficiale	77.647	63.736	89.474	70.588	70.33	90.909	50	81.481	74.157	60.274	75.862	81.481	74.419	79.545	88.608	88.312	87.5	87.179	54.545	100

Node	Group 1	Group 2	Simil.	Objects in group
1	*N. rufum*	*H. rupestris*	98.851	2
2	*N. caribaeum*	*N. erosum*	96.296	2
3	*H. craspedium*	*H. gardineri*	94.444	2
4	*H. munitum*	*H. murakoshii*	93.75	2
5	Node 2	*H. samoënse*	93.344	3
6	Node 3	*H. onkodes*	92.298	3
7	*H. boergesenii*	Node 4	91.745	3
8	Node 5	*N. rugulosum*	91.056	4
9	Node 7	*H. improcerum*	89.339	4
10	Node 8	*H. superficiale*	88.968	5
11	Node 9	Node 1	88.479	6
12	*L. falklandicum*	*L. subantarcticum*	88.372	2
13	*L. consociatum*	*H. reinboldii*	85.149	2
14	Node 11	Node 6	84.867	9
15	*H. breviclavium*	Node 13	83.402	3
16	Node 14	Node 10	81.72	14
17	Node 16	Node 15	78.542	17
18	Node 17	*H. megacystum*	63.301	18
19	Node 18	Node 12	50.768	20

Appendix 4.3. *Hydrolithon* – Bray Curtis, Distance matrix (excluding non-*Hydrolithon* taxa and taxa for which data was largely lacking)

	H. boergesenii	***N. caribaeum***	***H. craspedium***	***N. erosum***	***H. improcerum***	***H. gardineri***	***H. munitum***	***H. murakoshii***	***H. onkodes***	***H. reinboldii***	***N. rufum***	***N. rugulosum***	***H. rupestris***	***H. samoënse***	***H. superficiale***
H. boergesenii	0														
N. caribaeum	0.213	0													
H. craspedium	0.173	0.263	0												
N. erosum	0.178	0.037	0.229	0											
H. improcerum	0.085	0.2	0.22	0.163	0										
H. gardineri	0.157	0.247	0.056	0.213	0.204	0									
H. munitum	0.08	0.209	0.113	0.174	0.146	0.115	0								
H. murakoshii	0.085	0.176	0.16	0.14	0.089	0.163	0.063	0							
H. onkodes	0.111	0.222	0.067	0.187	0.179	0.087	0.089	0.095	0						
H. reinboldii	0.129	0.239	0.196	0.204	0.196	0.143	0.126	0.175	0.176	0					
N. rufum	0.13	0.133	0.184	0.095	0.136	0.167	0.128	0.091	0.14	0.137	0				
N. rugulosum	0.156	0.086	0.25	0.098	0.163	0.234	0.152	0.14	0.209	0.204	0.095	0			
H. rupestris	0.118	0.143	0.172	0.106	0.124	0.155	0.116	0.079	0.128	0.146	0.011	0.106	0		
H. samoënse	0.165	0.049	0.237	0.084	0.149	0.221	0.183	0.126	0.196	0.255	0.129	0.084	0.14	0	
H. superficiale	0.224	0.105	0.297	0.091	0.185	0.258	0.241	0.185	0.256	0.205	0.114	0.117	0.125	0.128	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	*N. rufum*	*H. rupestris*	0.011	2
2	*N. caribaeum*	*N. erosum*	0.037	2
3	*H. craspedium*	*H. gardineri*	0.056	2
4	*H. munitum*	*H. murakoshii*	0.063	2
5	Node 2	*H. samoënse*	0.067	3
6	Node 3	*H. onkodes*	0.077	3
7	*H. boergesenii*	Node 4	0.083	3

Node	Group 1	Group 2	Dissimil.	Objects in group
8	Node 5	*N. rugulosum*	0.089	4
9	Node 7	*H. improcerum*	0.107	4
10	Node 8	*H. superficiale*	0.11	5
11	Node 9	Node 1	0.115	6
12	Node 11	Node 6	0.151	9
13	Node 12	*H. reinboldii*	0.158	10
14	Node 13	Node 10	0.187	15

Appendix 44. ***Hydrolithon*** **– Percent Similarity, Similarity matrix (excluding non-*Hydrolithon* taxa and taxa for which data was largely lacking)**

