

# Morphology and systematics of two aberrant species of *Dictyota* (Dictyotaceae, Phaeophyta), including a discussion on the generic boundaries in the tribe Dictyoteae

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**Key words:** *Dictyota*, *Dictyotaceae*, morphology, systematics, generic boundaries

## Abstract

*Dictyota naevosa* (Suhr) Montagne and *D. radicans* Harvey possess characters that do not conform to the generic description of *Dictyota*. The generic boundaries in the tribe Dictyoteae are thus called into question. *Dictyota naevosa* differs from other *Dictyota* species by having more than one layer of cortical cells in the lower part of the thallus. The presence of a multilayered cortex is the only character distinguishing *Pachydictyon* from *Dictyota*. *Dictyota radicans* is characterised by the presence of terete surface proliferations, a feature used to distinguish *Glossophora* from *Dictyota*. Both *D. naevosa* and *D. radicans* have clear sister species that are currently placed in the genus *Dilophus*. The segregation of *Dilophus* from *Dictyota*, as still advocated by some authors, therefore becomes untenable. The morphological evidence leads us to question the generic status of *Pachydictyon*, *Glossophora* and *Glossophorella*, since the characters used to delineate these genera are commonly found in some species of *Dictyota*.

## Introduction

Within the brown algal family Dictyotaceae, two tribes are currently recognised, the Dictyoteae and Zonarieae, differentiated on the basis of the number of apical cells. In Dictyoteae there is a single apical cell, whereas in Zonarieae there is a marginal row or cluster of apical cells. Within the tribe Dictyoteae, J. Agardh (1848, 1882, 1894, 1897) recognised four genera: *Dictyota*, *Dilophus*, *Glossophora* and *Pachydictyon*, distinguished by the relative number of cortical and medullary layers and the presence of surface proliferations. Recently a new genus was added to the Dictyoteae, *Glossophorella* Nizamuddin & Campbell (1995). *Dictyota* Lamouroux (1809), as defined by Hörnig *et al.* (1992a), includes species characterised by a single lenticular, transversely orientated apical cell, and a parenchymatous thallus composed of a cortex and a medulla.

In the past, species characterised by a multilayered medulla, in at least some part of the thallus, were assigned to *Dilophus* J. Agardh (1882). The distinction, however, between *Dictyota* and *Dilophus*, was not clear-cut because the extent to which the medulla was multilayered varied substantially and some species were particularly hard to assign to one or the other genus (Setchell & Gardner, 1925; Taylor, 1945; Dawson, 1950). Eventually the two genera were merged by Hörnig *et al.* (1992a, b) on the basis of culture experiments that showed that the number of medullary layers can be altered in many species depending on the culture conditions. Although the merger has been accepted by several authors (e.g. Silva *et al.*, 1996; Wynne, 1998), some authors still recognise *Dilophus* as a separate genus (Phillips, 1992; Millar & Kraft, 1994; Huisman, 2000). *Pachydictyon* J. Agardh (1894) is characterised by a single-layered

medulla and multilayered cortex. Although the status of *Pachydictyon* has been questioned in the past (Setchell & Gardner, 1925; Dawson, 1950), it is still currently recognised. *Pachydictyon coriaceum* (Holmes) Okamura, a species from Japan and California, is characterised by a medulla which may comprise two layers of cells at the margins. Therefore, the species was transferred to *Glossophorella* Nizamuddin & Campbell (1995), which accommodates species with a multilayered cortex as well as a multilayered medulla. *Glossophora* J. Agardh (1882), a genus containing three species restricted to southern Australia and the Pacific coast of South America, is characterised by a unilayered cortex and medulla, but the surface is often densely beset with terete proliferations.

The morphology and taxonomy of *D. naevosa* (Suhr) Montagne and *D. radicans* Harvey was studied in the framework of a revision of the genus in the Indian Ocean (De Clerck, 1999). The results are discussed in this paper. Because these species possess characters that do not conform to the generic description of *Dictyota*, we have been led to reassess generic definitions in the tribe Dictyoteae.

## Materials & Methods

Specimens were collected by SCUBA or snorkelling during several trips in the Indian Ocean, Indonesia and Papua New Guinea since 1980 by ourselves. Material was prepared as herbarium specimens or preserved in 4% formalin/seawater and lodged in GENT. Additional specimens were examined from several herbaria (Appendix 1). Herbarium abbreviations follow Holmgren *et al.* (1990).

Morphological data result from morphometric analyses as described by De Clerck & Coppejans (1999).

## Results

### *Dictyota naevosa* (Suhr) Montagne 1840: 145

#### Description

Thallus completely erect, sparsely branched and very robust, 10–35 cm long (Fig. 1); attached by a

single stupose base from which one to several fronds (and usually a few narrow proliferations) arise; the base often with a velvet patch of rhizoids; colour *in situ* medium brown, bluish iridescent; dry specimens medium to dark brown. All straps of the thallus of similar width, reaching their maximum width in the middle part of the thallus, gradually tapering towards the base and apices; average width: (3.5–) 6.3–10.7 (–16.0) mm, proximal width: (2.0–) 3.8–6.5 (–11.0) mm, distal width: (3.0–) 8.7–15.0 (–22.0) mm, Wd/Wp: (1.9–) 2.2–2.5 (–2.6); length: (12.0–) 24.2–48.0 (–86.0) mm; L/W: (2.0–) 3.0–6.1 (–8.8). Apices rounded, apical segments very long (up to 135 mm) and spatulate, often eroded; apical cell protruding. Branching isotomous dichotomous to somewhat irregular (often as a result of damage), sparse, mostly to 2 or 3 orders; branching angle (15–) 25–40 (–50)°. Margins smooth, proliferations rare. Surface proliferations absent. Hair tufts common. Cortex and medulla predominantly unilayered, but several layers of both cortical and medullary cells frequently observed especially in Australian specimens (Figs. 2–4); Cortical cells (14–) 22–23 (–36) µm long, (10–) 14–16 (–24) µm wide, ratio: (1.3–) 1.4–1.6 (–1.9), and (22–) 23–26 (–29) µm high; medullary cells (77–) 112–120 (–197) µm long, (48–) 68–71 (–120) µm wide, ratio: (1.5–) 1.6–1.7 (–1.8), and (120–) 130–160 (–188) µm high.

Sporangia on both surfaces of the thallus, also present in the apical segments, grouped in conspicuous ovate to oblong sori, often surrounding one or two central hair tufts (most apparent in the apical segments and becoming more obscure near the basal parts of the thallus), hair tufts disappear in older parts; sori (433–) 716 (–1,435) µm wide, (340–) 1,640 (–5,740) µm long, ratio: (1.35–) 2.5 (–5.1) (Figs. 6, 7); sporangia more or less drop-shaped, not surrounded by an involucre, mature sporangia born on a single stalk cell, width: 60–100 µm, height: 110–130 µm (Fig. 8); divided sporangia frequently observed.

Male gametophytes with sori of antheridia evenly dispersed over the whole thallus, also present in the apical segments, often merging with other sori to form large coenosori (Figs. 9, 10); sori (272–) 325 (–758) µm wide, (400–) 725 (–1,846)

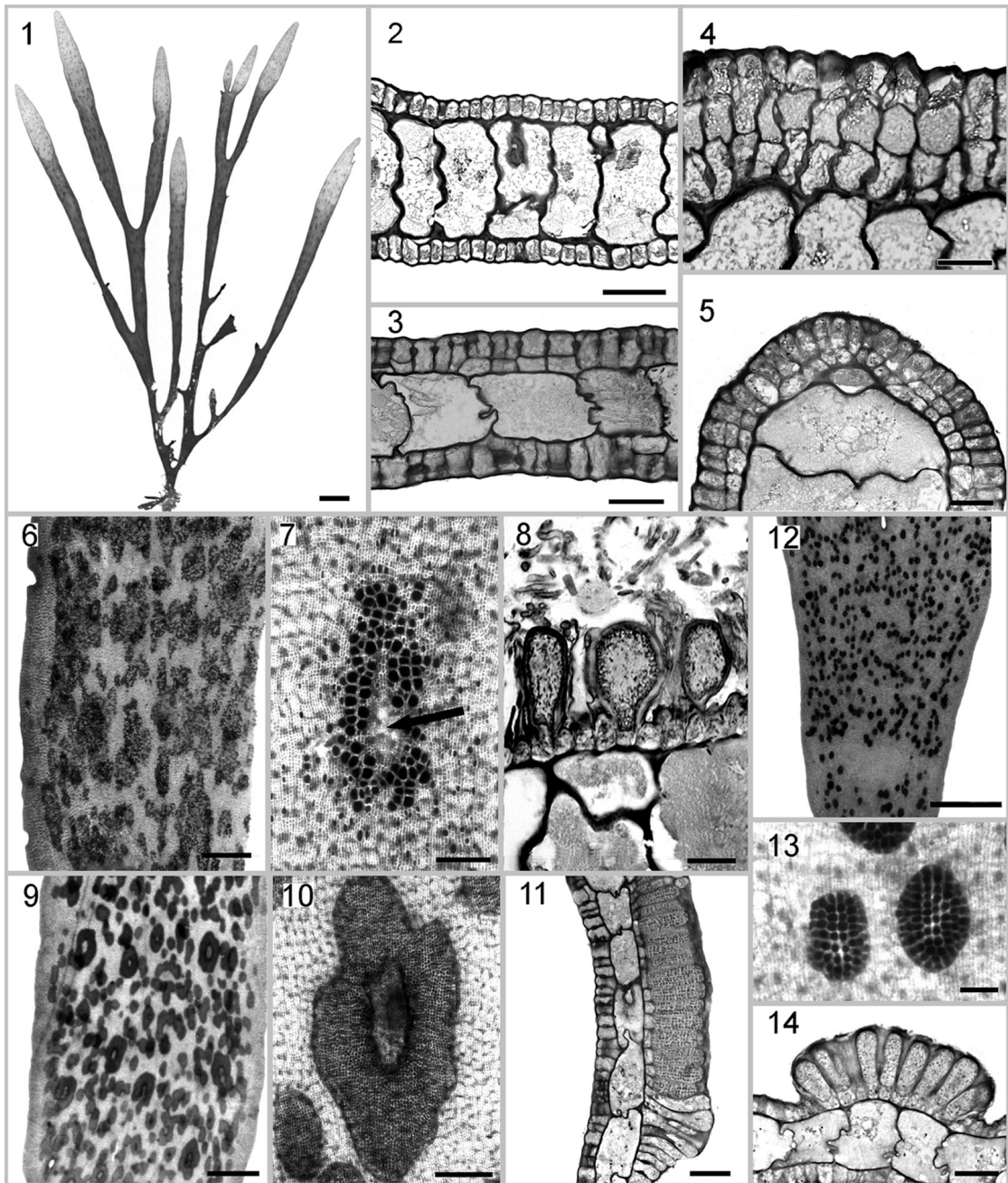


Plate 1. Morphology and anatomy of *Dictyota naevosa*.

*Fig. 1.* Habit of *D. naevosa* (HEC 11000) (scale: 1 cm).

*Fig. 2.* Transverse section showing unilayered cortex and medulla (scale: 100  $\mu$ m).

*Fig. 3.* Transverse section showing multiple duplications of the cortical layer (scale: 100  $\mu$ m).

*Fig. 4.* Transverse section of a three-layered cortex in the lower part of the thallus (scale: 50  $\mu$ m).

*Fig. 5.* Transverse section of a thallus margin with multiple duplications of the cortical layer (scale: 50  $\mu$ m).

*Fig. 6.* Surface view of tetrasporangial strap (scale: 2.5 mm).

*Fig. 7.* Detail of a tetrasporangial sorus with a central hair tuft (arrow) (scale: 500  $\mu$ m).

*Fig. 8.* Transverse section of a tetrasporangial sorus (scale: 50  $\mu$ m).

*Fig. 9.* Surface view of an antheridial strap (scale: 2.5 mm).

*Fig. 10.* Detail of an antheridial sorus with a central hair tuft (scale: 500  $\mu$ m).

*Fig. 11.* Transverse section of an antheridial sorus surrounded by 6 unicellular paraphyses (scale: 50  $\mu$ m).

*Fig. 12.* Surface view of an oogonial strap (scale: 2.5 mm).

*Fig. 13.* Detail of oogonial sori (scale: 100  $\mu$ m).

*Fig. 14.* Transverse section of an oogonial sorus (scale: 50  $\mu$ m).

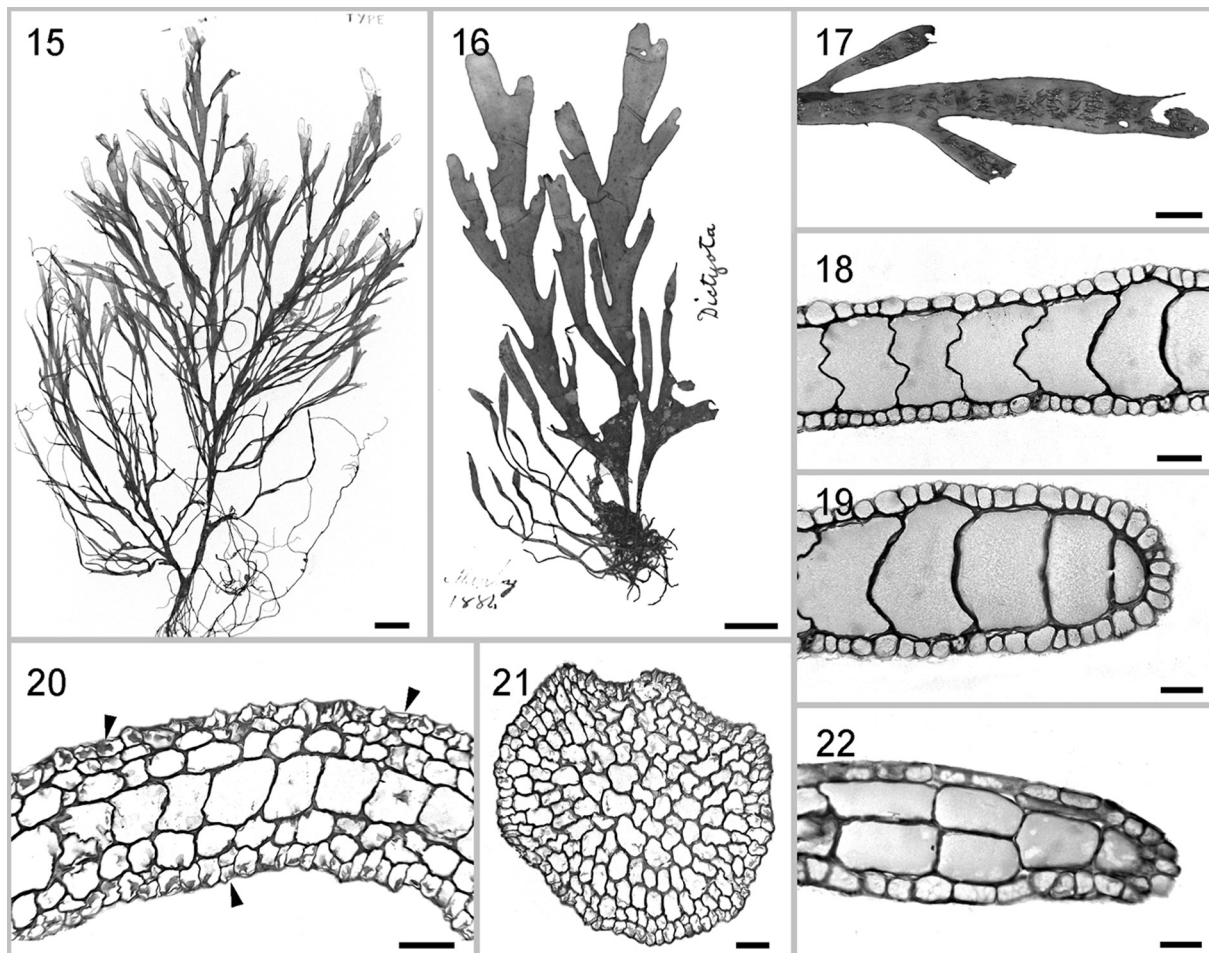


Plate 2. Morphology and anatomy of *D. radicans*.

Fig. 15. Lectotype specimen of *D. radicans* (TCD Harvey 69A) (scale: 1 cm).

Fig. 16. Habit of a broad specimen (MEL 16991) (scale: 1 cm).

Fig. 17. Detail of an apical portion of the thallus with multiple surface proliferations (scale: 5 mm).

Fig. 18. Transverse section through the thallus showing a unilayered cortex and medulla (scale: 50  $\mu$ m).

Fig. 19. Transverse section of a thallus margin (scale: 50  $\mu$ m).

Fig. 20. Transverse sections of a transition zone between a normal strap and a terete stolonoidal fibre (scale: 50  $\mu$ m).

Fig. 21. Transverse section of a terete stolonoidal fibre (scale: 100  $\mu$ m).

Fig. 22. Longitudinal section of a terete surface proliferation showing a multilayered medulla (scale: 50  $\mu$ m).

$\mu$ m long, L/W: (0.9–) 2.3 (–4.3); antheridia, born on a single stalk cell, 22  $\mu$ m wide, 65  $\mu$ m high; antheridia per sorus: (31–) 52 (–94); sori surrounded by 3–6 rows of unicellular paraphyses (Fig. 11).

Female gametophytes, with sori of oogonia evenly distributed over the whole surface, also present in the apical segments, resembling sori of tetrasporangia but not associated with hair tufts (Figs 12, 13); sori (237–) 296 (–401)  $\mu$ m wide, (340–) 415 (–495)  $\mu$ m long, L/W: (1.1–) 1.4

(–1.7); oogonia 65  $\mu$ m wide, 140  $\mu$ m high; oogonia per sorus: (39–) 65 (–88) (Fig. 14).

*Remarks*

The distribution of *D. naevosa* is limited to South Africa and Australia. *Dictyota naevosa* is the only species occurring in the Indian Ocean characterised by sporangia that are grouped in ovate to oblong sori. Apart from this reproductive character, the large size, sparse branching and the

extremely long apical segments are distinctive. Only *D. hauckiana* Nizamuddin attains a similar size, with long and broad internodes, but the latter species has conspicuously dentate margins and does not occur in either South Africa or Western Australia (Hauck, 1884, as *D. atomaria* Hauck; Børgesen, 1932, as *D. atomaria*; De Clerck & Coppejans, 1999). *Dictyota naevosa* closely resembles *D. diemensis* Kützing, a southern Australian species recorded from Point Sinclair, South Australia to Port Phillips, Victoria and Tasmania (Womersley, 1987; Phillips *et al.*, 1990).

There is, however, an overlap in the distribution of these species as *D. naevosa* occurs from Western Australia to the Gulf of St Vincent. Kützing (1859) distinguished both species on the shape of the apices. Womersley (1987) distinguishes *D. naevosa* from *D. diemensis* on colour differences, thallus size, the length of the apical segments and the degree of branching. However, the distinction between both taxa should be re-examined as some specimens are particularly hard to assign to either of the two species. *Dictyota naevosa* might also be closely related to *D. phlyctaenodes* Montagne (1852) from the Juan Fernandez Islands, although the morphology of the sporangial sori has not been described in detail (Levring, 1941). *Dictyota naevosa* occasionally forms a multilayered cortex near the basal parts of the thallus. In South African specimens this is usually restricted to a duplication of a cortical cell by means of a tangential division (Fig. 3), but Australian specimens sometimes form a multilayered cortex up to four cells thick (Fig. 4).

*Dictyota intermedia* Zanardini, a species known from Queensland, New South Wales and Lord Howe Island (Allender & Kraft, 1983, as *Dil. intermedius* (Zanardini) Allender & Kraft; Millar & Kraft, 1994, as *Dil. intermedius*), is clearly distinct from *D. naevosa* by the constant presence of a multilayered medulla near the margins, numerous surface proliferations, and reproductive structures which form tiers across the width of the straps. *Dictyota naevosa* sometimes forms a multilayered medulla near the margins of the straps in the basal part of the thallus. This is not a constant feature, however, and several specimens fail to reveal a mul-

tilayered medulla. Nevertheless, both species have a many characters in common: sporangia grouped in sori associated with hair tufts, drop-shaped sporangia, spatulate apices and a locally multilayered cortex (Phillips, 1992, as *Dil. intermedius*). Several of these characters, especially the formation of the sporangial sori, are unique in *Dictyota* (apart from *D. diemensis* and possibly *D. phlyctaenodes*), indicating a close relationship between the two species.

### *Dictyota radicans* Harvey 1855: 536

#### *Description*

Thallus completely erect, 8–20 cm long; attached by means of numerous, long, entangled, terete stolonoid fibres (Figs. 15, 16); fibres not restricted to the basal parts, but often originating from transformed apices, ca. 300–600 µm in diameter, multilayered; colour *in situ* medium brown, non-iridescent, often covered by encrusting Corallinales; dry specimens medium to pale brown. Straps variable in width, some tapering abruptly and forming terete stolonoid fibres, others gradually widening towards the apices; average width: (1.5–) 2.9–4.8 (–9.2) mm, proximal width: (1.0–) 1.8–3.0 (–6.5) mm, distal width: (1.8–) 4.2–5.8 (–12.2) mm, Wd/Wp: (1.6–) 1.9–2.2 (–2.6); length: (8.0–) 10.4–14.5 (–18.0) mm; L/W: (1.6–) 2.7–3.6 (–8.8). Apices broadly rounded to acute; apical segments sometimes very long and spatulate (Fig. 17) or tapering to an acute apex and forming stolonoid fibres; apical cell level or in a slight depression. Branching anisotomous dichotomous, often appearing irregular due to the formation of stolonoid fibres; branching angle (25–) 30–50 (–60)°. Margins smooth, marginal proliferations common; terete surface proliferations common to numerous (often associated with sporangia, some developing into new straps or stolonoid fibres) (Figs. 17, 22–25); surface of the thallus undulated in fully grown parts of the thallus. Hair tufts common. Cortex and medulla unilayered (Figs. 18, 19), medulla becoming multilayered when apices taper into stolonoid fibres (Figs. 20, 21); straps generally thicker near

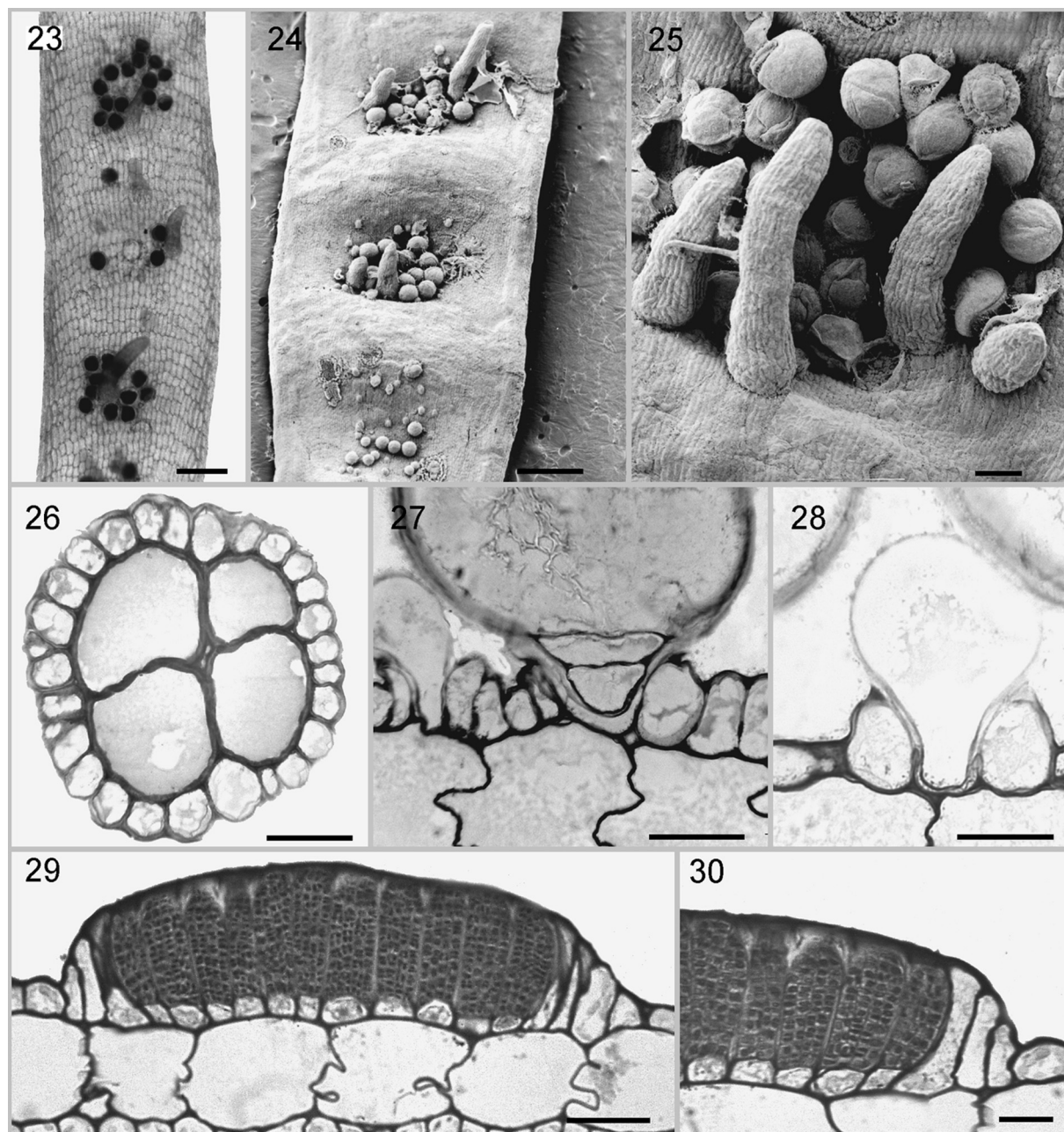


Plate 3. Reproductive morphology of *D. radicans*.

*Fig. 23.* Surface view of a strap with block-like tetrasporangial sori and surface proliferations (scale: 2 mm).

*Fig. 24.* SEM of tetrasporangial sori confined to the concavities of the undulated thallus (scale: 1 mm).

*Fig. 25.* SEM detail a tetrasporangial sorus with some terete surface proliferations (scale: 100  $\mu$ m).

*Fig. 26.* Transverse section of a surface proliferation (scale: 100  $\mu$ m).

*Fig. 27.* Transverse section of a tetrasporangium showing 2 stalk cells (scale: 50  $\mu$ m).

*Fig. 28.* Transverse section of a young tetrasporangium prior to the formation of the stalk cells (scale: 25  $\mu$ m).

*Fig. 29.* Transverse section of an antheridial sorus (scale: 50  $\mu$ m).

*Fig. 30.* Detail of an antheridial sorus surrounded by 3 rows of unicellular paraphyses (scale: 25  $\mu$ m).

the margins (up to 175  $\mu\text{m}$ ) compared to the central parts (up to 125  $\mu\text{m}$ ); cortical cells (31–) 44–51 (–77)  $\mu\text{m}$  long, (15–) 21–23 (–26)  $\mu\text{m}$  wide, ratio: (1.8–) 2.2–2.4 (–2.7) and (18–) 21–23 (–26)  $\mu\text{m}$  high; medullary cells (102–) 151–170 (–199)  $\mu\text{m}$  long, (51–) 60–67 (–82)  $\mu\text{m}$  wide, ratio: (2.0) 2.3–2.6 (–2.9) and (65–) 95–115 (–135)  $\mu\text{m}$  high.

Sporangia on both surfaces of the thallus, grouped in more or less square, block-like patches in the concavities of the undulated straps, most common in the apical and subapical parts (Figs. 23–25); mature sporangia borne on two-celled stalks, surrounded by an inconspicuous involucre, width: 160–198  $\mu\text{m}$ , height: 150–185  $\mu\text{m}$ ; divided sporangia observed (Figs. 27, 28).

Male gametophytes with antheridia in similar alternating, concave patches to the sporangia, sori ovate to irregular in shape, 200–500  $\mu\text{m}$  wide, 250–600  $\mu\text{m}$  long, surrounded by 2–3 rows of unicellular paraphyses; antheridia 70–90  $\mu\text{m}$  long, 20–30  $\mu\text{m}$  wide.

Female gametophytes never observed.

#### Remarks

Womersley (1967; 1987) treated *D. radicans* Harvey as a synonym of *D. prolifera* Lamouroux. However, the latter species is a synonym of *D. crispata* Lamouroux (De Clerck, 1999). As pointed out by De Clerck & Coppejans (1997), *D. radicans* may superficially resemble *D. crispata* but differs fundamentally in the presence of basal stolonoidal fibres, the absence of involucre surrounding the sporangia, the presence of two sporangial stalk cells, and the grouping of sporangia in block-like sori.

*Dictyota radicans* is an Australian species characterised by the abundant presence of stolonoidal fibres, terete surface proliferations and sporangia confined to the concavities of the undulated straps. In the Indian Ocean, two other species are characterised by extensive stolonoidal fibres, *D. subrii* Murray and *D. stolonifera* Dawson (De Clerck & Coppejans, 1999). In both species, however, stolonoids are restricted to the basal parts, whereas in *D. radicans* stolonoidal fibres are often formed

on apical segments or result from terete surface proliferations. Furthermore, *D. stolonifera* lacks the undulated straps and surface proliferations. Straps of *D. subrii*, a South African species, are also undulated and sporangia are confined to block-like patches and subtended by 2-celled stalks similar to *D. radicans*. *Dictyota subrii*, however, is characterised by a medulla that is multilayered near the base of the thallus, but which becomes multilayered in the middle and upper apical portion of the thallus only near the margins (De Clerck, 1999). *Dictyota rugulosa* Lucas has similar undulated straps and surface proliferations (especially when fertile), but this species lacks the abundant stolonoidal fibres and has a multilayered marginal medulla (Lucas, 1935; Phillips, 1992, as *Dil. marginatus*).

Transverse sections of the transition zone between a normal strap and a terete stolonoidal fibre demonstrate that the multilayered nature of the fibres is not just the result of duplications of the medullary cells. In fact, both the cortical cells and medullary cells divide to produce a multilayered thallus. Medullary cells in stolonoidal fibres are much smaller than those of ordinary straps and the size difference between cortical and medullary cells becomes reduced.

#### Discussion

*Dilophus* was described by J. Agardh (1882) on the basis of a multilayered medulla. Initially 5 species were included in the genus, *Dil. alternans* J. Agardh [= *D. pinnatifida* Kützinger], *Dil. fastigiatus* (Sonder) J. Agardh [= *D. fastigiata* Sonder], *Dil. gunnianus* J. Agardh [= *D. gunniana* (J. Agardh) Hörnig, Schnetter & Prud'homme van Reine, the lectotype of *Dilophus* (De Toni, 1891)], *Dil. opacus* [= *D. fastigiata* Sonder], and *Dil. repens* (J. Agardh) J. Agardh [= *D. fasciola* (Roth) Lamouroux var. *repens* (J. Agardh) Ardissoni]. Apparently, the extent to which the medulla was multilayered was of no importance. *Dictyota fastigiata*, *D. gunniana* and *D. pinnatifida* are characterised by a medulla that is multilayered near the margins throughout the whole length of the thallus. At least near the base, this medulla is multilayered over the whole width

of the straps. The number of layers in the central part of the straps of the middle and apical parts of the thallus is variable in at least *D. fastigiata* and *D. gunniana*, ranging from 1–7 (Womersley, 1987; Phillips, 1992). The medulla of *D. fasciola* var. *repens* on the other hand is only multilayered in the stoloniferous holdfast and the basal regions of the erect parts (Feldmann, 1937; Nizamuddin, 1981). The latter situation, in particular, caused much confusion because several *Dictyota* species often exhibit a multilayered medulla in the extreme basal parts of the thallus (Schnetter & Bula-Meyer, 1982; Hörnig *et al.*, 1992a). The anatomy of *D. naevosa* and *D. binghamiae* further complicates the distinction between *Dictyota* and *Dilophus*, because in both species the medulla often becomes multilayered near the margins of the basal thallus parts (this paper; Dawson, 1950).

J. Agardh (1894) subdivided *Dilophus* according to whether the margins were thicker than the central part of the thallus or whether the thallus had a uniform thickness over the entire width of the straps. According to Womersley (1987), the presence of thicker margins is usually restricted to species with one central medullary layer and several marginal medullary layers. The morphology of *D. radicans* is, in this respect, extremely interesting because the straps are typically thicker near the margins, despite the presence of only a single medullary layer. Having shown by means of culture experiments that the presence of a multilayered medulla can easily be induced in many *Dictyota* species (including *D. dichotoma*, the generic type), Hörnig *et al.* (1992a) reduced *Dilophus* to a synonym of *Dictyota*. This decision, however, was not unanimously accepted by all authors (e.g. Phillips, 1992; Millar & Kraft, 1994; Huisman, 2000).

Apart from the fact that some species are difficult to assign to either of the two genera due to the occasional or local presence of a multilayered medulla, the morphology and anatomy of *D. naevosa* and *D. radicans* indicate that close phylogenetic relationships exist between members of the two genera. Reproductive structures have generally not been used to define generic boundaries in the Dictyotales (Phillips, 1997). Nevertheless, some interesting similarities in tetrasporangial morphol-

ogy and arrangement have been observed, which cross existing generic boundaries in the Dictyoteae. Phillips (1992) revealed the presence of two-celled stalks as opposed to one-celled stalks in at least three species (*D. fastigiata*, *D. rugulosa* and *D. robusta*) characterised by a multilayered medulla. In this study, it is shown that *D. radicans*, always treated as a species of *Dictyota sensu stricto*, is also characterised by sporangia subtended by two stalk cells. Similarly, the presence of an involucre which is either present or absent in both *Dictyota sensu stricto* and *Dilophus*, does not differentiate the two genera. Perhaps more remarkable is the arrangement of tetrasporangia in oblong sori surrounding one to several hair sori in *D. naevosa*. An identical sporangial arrangement is encountered in the closely related *D. diemensis* (Phillips *et al.*, 1990) and *D. intermedia* (Phillips, 1992). The latter species, however, is invariably characterised by a multilayered medulla.

Although criticised in the past (Setchell & Gardner, 1925; Dawson, 1950), the generic status of *Pachydictyon* was not discussed by Hörnig *et al.* (1992a). The only character put forward by J. Agardh (1894; 1897) to characterise *Pachydictyon* was the presence of a multilayered cortex. The genus contains at present four species, *P. polycladum* Kützinger, *P. paniculatum* (J. Agardh) J. Agardh, both from southern Australia, *P. coriaceum* (Holmes) Okamura from Japan and California and *P. aegerrime* Allender & Kraft from Lord Howe Island, Australia.

The lectotype of the genus, *P. furcellatum* J. Agardh, a synonym of *P. polycladum* (Kützinger) Womersley, is characterised by a multilayered cortex in the lower part of the thallus. The cortex in young plants is initially unilayered, becoming two to four cells thick with age by periclinal divisions in the larger basal axes only (Womersley, 1987). Cortical development in *P. paniculatum* is very similar, differing only in thickness (three to five cells). *Pachydictyon aegerrime*, on the other hand, is characterised by a unilayered cortex. Division of cortical cells only occurs near the margins in the basal part of the thallus, where a two-layered cortex can be observed.

Most species of *Dictyota* have a uniformly uni-



layered cortex as in the type of the genus, *D. dichotoma* (Hudson) Lamouroux. However, *D. naevosa*, may produce a cortex up to six cells thick near the basal parts (Womersley, 1987; this paper). Also, *D. binghamiae* J. Agardh, which was regarded conspecific with *P. coriaceum* by Dawson (1950), produces a multilayered cortex near the base. Further examples of local duplication of cortical cells near the margins of the thallus, similar to the situation in *P. aegerrime*, are offered by *D. radicans* (this study), *D. robusta* J. Agardh and *D. rugulosa* Lucas (Phillips, 1992, as *Dil. robustus* (J. Agardh) J. Agardh and *Dil. marginatus* J. Agardh). Similarly, Womersley (1987) noted that *G. nigricans* (J. Agardh) Womersley shows duplications of the cortex layer near the basal (especially marginal) parts of the thallus. Further studies, preferably based on the type species of *Pachydictyon* (*P. polycladum*), should clarify the generic status of the genus and its relationship with *Dictyota*. The decision to erect a new genus, *Glossophorella*, to accommodate species which show a multilayered medulla as well as a multilayered cortex, as advocated by Nizamuddin & Campbell (1995), only further complicates generic placement of certain species.

Typically, the surface of mature thalli of *Glossophora* is moderately to densely covered with terete to compressed proliferations (J. Agardh, 1882; Levring, 1941; Womersley, 1987). When terete, these surface proliferations show a multilayered medulla. