

***Tapeinodasya* Weber-van Bosse (Ceramiales,  
Rhodophyta): Redescription of an Enigmatic Genus of the  
Dasyaceae.**

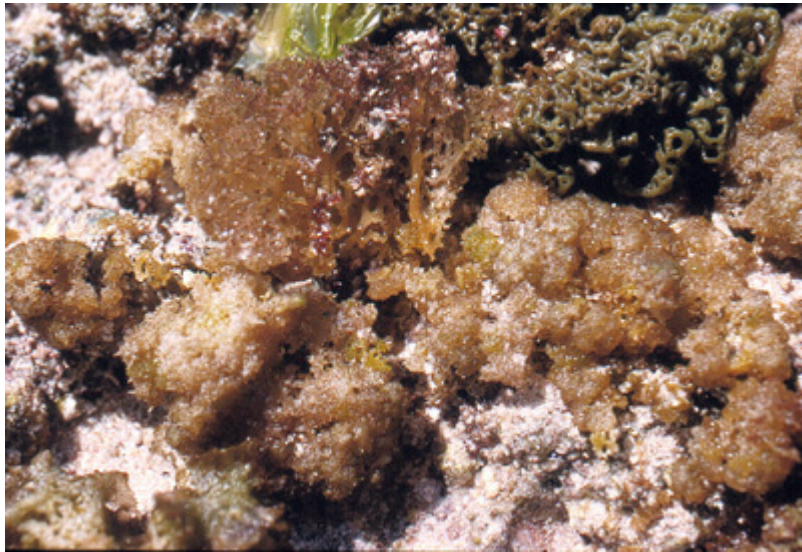
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**ABSTRACT**

The genus *Tapeinodasya*, originally described by Weber-van Bosse (1904) from Indonesia and the Sulu Archipelago (Philippines), has remained one of the least known genera of the Dasyaceae. Based on recent collections from the East African coast, vegetative and tetrasporangial structures are described in detail for the first time and the placement of *Tapeinodasya* in the Dasyaceae based on cellulosympodial growth is confirmed. The genus is separated from all other genera of the Dasyaceae by a distinctive cauliflower-like habit, complete absence of monosiphonous filaments, extensively corticated tetrasporangial stichidia and the presence of both pre- and postsporangial cover cells. *Tapeinodasya* appears to be related to the *Heterosiphonia*-like genera, based on an alternate sequence of periaxial cell formation, a primary alternate-

distichous arrangement of holoblastic branches, and branches separated from one another by one or more unbranched segments. Placement of *Tapeinodasya* in a clade with *Thuretia* and *Dictyurus* as recently hypothesized is verified by the recognition of a clockwise mode of alternate periaxial cell formation and a primary bilateral organisation. Comparison of the East African specimens with the type collections of the other known species, shows that the Tanzanian specimens belong to the Indonesian *Tapeinodasya bornetii* rather than to *T. etheliae* which was described from the Amirante Islands. The presence of *T. bornetii* in Tanzania represents a substantial range extension and a new record for the Indian Ocean.

## INTRODUCTION

*Tapeinodasya*, a genus of the red algal family Dasyaceae, was first described by Weber-van Bosse and is at present composed of two species: the type, *T. bornetii* Weber-van Bosse (1904) from the Malayan region, and *T. etheliae* Weber-van Bosse (1913, as *T. ethelae*) from the Amirante Islands, Seychelles. Main characteristics of the genus are the overall 'cauliflower-like' habit, spinous branches and presence of only two sporangia per segment in the stichidia. Despite the distinctive morphology, subsequent reports and descriptions of the two species are virtually non-existent. *Tapeinodasya bornetii* is only known from its original description and a single report from Indonesia, based on collections from the Siboga-Expedition (Weber-van Bosse 1904, 1923). *Tapeinodasya etheliae*, which was described from the Amirante Islands north of Madagascar based on material collected by Gardiner on the 'Sealark' Expedition, has never been reported again. All subsequent reports of both species are basically repetitions of the original accounts (Weber-van Bosse 1914; De Toni 1905; 1924; Kylin 1956; Velasquez et al. 1975; Silva et al. 1987; Silva et al. 1996). According to Weber-van Bosse (1913) *T. etheliae* differs from *T. bornetii* by a less dense ramification, the short adventitious branches in the axils of lateral branches and a less conspicuous dorsiventral organisation.

Several studies have focussed on phylogenetic relationships of the entire family Dasyaceae, with respect to the Ceramiaceae, Delesseriaceae, and Rhodomelaceae (Falkenberg 1901; Kylin 1930; Hommersand 1963; Saunders et al. 1996; Jong et al. 1998) or on evolutionary affinities of the genera of Dasyaceae (Parsons 1975; Jong 1997). From the latter studies, however, it became evident that our knowledge of the genera of the Dasyaceae is not evenly distributed. Data on some genera are primarily based on old accounts and are incomplete in several ways, hence precluding a better understanding of the intra- and interfamilial relationships of the Dasyaceae. Collections of *Tapeinodasya bornetii*, the type of the genus, from the East African coast enable us to re-examine the morphology and structure of *Tapeinodasya* and reconsider its position in the Dasyaceae. Additionally, the specimens from East Africa were compared with the type material of *T. bornetii* and *T. etheliae*.

## MATERIALS AND METHODS

The plants of *Tapeinodasya bornetii* were collected over a period of several years by E. Coppejans, O. Dargent, O. De Clerck and C. Van den heede in the framework of a series of marine algal biodiversity studies in the Indian Ocean (Kenya, Tanzania). Specimens were immediately processed as herbarium specimens as well as small amounts being preserved in 4% Formalin/seawater. Slide material was stained in a mixture of 1 g aniline blue powder, 50 ml Karo®, 45 ml distilled water, 5 ml acetic acid and has been deposited in the Herbarium of

the Ghent University (GENT) and the National Herbarium of the Netherlands, Leiden (L). Line-drawings were prepared using a camera lucida mounted on a Zeiss Research microscope. Agfa APX25 was used in making black and white photographs. Original material of both *T. bornetii* and *T. etheliae* deposited in L was used for comparison.

## RESULTS

### *Tapeinodasya bornetii* Weber-van Bosse

#### Specimens examined

Tanzania. Mafia Island, Chole Bay, Juani Islet, epilithic, subtidal, -2 m (Leg. Coppejans and Van den heede, 30 July 1993, GENT HEC 9783). Pemba Island, Misali Islet, NE-coast, epiphytic on *Laurencia* sp., horizontal rock surface on intertidal coral platform with very large, shallow pools at low tide (Leg. Coppejans and De Clerck, 21 January 1996, GENT HEC 11392). Pemba Island, Tondooni, Verani, epiphytic on *Laurencia* sp., low intertidal rock pool (Leg. Coppejans and De Clerck, 24 January 1996, GENT HEC 11475). Zanzibar. Paje, epilithic, seaward slope of the fringing reef, just exposed at spring low tide (Leg. Coppejans and Dargent, 23 July 1997, GENT HEC 12018).

#### Description

**Habitus and external morphology.** Plants are of a pale straw colour on the upper side, pinkish red on the downward (shaded side), forming semiprostrate cushions, 4-6 cm high and up to 15 cm in diameter. Thalli are ascending, attached at several points near the base. Plants are generally cauliflower-like with frequently branching, thick, terete, denuded basal axes on the inside, surrounded by a peripheral layer of extremely densely branched ultimate axes (**Habit**; [Figs. 1, 2](#)). Distinct percurrent axes are lacking. Basal axes are cartilaginous, 2-3 mm wide near the base, tapering gradually towards the apices. All axes are entirely corticated from several cells near the apex onwards. Monosiphonous filaments are absent, the pseudolaterals themselves being completely corticated.

**Branching.** Three types of axes can be distinguished: 1. Bilaterally organised, compressed sympodial axes, which grow in a more or less horizontal position ([Figs. 3, 4, 13](#)); 2. adventitious sympodial axes arising on the most basal axial cell of a pseudolateral of a bilaterally organised axis; 3. radially organised indeterminate axes taking the place of a pseudolateral on radially organised axes. Although complicated at first sight and without an apparent structure, the branching system generally follows a rather strict pattern. This, however, is only clearly observed in the apical parts of the thallus. The morphology of the horizontally orientated holoblastic sympodial branches is bilateral with pseudolaterals deflected to two opposite sides of the sympodial main axis ([Figs. 4, 12](#)). The distance between two successive pseudolaterals is 375-750  $\mu\text{m}$ . The axial cells of basal segments of pseudolaterals can give rise to new, apparently radially organised, adventitious sympodial axes, directed upward and of limited growth (600-1300  $\mu\text{m}$ ), with short distances between the pseudolaterals (100-150  $\mu\text{m}$ ). One of the pseudolaterals of such an adventitious sympodial axis might grow into another horizontally orientated bilateral sympodial main axis. Radially organised indeterminate axes seem to be formed at random, but are always replacing a pseudolateral of an adventitious sympodial axis. Anastomosis between axes in the lower part of the thallus is observed occasionally, but does not seem to follow a strict pattern ([Fig. 9](#)). Neither does it involve the formation of specialised connective cells. At times indeterminate

axes bend down, stop forming side branches and grow towards the substrate, eventually continuing growth as prostrate axes (Fig. 8).

**Apical organisation and periaxial cell formation.** Except for the vertically arranged adventitious sympodial axes, which arise endogenously on the pseudolaterals, branching is essentially holoblastic. Pseudolaterals are formed every other segment, with occasionally two, rarely three segments separating successive pseudolaterals (Figs. 5, 12). Pseudolaterals are primarily deflected in a bilateral manner. In radially arranged axes however, pseudolaterals are secondarily displaced due to asymmetric cortex development. Pseudolaterals remain unbranched. Four periaxial cells are developed, cut off in an alternating clockwise sequence. After a first periaxial cell is cut off, a second periaxial cell is formed adjacent to the first periaxial cell, followed by a third periaxial cell being cut off at the opposite side of the first periaxial cell, and diametrically opposite to the second periaxial cells. A fourth periaxial cell is situated opposite to the first periaxial cell. In a next segment this order of periaxial cell formation remains exactly the same if no pseudolateral is formed. If a pseudolateral is formed the position of the first periaxial cell switches 180° (Fig. 12). The first periaxial cell is often cut off from the second segment onward; the periaxial cells are already surrounded by an extensive cortex in the subapical parts. The cortex can be up to 5 layers thick and is differentiated into a cortical and a subcortical layer in the main axes.

**Reproductive structures.** Tetrasporangial stichidia develop from the pseudolaterals, and consist of 16-26 fertile segments, each one producing 2 tetrasporangia (Fig. 6). Often, however, a segment may produce only one sporangium, or none at all. Stichidia are unbranched, spindle-shaped, 300-340 µm wide and 900-1700 µm long. Four periaxial cells are formed in an alternating sequence as in the axes, but only the second and third periaxial cell may cut off a tetrasporangium. A presporangial cover cell is cut off at the distal end of the periaxial cell before the latter divides transversely into an upper tetrasporangial initial and a lower stalk cell (Figs. 7, 15). Subsequently a second and a third cover cell are produced, after which all cover cells and their daughter cells divide numerous times resulting in a densely corticated stichidium, morphologically similar to sterile pseudolaterals (Fig. 16). Mature tetrasporangia are 110-135 µm in diameter.

Spermatangial branches were not observed.

Female reproductive structures. Procarps and young stages of cystocarp development were not observed. Mature cystocarps are sessile, globose (1100-1350 µm in diameter), with a short spout (Fig. 10). Carposporangia are obovate (80 µm wide, 130 µm long), maturing basipetally and formed in rows on monopodially branched gonimoblast filaments.

## Ecology

Specimens of *T. bornetii* were collected in midlittoral pools of extensive subhorizontal reef flats along the East African coast.

## DISCUSSION

Comparison with the type material of *Tapeinodasya bornetii* shows that the East African specimens are almost identical to Indo-Malayan specimens (Figs. 17-19). Hence, this detailed report confirms a major range extension of this species, which was already mentioned by Copejans et al. (2001). The type (and probably the only) specimen of *T. etheliae* (Fig. 21)

was found to be practically identical to *T. bornetii* in thallus structure, branching pattern, and number and formation of periaxial cells. However, the general morphology of the axes differs substantially between the species. In *T. etheliae* the horizontally orientated axes are less well developed compared to *T. bornetii*, whereas the vertically orientated axes appear to be better developed. Consequently, the thallus of *T. etheliae* has a more slender, erect habit than *T. bornetii*. Further differences include a more compressed nature (although difficult to judge from herbarium specimens), and a larger width of the axes in *T. etheliae*, 3-5 mm versus 2-3 mm in *T. bornetii*. Observations on the type material of *T. etheliae* are congruent with the original account of Weber-van Bosse (1913), but a few discrepancies were noticed. The number of axial cells between two succeeding branches appears to be two rather than three as suggested by Weber-van Bosse (1913). Also, Weber-van Bosse's characterization of the apical organization as primarily radial and secondarily bilateral appears to be incorrect. The primary organisation of the axes is bilateral. However, as opposed to the situation in *T. bornetii* where some axes develop a secondarily derived radial structure, the entire thallus in *T. etheliae* remains bilaterally organised.

*Tapeinodasya* has traditionally been included in the Dasyaceae on the basis of the cellulosympodial growth (sensu Norris et al. 1984), the original character separating the Dasyaceae from the Ceramiaceae, Delesseriaceae and Rhodomelaceae (Falkenberg 1901; Rosenberg 1933; Kylin 1956). Unfortunately additional differentiating characters of the Dasyaceae, related to the early developmental stages of the female reproductive structures and postfertilisation events (see Rosenberg 1933; Hommersand 1963; Parsons 1975), could not be verified. However, the absence of trichoblasts and the presence of tetrasporangial stichidia are also characteristic of the Dasyaceae. Within the family the genus is easily recognised by: 1. A unique cauliflower-like habit. 2. An entirely polysiphonous and densely corticated thallus. 3. Completely polysiphonous pseudolaterals. Most genera of the Dasyaceae have pseudolaterals which are either entirely monosiphonous (e.g., *Dasya*, *Dasysiphonia*, *Dictyurus*, *Dipterocladia*, *Rhodoptilum*, and *Thuretia*) or have one to a few polysiphonous segments near the base (*Dasyella*, *Eupogodon* and *Heterosiphonia*). Only in some species of *Heterosiphonia* are pseudolaterals largely polysiphonous, with only the ultimate segments being monosiphonous e.g., *H. berkeleyi* Montagne, *H. dubia* (Suhr) Falkenberg, and *H. pellucida* (Harvey) Falkenberg (Ricker 1987; Stegenga et al. 1997). 4. The formation of only two tetrasporangia per segment. Although the number of periaxial cells in vegetative axes is not necessarily similar to the number of periaxial cells in stichidial axes, and partial maturing of periaxial cells in stichidia is not uncommon, in Dasyaceae the number of tetrasporangia per segment equals the number of periaxial cells in the stichidia (Jong 1997). The situation of *Tapeinodasya* with four periaxial cells being formed of which only two give rise to tetrasporangia is to be found only in *Halodictyon* (Coppejans 1975), a delicate net-forming species, of which the position in the Dasyaceae is seriously doubted (Jong et al. 1998). 5. The structure of the tetrasporangial stichidia. In the Dasyaceae tetrasporangial cover cells are cut off from the fertile periaxial cell either prior to or after the formation of a tetrasporangium. Postsporangial cover cells are found in most genera: *Dasya*, *Dasysiphonia*, *Dipterocladia*, *Eupogodon*, and some species of *Heterosiphonia* (Rosenberg 1933; Lee and West 1979; Kajimura 1992; Millar 1996; Jong et al. 1997; Jong et al. 1998). Presporangial cover cells are found in *Dasyella*, *Dictyurus*, *Heterosiphonia*, and *Thuretia* (Aregood and Hackett 1971; Coppejans and Boudouresque 1984; Parsons 1975; Jong et al. 1998).

The presence of both pre- and postsporangial cover cell groups has not yet been recorded in any genus of the Dasyaceae, but is fairly common in the Rhodomelaceae. Numerous members of the latter family often show two large, rectangular cover cells, produced before the

tetrasporangium is cut off. A third postsporangial cover cell is usually small and triangular (Hommersand 1963). In many genera of the Rhodomelaceae, however, the additional postsporangial cover cell is absent. Because of the variation in cover cell formation, in both the Dasyaceae and Rhodomelaceae, this character is generally not regarded to be important on a family level. One more difference exists between *Tapeinodasya* and the other genera of the Dasyaceae with respect to the tetrasporangial stichidia. All the other genera show cover cells remaining undivided or dividing only once. In *Tapeinodasya*, however, the original cover cells become embedded in a 2-3 layered cortex. According to Hommersand (1963) this is an ancestral character, also present in primitive genera of the remaining families of the Ceramiales such as *Carpoblepharis* (Ceramiaceae) and *Bostrychia* (Rhodomelaceae). It therefore can be hypothesized that *Tapeinodasya* represents a primitive member of the Dasyaceae. Based on cladistic analysis *Tapeinodasya* was assigned to the *Heterosiphonia*-related genera (Jong et al. 1998), which are thought to contain more plesiomorphic characters of the Dasyaceae (Hommersand 1963; Jong et al. 1998).

Ancestral characters defining the *Heterosiphonia*-related genera present in *Tapeinodasya* are: a primary alternate-distichous arrangement of holoblastic branches, partly or completely polysiphonous pseudolaterals, holoblastic branches separated from one another by one or more unbranched segments, and an alternate sequence of periaxial cell formation. A phylogeny of the genera of the Dasyaceae based on morphological and reproductive characters places *Tapeinodasya* in an unresolved clade with *Dictyurus* and *Thuretia* (Jong et al. 1998). The latter two, and especially *Dictyurus*, have been considered to be isolated genera and only distantly related to *Heterosiphonia*. The close relationship between *Tapeinodasya* and the *Dictyurus-Thuretia* group is primarily based on the sequence of periaxial cell development and the number of periaxial cells. Additional support for the clade was given by the presence of anastomosis in all three genera. However, whereas in *Dictyurus* and *Thuretia* pseudolaterals are secondarily united to form a delicate and highly regular network, the anastomosis in *Tapeinodasya*, occurs in an irregular manner and never results in a lace-like network. Also the specialised lateral cells accomplishing the anastomosis of pseudolaterals in *Dictyurus* and *Thuretia* (Parsons 1975; Parsons and Womersley 1998), are absent in *Tapeinodasya*. The homology of this character is therefore doubted in those genera.

The Dasyaceae are characterised by holoblastic branching, in which an apical cell cuts off a subapical cell, which becomes the initial of a lateral branch prior to the formation of periaxial cells (Hommersand 1963, Parsons 1975). Due to the sympodial construction of the thallus, those holoblastic branches are modified and become sympodial monosiphonous or polysiphonous branches, called pseudolaterals. As the plane of division of the apical cell determines the side to which a branch is formed, the primary branching pattern is defined by the division of the apical cell into a new apical cell and a subapical cell. In all genera of the Dasyaceae the first periaxial cell is formed to one side of a pseudolateral, the second periaxial cell to the other side of and slightly underneath the pseudolateral (Jong et al. 1997). As a result a relationship exists between the primary branching pattern and the sequence of periaxial cell formation, limiting the number of possible patterns. On morphological grounds two different primary thallus organisations can be distinguished: a radial and an alternate-distichous pattern. Thallus architecture can be further categorised based on the morphology of the pseudolaterals, which can be entirely monosiphonous to largely polysiphonous (Fig. 22). In certain genera further modifications of these basic patterns of thallus organisation have occurred by means of anastomosis of the pseudolaterals (e.g., *Dictyurus* and *Thuretia*). In species with a primary radial structure, the position where the first periaxial cell is formed follows the spiral of pseudolaterals (often a 2/5 spiral). The periaxial cells therefore are

formed in a circular sequence ([Fig. 23](#)). This is true for all primary radially organised genera of the Dasyaceae: *Dasya*, *Eupogodon*, and *Rhodoptilum*. Genera of the Dasyaceae characterised by a dorsiventral or a bilateral symmetry do not differ in the position of the pseudolaterals. In both cases pseudolaterals are deflected distichously. However, the sequence of periaxial cell formation differs between dorsiventral and bilaterally organised thalli. In *Colacodasya*, *Dasysiphonia*, and *Heterosiphonia* the first periaxial cell is always formed on the same side of the thallus, the dorsal side. The other periaxial cells are alternately formed on the left or right side of the first periaxial. The last periaxial cell is cut off opposite the first, on the ventral side of the thallus. This sequence of periaxial cell formation is referred as alternating-switching by Jong et al. (1998). In the genera characterised by a primary bilateral organisation, *Dictyurus*, *Dipterocladia*, *Tapeinodasya* and *Thuretia*, the position of the first periaxial cells shifts from the dorsal to the ventral side of the thallus, but the relative position of the periaxial cells does not switch as in dorsiventrally organised taxa. The mode of periaxial cell formation encountered in bilateral genera is referred to by Jong et al. (1998) as alternating-clockwise.

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### Note added in proof:

*Tapeinodasya bornetii* has since been collected from south-western Madagascar by the last author, indicating that the species is even more widespread than indicated in this paper. Specimen details: Madagascar, Beravy, 18 km North of Tuléar, growing on horizontal rock substrate of the reef flat, just exposed at spring low water, (Coppejans, Douterlungne & Razanakoto, 22.viii.2002, GENT HEC 15151).

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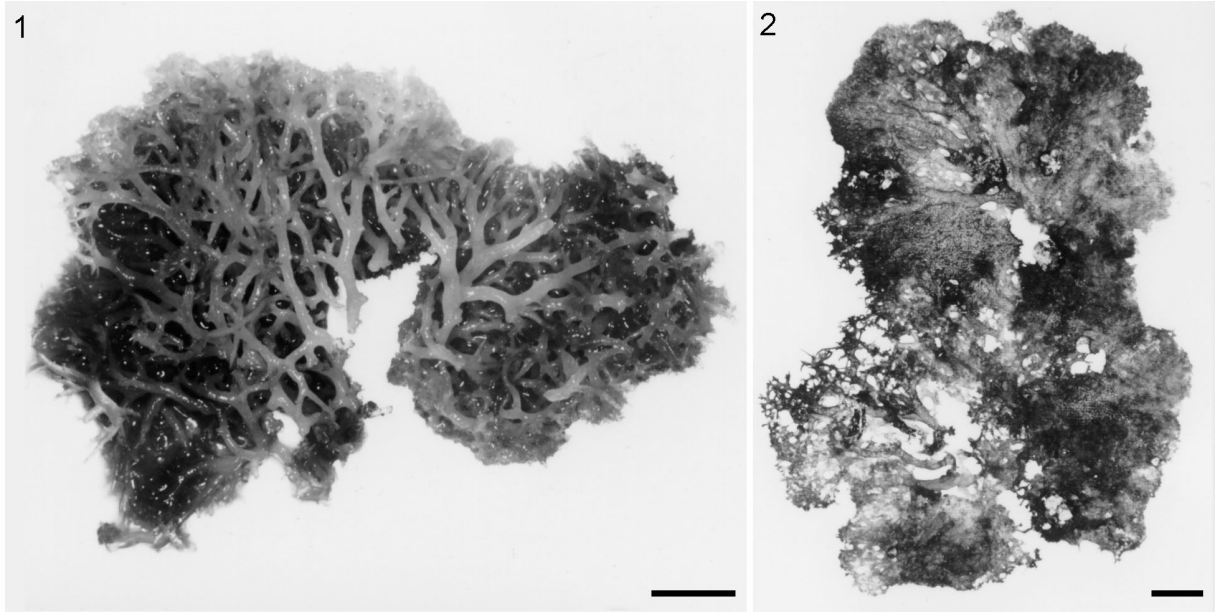
## REFERENCES

- Aregood, C.C. and Hackett, H.E. 1971.  
A new *Dictyurus* (Rhodophyceae, Dasyaceae) from the Maldive Islands, Indian Ocean. *Journal of the Elisha Mitchell Scientific Society* 87: 91–96.
- Coppejans, E. 1975.  
Végétation marine de l'île de Port-Cros (Parc National). XI. Sur *Halodictyon mirabile* Zanard. (Rhodophyceae). *Biologisch Jaarboek (Dodonaea)* 43: 116–126.
- Coppejans, E. and Boudouresque, C.F. 1984.  
Découverte du gamétophyte et du tétrasporophyte de *Dasyella gracilis* Falkenberg (Rhodophyta: Ceramiales). *Bulletin de la Société Royale de Botanique de Belgique* 117: 8–18.
- Coppejans, E., De Clerck, O., Leliaert, F. and Dargent, O. 2001.  
Progress of the taxonomic research on benthic marine algae (Chlorophyta, Phaeophyta and Rhodophyta) along the East African coast. In Richmond, M.D. and Francis, J. (eds.), *Marine Science Development in Tanzania and Eastern Africa. Proceedings of*

- the 20th Anniversary Conference on Advances in Marine Science in Tanzania. 28 June - 1 July, 1999, Zanzibar, Tanzania. University of Dar es Salaam/SIDA-SAREC/CIDA/USAID/ WIOMSA. Pp. 401–418.*
- De Toni, G.B. 1905.  
*Sylloge algarum ... Vol. IV. Florideae. Sectio IV. Patavii. 1523–1973.*
- De Toni, G.B. 1924.  
*Sylloge algarum ... Vol. VI. Florideae. Additamenta. Patavii. xi + 767 pp.*
- Falkenberg, P. 1901.  
*Die Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeres-abschnitte. Frielander und Sohn, Berlin. xvi + 754 pp.*
- Holmgren, P.K., Holmgren, N.H., and Barnett, L.C. 1990.  
*Index Herbariorum, I. The Herbaria of the World, 8<sup>th</sup> ed. New York Botanical Garden, New York. x + 693 pp. [Regnum Vegetabile vol. 120].*
- Hommersand, M.H. 1963.  
The morphology and classification of some Ceramiaceae and Rhodomelaceae.  
*University of California Publications in Botany 35: 165–366.*
- Jong, Y.S.D.M. de 1997.  
Studies on Dasyaceae. 1. Reproductive structures of *Eupogodon planus* and *E. spinellus* (Ceramiaceae, Rhodophyta) from Corsica (Mediterranean). *Phycologia 36: 281–292.*
- Jong, Y.S.D.M. de, Prud'homme van Reine, W.F., and Lokhorst, G.M. 1997.  
Studies on Dasyaceae. 2. A revision of the genera *Eupogodon* and *Dipterocladia* gen. nov. (Ceramiaceae, Rhodophyta). *Botanica Marina 40: 421–450.*
- Jong, Y.S.D.M. de, Prud'homme van Reine, W.F., Van Der Wurff, A.W.G., Stam, W.T., and Olsen, J.L. 1998.  
Studies on Dasyaceae. 3. Towards a phylogeny of the Dasyaceae (Ceramiaceae, Rhodophyta), based on comparative rbcL gene sequences and morphology. *European Journal of Phycology 33: 187–201.*
- Kajimura, M. 1992.  
A new species of *Dasysiphonia* (Dasyaceae, Rhodomelaceae) from the Sea of Japan. *Botanica Marina 35: 407–413.*
- Kylin, H. 1930.  
Über die Entwicklungsgeschichte der Florideen. *Lunds Universitets Årsskrift N. F. Avd. 2 26: 1–104.*
- Kylin, H. 1956.  
*Die Gattungen der Rhodophyceen. Gleerups, Lund. xv + 673 pp.*
- Lee, I.K. and West, J.A. 1979.  
*Dasysiphonia chejuensis* gen. et sp. nov. (Rhodophyta, Dasyaceae) from Korea. *Systematic Botany 4: 115–129.*
- Millar, A.J.K. 1996.  
*Dasya roslyniae* sp. nov. (Dasyaceae, Rhodophyta), with a discussion on generic distinctions among *Dasya*, *Eupogodon*, *Rhodoptilum* and *Pogonophorella*. *Journal of Phycology 32: 145–157.*
- Norris, R.E., Wollaston, E.M., and Parsons, M.J. 1984.  
New terminology for sympodial growth in the Ceramiaceae (Rhodophyta). *Phycologia 23: 233–237.*
- Parsons, M.J. 1975.  
Morphology and taxonomy of the Dasyaceae and Lophothaliae (Rhodomelaceae) of the Rhodophyta. *Australian Journal of Botany 23: 549–713.*
- Parsons, M.J. and Womersley, H.B.S. 1998.



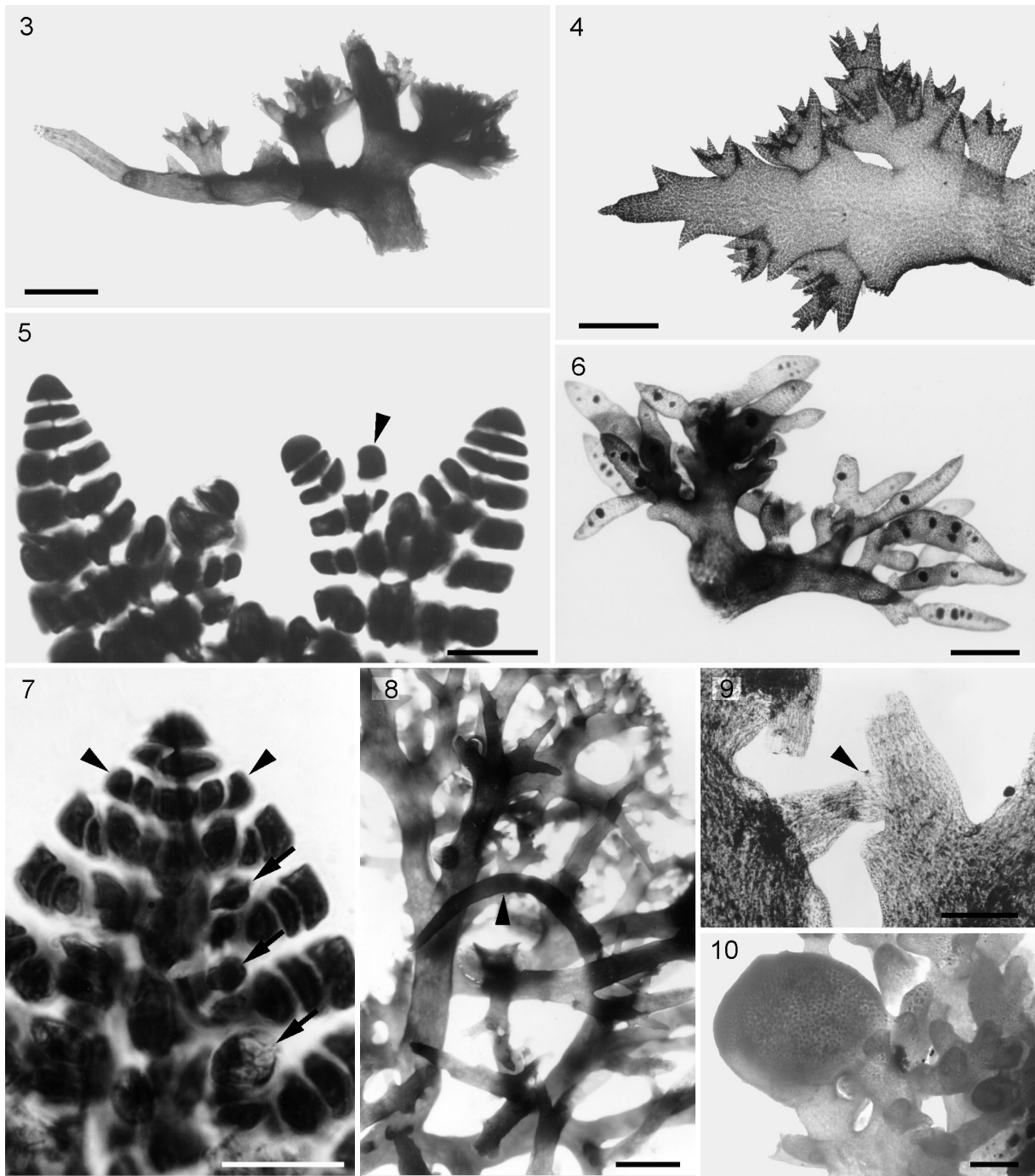
- The family Dasyaceae Kützing 1843: 413, 414. In: (H.B.S. Womersley) *The Marine Benthic Flora of Southern Australia. Part IIIC*. State Herbarium of Australia. 422–510 pp.
- Ricker, R.W. 1987.  
*Taxonomy and Biogeography of Macquarie Island Seaweeds*. British Museum (Natural History), London. 344 pp.
- Rosenberg, T. 1933.  
*Studien über Rhodomelaceae und Dasyaceae*. Gleerups, Lund. 87 pp., 25 pls.
- Saunders, G.W., Strachan, I.M., West, J.A., and Kraft, G.T. 1996.  
Nuclear small-subunit ribosomal RNA gene sequences from representative Ceramiaceae (Ceramiales, Rhodophyta). *European Journal of Phycology* 31: 23–29.
- Silva, P.C., Meñez, E.G., and Moe, R.L. 1987.  
Catalog of the benthic algae of the Philippines. *Smithsonian Contributions to the Marine Science* 27: iv + 179 pp.
- Silva, P.C., Basson, P.W., and Moe, R.L. 1996.  
Catalogue of the benthic marine algae of the Indian Ocean. *University of California Publications in Botany* 79: xiv + 1259 pp.
- Stegenga, H., Bolton, J.J., and Anderson, R.J. 1997.  
Seaweeds of the South African west coast. *Contributions from the Bolus Herbarium* 18: 1–655.
- Velasquez, G.T., Trono, G.C. Jr., and Doty, M.S. 1975.  
Algal species reported from the Philippines. *Philippine Journal of Science* 101: 115–169.
- Weber-van Bosse, A.A. 1904.  
Note sur deux algues de l'Archipel Malaisien. *Receuil des Travaux Botanique Néerlandais* 1: 96–105.
- Weber-van Bosse, A.A. 1913.  
IV. Marine algae, Rhodophyceae of the 'Sealark' Expedition, collected by Mr. J. Stanley Gardiner. *Transactions of the Linnean Society of London, Second Series, Botany* 8: 105–142.
- Weber-van Bosse, A.A. 1914.  
[The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner, M.A. Reports:] No. XIV. Marine algae, Rhodophyceae. *Transactions of the Linnean Society of London, Second Series, Zoology* 16: 269–306.
- Weber-van Bosse, A.A. 1923.  
Liste des Algues du Siboga. III. Rhodophyceae, part 2. Ceramiales. *Siboga-Expeditie Monographie* 59c: 311–392.



**Figs 1-2.** Vegetative morphology *Tapeinodasya bornetii*.

Fig. 1. Habit of wet preserved specimen from Tanzania seen from underneath (HEC 11475).  
Scale = 1 cm.

Fig. 2. Habit of a herbarium specimen from Tanzania (HEC 12018). Scale = 1 cm.



**Figs 3-10.** Vegetative and reproductive morphology of *T. bornetii*.

Fig. 3. Lateral view of a horizontally orientated axis with radially arranged axes developing from its upper surface. Scale = 500  $\mu$ m.

Fig. 4. Surface view of a horizontally orientated axis with radially arranged axes developing from the axils of the pseudolateral (arrows). Scale = 500  $\mu$ m.

Fig. 5. Detail of the sympodial apical organisation (arrowhead): newly formed apex). Scale = 50  $\mu$ m.

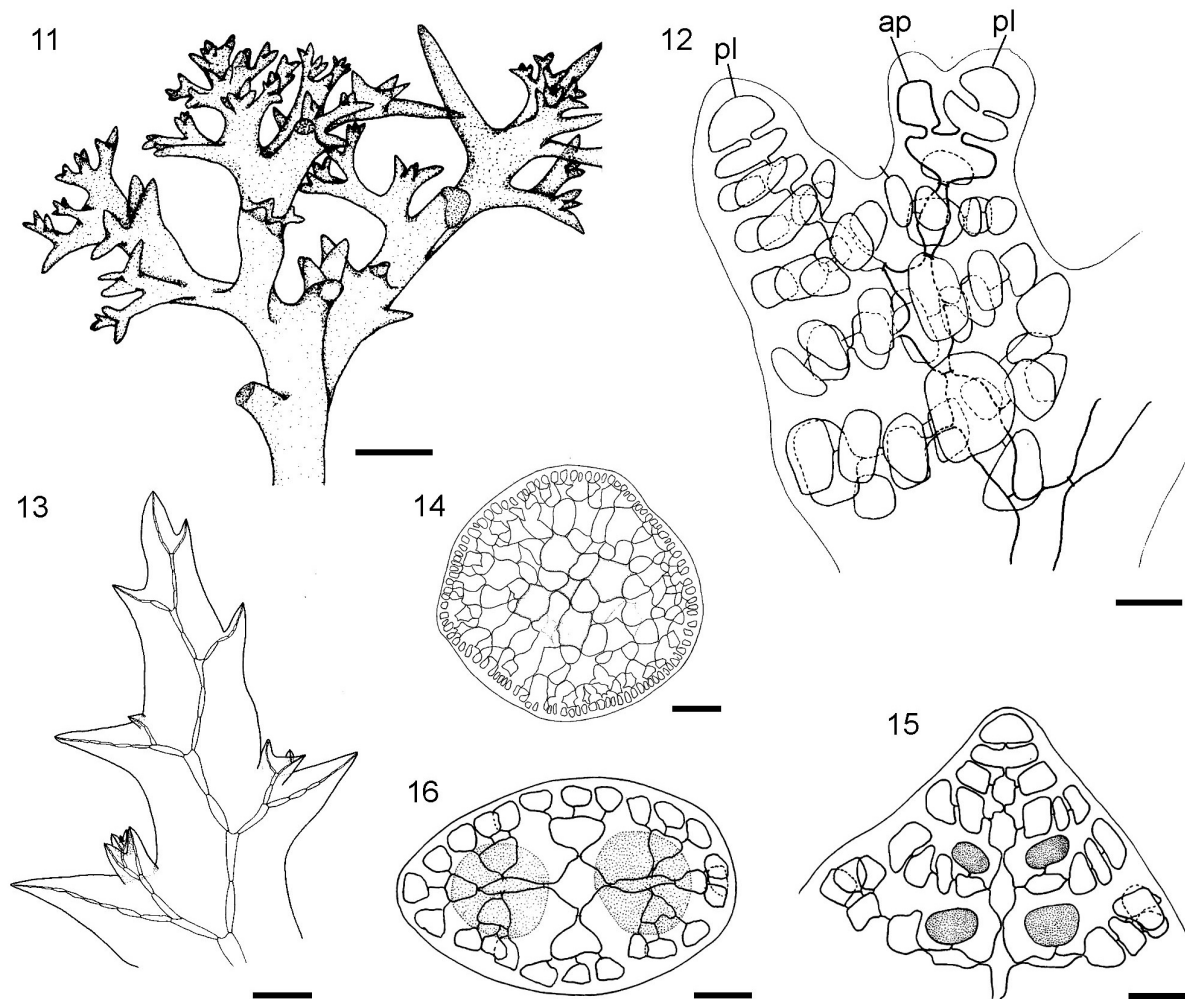
Fig. 6. Detail of the apical part of the thallus with abundant tetrasporangial stichidia. Scale = 500  $\mu$ m.

Fig. 7. Detail of the apical part of a stichidium showing the production of a cover cell (arrowhead) prior to the formation of the tetrasporangium (arrows). Scale = 50  $\mu$ m.

Fig. 8. Recurved branch (arrowhead) developing in the middle part of the thallus. Scale = 2 mm.

Fig. 9. Detail of two anastomosing axes. Scale = 200  $\mu$ m.

Fig. 10. Detail of a mature cystocarp. Scale = 250  $\mu$ m.



**Figs 11-16. Vegetative and reproductive morphology of *T. bornetii*.**

Fig. 11. Detail of an apical part of the thallus. Scale = 1 mm.

Fig. 12. Detail of a vegetative apex showing cellulosympodial growth and an alternating-clockwise sequence of periaxial cell formation. Scale = 10 µm

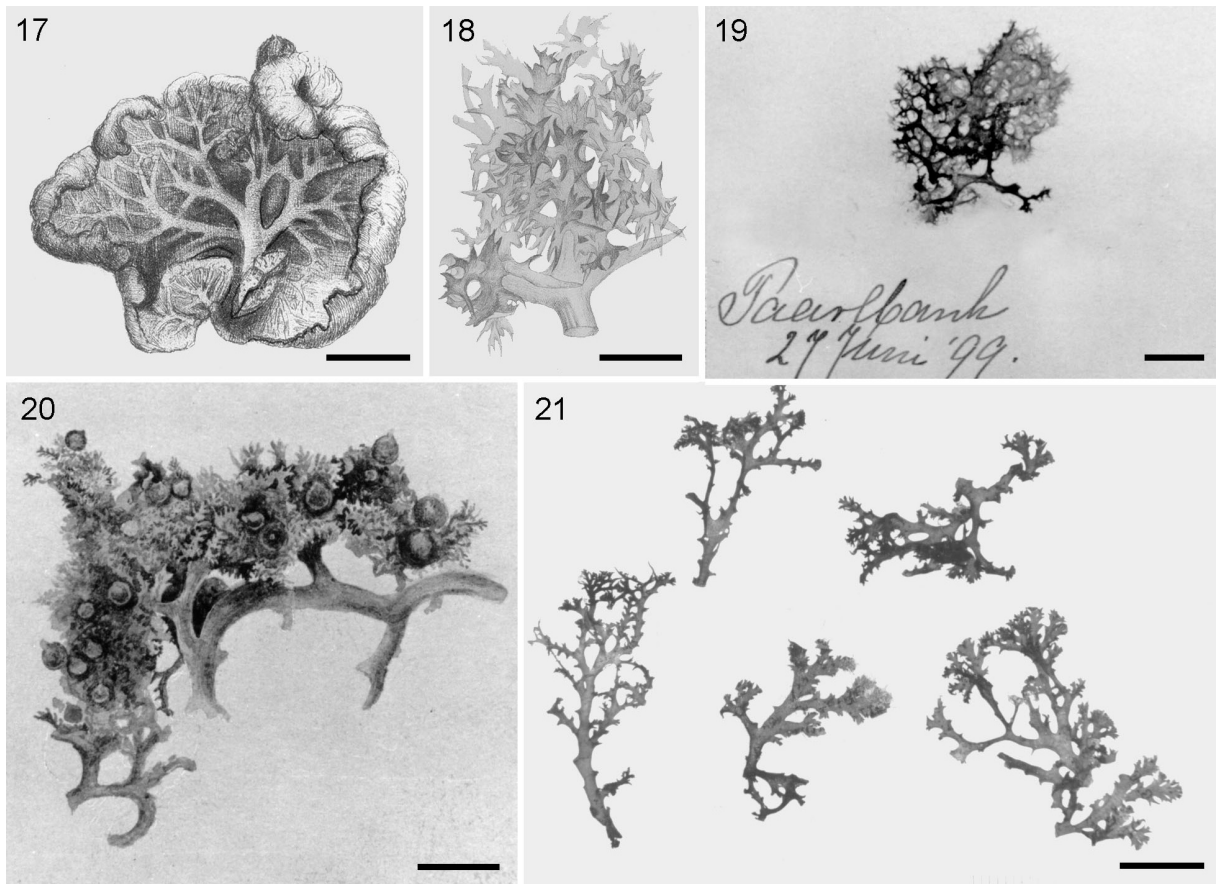
Fig. 13. Schematic representation of the branching pattern of a bilaterally organised sympodial main axis with apparently radially organised adventitious sympodial axes developing endogenously in the axils of the pseudolaterals. Scale = 250 µm.

Fig. 14. Transverse section of an older portion of an axis showing the axial cell surrounded by 4 periaxial cells and extensive cortical layers. Scale = 100 µm.

Fig. 15. Apex of a tetrasporangial stichidium showing the formation of a cover cell prior to the formation of a tetrasporangium from the second and third periaxial cell (first and fourth periaxial cells and derivatives are not illustrated). Scale = 25 µm.

Fig. 16. Cross section through a mature part of a tetrasporangial stichidium. Scale = 50 µm.

Abbreviations: ap : apex; pl : pseudolateral.



**Figs 17-21.** Type material and original illustrations of *T. bornetii* and *T. etheliae*.

Fig. 17. Original drawing of *T. bornetii* by Weber-van Bosse (1923: pl. x, fig. 1). Scale = 1 cm.

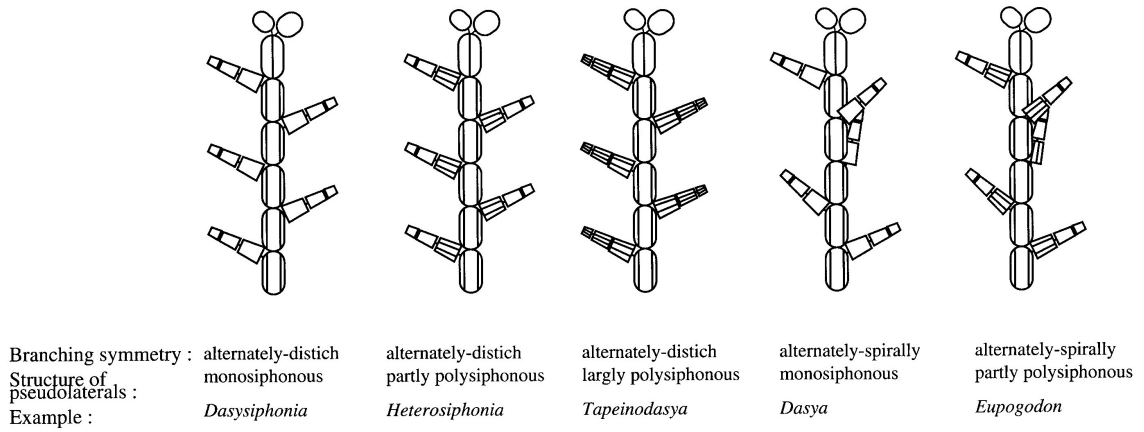
Fig. 18. Original drawing of an apical part of *T. bornetii* by Weber-van Bosse (1923: pl. x, fig. 2). Scale = 5 mm.

Fig. 19. Lectotype of *T. bornetii* from the Sulu Archipelago, Philippines (L 941.155-155). Scale = 1 cm.

Fig. 20. Original drawing of a cystocarpic specimen by Weber-van Bosse (unpublished). Scale = 5 mm.

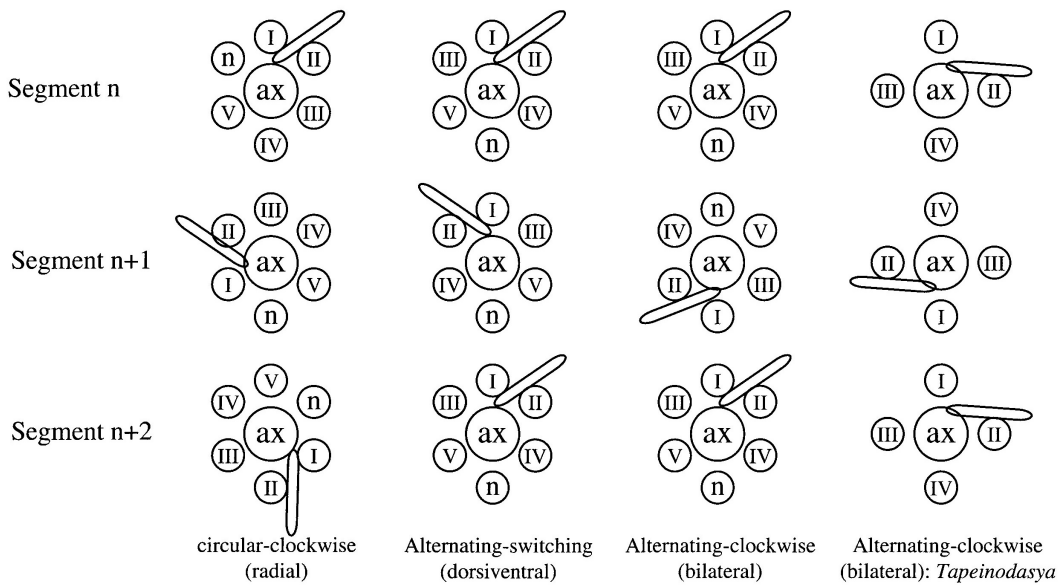
Fig. 21. Holotype of *T. etheliae* from the Amirante Islands, Seychelles (L. 950.45-180). Scale = 1 cm.

Fig. 22



**Fig. 22.** Schematic representation of the different thallus structures in the Dasyaceae.

Fig. 23



**Fig. 23.** Schematic representation of the relationship between the deflection of the pseudolaterals (grey bar) and the mode of periaxial formation in the Dasyaceae.