	H. boergesenii	***N. caribaeum***	***H. craspedium***	***N. erosum***	***H. improcerum***	***H. gardineri***	***H. munitum***	***H. murakoshii***	***H. onkodes***	***H. reinboldii***	***N. rufum***	***N. rugulosum***	***H. rupestris***	***H. samoënse***	***H. superficiale***
H. boergesenii	100														
N. caribaeum	78.652	100													
H. craspedium	82.692	73.684	100												
N. erosum	82.222	96.296	77.083	100											
H. improcerum	91.489	80	78	83.721	100										
H. gardineri	84.314	75.269	94.444	78.723	79.592	100									
H. munitum	92	79.121	88.679	82.609	85.417	88.462	100								
H. murakoshii	91.489	82.353	84	86.047	91.111	83.673	93.75	100							
H. onkodes	88.889	77.778	93.333	81.319	82.105	91.262	91.089	90.526	100						
H. reinboldii	87.129	76.087	80.374	79.57	80.412	85.714	87.379	82.474	82.353	100					
N. rufum	86.957	86.747	81.633	90.476	86.364	83.333	87.234	90.909	86.022	86.316	100				
N. rugulosum	84.444	91.358	75	90.244	83.721	76.596	84.783	86.047	79.121	79.57	90.476	100			
H. rupestris	88.172	85.714	82.828	89.412	87.64	84.536	88.421	92.135	87.234	85.417	98.851	89.412	100		
H. samoënse	83.516	95.122	76.289	91.566	85.057	77.895	81.72	87.356	80.435	74.468	87.059	91.566	86.047	100	
H. superficiale	77.647	89.474	70.33	90.909	81.481	74.157	75.862	81.481	74.419	79.545	88.608	88.312	87.5	87.179	100

Node	Group 1	Group 2	Simil.	Objects in group
1	*N. rufum*	*H. rupestris*	98.851	2
2	*N. caribaeum*	*N. erosum*	96.296	2
3	*H. craspedium*	*H. gardineri*	94.444	2
4	*H. munitum*	*H. murakoshii*	93.75	2
5	Node 2	*H. samoënse*	93.344	3
6	Node 3	*H. onkodes*	92.298	3

Node	Group 1	Group 2	Simil.	Objects in group
7	*H. boergesenii*	Node 4	91.745	3
8	Node 5	*N. rugulosum*	91.056	4
9	Node 7	*H. improcerum*	89.339	4
10	Node 8	*H. superficiale*	88.968	5
11	Node 9	Node 1	88.479	6
12	Node 11	Node 6	84.867	9
13	Node 12	*H. reinboldii*	84.174	10
14	Node 13	Node 10	81.333	15

Appendix 45. ***Hydrolithon*** **(only real taxa) – Bray Curtis, Distance matrix**

	H. boergesenii	***H. craspedium***	***N. erosum***	***H. improcerum***	***H. gardineri***	***H. munitum***	***H. onkodes***	***H. reinboldii***	***H. rupestris***	***H. superficiale***
H. boergesenii	0									
H. craspedium	0.162	0								
N. erosum	0.187	0.229	0							
H. improcerum	0.095	0.22	0.163	0						
H. gardineri	0.146	0.056	0.213	0.204	0					
H. munitum	0.069	0.113	0.174	0.146	0.115	0				
H. onkodes	0.1	0.067	0.187	0.179	0.087	0.089	0			
H. reinboldii	0.118	0.196	0.204	0.196	0.143	0.126	0.176	0		
H. rupestris	0.106	0.172	0.106	0.124	0.155	0.116	0.128	0.146	0	
H. superficiale	0.233	0.297	0.091	0.185	0.258	0.241	0.256	0.205	0.125	0

Node	Group 1	Group 2	Dissimil.	Objects in group
1	*H. craspedium*	*H. gardineri*	0.056	2
2	*H. boergesenii*	*H. munitum*	0.069	2
3	Node 1	*H. onkodes*	0.077	3
4	*N. erosum*	*H. superficiale*	0.091	2
5	Node 2	*H. rupestris*	0.111	3
6	Node 5	*H. improcerum*	0.121	4
7	Node 6	*H. reinboldii*	0.146	5
8	Node 7	Node 3	0.153	8
9	Node 8	Node 4	0.204	10

Appendix 46. *Hydrolithon* (only real taxa) – Percent Similarity, Similarity matrix

	H. boergesenii	***H. craspedium***	***N. erosum***	***H. improcerum***	***H. gardineri***	***H. munitum***	***H. onkodes***	***H. reinboldii***	***H. rupestris***	***H. superficiale***
H. boergesenii	100									
H. craspedium	83.81	100								
N. erosum	81.319	77.083	100							
H. improcerum	90.526	78	83.721	100						
H. gardineri	85.437	94.444	78.723	79.592	100					
H. munitum	93.069	88.679	82.609	85.417	88.462	100				
H. onkodes	90	93.333	81.319	82.105	91.262	91.089	100			
H. reinboldii	88.235	80.374	79.57	80.412	85.714	87.379	82.353	100		
H. rupestris	89.362	82.828	89.412	87.64	84.536	88.421	87.234	85.417	100	
H. superficiale	76.744	70.33	90.909	81.481	74.157	75.862	74.419	79.545	87.5	100

Node	Group 1	Group 2	Simil.	Objects in group
1	*H. craspedium*	*H. gardineri*	94.444	2
2	*H. boergesenii*	*H. munitum*	93.069	2
3	Node 1	*H. onkodes*	92.298	3
4	*N. erosum*	*H. superficiale*	90.909	2
5	Node 2	*H. rupestris*	88.891	3
6	Node 5	*H. improcerum*	87.861	4
7	Node 6	*H. reinboldii*	85.361	5
8	Node 7	Node 3	84.681	8
9	Node 8	Node 4	79.612	10

GENERAL DISCUSSION

1. Taxonomic Implications

As noted by Chamberlain (1991), recent taxonomic studies are suggesting that a considerable reduction in the number of real species will occur after thorough study of types and modern material. This is particularly true when one considers the vast number of previously poorly described taxa (Woelkerling 1984; Chamberlain et al. 1991) of which Woelkerling & Lamy (1998) provide some reasons. While these authors cite examples from the older literature, many of these problems still persist in the modern research despite continued calls (e.g. Keats 1997; Keats et al. 1997) to describe as many species characters in sufficient detail so that future researchers will be able to assess species without having to resort to an analysis of type specimens.

In this review of the genera Porolithon (defunct) and Hydrolithon, the present research has tried to describe all taxa in sufficient detail. Although this has been possible with most taxa under review, it has, however, not been possible with others for reasons mentioned in text. Nonetheless, as Chamberlain (1991) had noted, I have found a large number of taxa to be conspecific. This has largely been due to the fact that Foslie (and similarly Lemoine) had described large numbers of species largely or solely on apparent differences 1) in external morphology, 2) sporangial conceptacle size and shape and 3) internal vegetative anatomy (see Woelkerling 1984). While Foslie (1905) himself concluded that many of his earlier taxa were probably synonymous (alluding that “a considerable reduction was necessary”) he continued to distinguish and describe species based solely on external morphology (see Woelkerling 1984).

1.1 **Porolithon** (defunct)

Based on the collective analyses of the taxa described in Paper 1, the characteristics of the taxa ascribed to Porolithon are:

1. thallus non-geniculate;
2. cells of contiguous vegetative filaments normally joined by cell fusions;
3. secondary pit connections absent or rare;
4. sporangia lacking apical plugs and borne within uniporate conceptacles.

The above four characters group this taxon into the subfamily Mastophoroideae (Setchell 1943: 134 - as 'Mastophoreae')

5. thallus monomerous or dimerous and lacking a basal layer of palisade cells throughout;
6. in monomerous thalli, medulla predominantly plumose (non-coaxial);
7. trichocytes present, occurring singly, in small horizontal groups separated by vegetative filaments, in long vertical chains, or in large tightly packed, pustulate horizontal fields lacking vegetative filaments interspersed among the trichocytes;
8. the base of sporangial conceptacle pore canals are lined by a ring of conspicuous, enlarged, domed cells;
9. these enlarged cells do not protrude into the pore canal, and are oriented more-or-less perpendicularly to the roof surface;
10. the sporangial conceptacle roof is formed from filaments interspersed among the sporangia and not peripheral to them;
11. the sporangial pore canal is not usually lined by narrow filaments that tilt into the pore canal and create the appearance of papillae,

12. Spermatangial conceptacles containing simple spermatangial systems that are restricted to the conceptacle floor;
13. gonimoblast filaments borne from the margin of the fusion cell.

The latter nine characters are collectively diagnostic of Hydrolithon (sensu strictu) as proposed by Penrose & Wolkerling (1988, 1992). Based on the above analyses, however, there appears to be two groups of taxa within the confines of the genus Hydrolithon (sensu strictu). These two groups separate out from one another based collectively on: 1) the number of epithallial cell layers; 2) the trichocyte arrangement and 3) the thallus construction (see Paper 1). It seems logical to suggest, therefore, that within the genus Hydrolithon, there are at least two subgenera: Group 1 should comprise the subgenus Hydrolithon with H. reinboldii representative of the subgenus; and Group 2 should comprise the subgenus Porolithon with H. onkodes representative of this subgenus (see also Paper 3). While this pattern is not evident from the phenograms for Hydrolithon it should be remembered that in the cluster analysis, characters have no weighting; species' character similarities and distances will quite often overshadow differences between clusters.

The following taxa conformed well to the present-day diagnosis of the genus Hydrolithon; H. boergesenii, H. craspedium, H. gardineri, H. improcerum, H. onkodes, and H. reinboldii. Although successfully transferred, some of the above taxa were transferred without any taxonomic study. Lithophyllum africanum, on the other hand, underwent a detailed taxonomic revision and subsequent transfer by Afonso-Carrillo et al. (1993) to the genus Spongites. Afonso-Carrillo (pers. comm. in Woelkerling et al. 1998: 123) later questioned this transfer and suggested that L. africanum probably belongs to Hydrolithon as delimited by

Penrose (1996). This transfer was never affected. The results of the present research supports Afonso-Carrillo et al's (1993) original diagnosis as this taxon does conforms to the genus Spongites (sensu strictu). The current research has also showed that nine taxa are conspecific with H. craspedium (P. castellum), H. gardineri (L. aequinoctiale, L. coarctatum, L. praetextatum and P. marshallense) and H. onkodes (L. antillarum, L. pachydermum, L. sandvicense, and P. cocosicum). A single new combination was also found. Lithophyllum oligocarpum conforms to the genus Spongites and should be referred to as Spongites oligocarpus (Foslie) Maneveldt & Keats comb. nov.. For various reasons we were unable to obtain four type specimens (P. colliculosum, P. orbiculatum, P. somaliae and P. sonorense) and have commented as much as possible on these taxa based on previous research (see Paper 1).

1.2 Hydrolithon

It was only recently that the generic delimitation of Hydrolithon was resolved (Penrose 1991, 1992; Penrose & Woelkerling 1991, 1992; Penrose & Chamberlain 1993). Hydrolithon has undergone substantial revision since 1909 and it is presently characterised by the pattern of its tetrasporangial conceptacle roof development. In Hydrolithon, the pore canals of the tetrasporangial conceptacles are lined by a ring of conspicuous, enlarged cells that arise from filaments interspersed among the sporangial initials. These cells do not protrude into the pore canal, but are oriented more-or-less perpendicular to the roof surface. Based on this feature Hydrolithon and Porolithon are considered congeneric and Porolithon has been subsumed into Hydrolithon.

Porolithon onkodes, the type species of the former Porolithon, was the only species examined which was formally transferred to Hydrolithon. A few other Porolithon taxa have also been transferred (see Paper 1), but without any review; the larger number have still not been formally transferred. In addition, a host of other species have since been included in Hydrolithon. The current research has attempted to reassess as many taxa as possible that have been ascribed to the genus Hydrolithon (excluding Fosliella-state Hydrolithon) as well as taxa found to conform to the generic delimitation of Hydrolithon. This has been hampered by a lack of type material supplied from various herbaria, a lack of representative material from type localities, and inadequate descriptions of even recently described taxa.

Not-with-standing, the following taxa have been found to have been successfully transferred to, and conform well to the present-day diagnosis of Hydrolithon; H. boergesenii, H. craspedium, H. gardineri, H. improcerum, H. munitum, H. onkodes, H. reinboldii, H. rupestris and H. superficiale (see Paper 2). A number of taxa that have been ascribed to Hydrolithon do not, however, conform to the genus and these have been described under different combinations (see Paper 2). Hydrolithon breviclavium has been found to conform to the genus Spongites and is consequently referred to as Spongites brevicalvius (Foslie) Maneveldt & Keats comb. nov.. Hydrolithon consociatum and H. subantarcticum are found to be conspecific, the former having nomenclatural priority. Previous research has, however, considered these two taxa synonymous with Spongites discoideus. An investigation into the sporangial conceptacle roof development of these two taxa show that they belong within the confines of the genus Pneophyllum instead, and should therefore be referred to as Pneophyllym consociatum (Foslie) Maneveldt & Keats comb. nov..

In addition, the current research has found that the following taxa conform to the present-day delimitation of Hydrolithon: Neogoniolithon caribaeum, N. erosum and N. rugulosum. These taxa have, however, all been found to be conspecific and subsequently are all referred to as Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov. Similarly, Hydrolithon samöense (Lithophyllum samoënse Foslie 1906: 20) has also been found to be conspecific with Hydrolithon erosum (Foslie) Maneveldt & Keats comb. nov. (Lithophyllum erosum Foslie 1906: 20) the latter having nomenclatural priority. Hydrolithon samoënse was and still is, however, very widely used and it may be argued that the epithet samoënse instead be given priority; this suggestion requires further investigation. The current research has also showed that a number of other taxa are conspecific with H. munitum (H. murakoshii) and H. rupestris (N. rufum) (see Paper 2).

2. Ecological Implications

The ecological importance of non-geniculate coralline algae as cementers of the coral reef margin has been widely documented (Setchell 1926; Taylor 1950; Lee 1967; Littler & Doty 1975; Adey et al. 1982; Keats et al. 1997; Littler & Littler 2000, 2003). Species ascribed to the defunct genus Porolithon Foslie, in particular, have been highlighted as being very important (Lee 1967; Adey 1978; Littler 1973). In the tropical Indo-Pacific and tropical eastern Atlantic regions, Hydrolithon onkodes has been reported to be the single most important ecological species because of its wide distribution (Lee 1967; Littler 1973; Littler & Doty 1975; Gordon et al. 1976; Adey et al. 1982; Ballesteros & Afonso-Carrillo 1995). Similarly, Porolithon pachydermum has been documented as the single most important ecological species in the tropical western Atlantic (Adey 1978; Littler et al. 1995; Littler & Littler 2000). As these taxa have now been shown to be conspecific, it seems logical to suggest that on a global scale, Hydrolithon onkodes is probably the single most important cementer of coral reefs.

A three-dimensional honey-combed form of Hydrolithon onkodes occurs in some shallow South Pacific coral reef areas in which upright lobes are produced (see also Littler & Littler 2003). At the bases of these upright lobes are found the tubular burrows of the chiton Cryptoplax larvaeformis. This form is evidently caused by growth in response to the grazing activities of this chiton. Similarly, on some Caribbean reefs, Hydrolithon onkodes (as Porolithon pachydermum) has been reported to have the same castle-like, three-dimensional honey-combed structure. At the bases of the coralline are found the tubular burrows of the chiton, Choneplax lata (Littler et al. 1995; Littler & Littler 2000). This form too is evidently caused by growth in response to the grazing activities of this chiton (Littler et al. 1995). In this coralline-herbivore interaction, the importance of Hydrolithon onkodes as a source of food and refuge for the two species of chiton is clearly evident (see Littler et al. 1995). Similar such interactions have been documented (e.g. Steneck 1982; Maneveldt et al. in press) and symbiont fidelity may be more common than previously assumed.

In conclusion, the apparent conspecificity of a number of taxa ascribed to the genera Porolithon and Hydrolithon will clearly also have both biogeographic and biodiversity implications. While this study has certainly increased the geographic range of a number of taxa, it has also resulted in the reduction of the number of real taxa and many checklists will no doubt need to be revised. Chamberlain (1991) had already concluded that recent studies would show a considerable reduction in the number of taxa described. This has not only become true for the genus Hydrolithon, but for a number of other taxa worldwide (e.g. Woelkerling 1997).

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Table 1. A selection of comparable thallus terminologies used by various authors.

Foslie, Mikael H.	Lemoine, Marie	Adey, Walter H.	Johansen, H. William	Woelkerling, William J. (et al.)	Chamberlain, Yvonne M. (et al.)[1]
multi-layered hypothallium	multi-layered hypothallium	multi-layered hypothallium	multistromatic hypothallium	monomerous	monomerous
single-layered hypothallium	single-layered hypothallium	single-layered hypothallium	monostromatic hypothallium	dimerous	dimerous
epithallium	epithallium	epithallium	epithallus	epithallial cells	epithallial cells/epithallus
		meristem cells		subepithallial initial	subepithallial initial
perithallium	perithallium	perithallium	perithallus + cortex	peripheral region	cortex
hypothallium	hypothallium	hypothallium	hypothallus + medulla	ventral/central core	medulla
-	-	coaxial hypothallium	coaxial hypothallus	coaxial ventral/central core	coaxial medulla
-	-	plumose	noncoaxial	noncoaxial	noncoaxial, plumose
-	-	hypothallium	hypothallus	primigenous filaments (of dimerous thalli)	basal filaments (of dimerous thalli)
-	-	perithallium	perithallus	postigenous filaments (of dimerous thalli)	erect filaments (of dimerous thalli)
-	-	hypothallium	medullary filaments	core filaments (of monomerous thalli)	medullary filaments (of monomerous thalli)
-	-	perithallium	cortical filaments	peripheral derivatives of core filaments (of monomerous thalli)	cortical filaments (of monomerous thalli)
heterocyst	heterocyst	heterocyst	trichocyte	trichocyte	trichocyte

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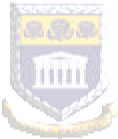
[1] Thallus terminology in this dissertation follows Chamberlain (1990) unless otherwise stated.



APPENDIX 1.

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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.

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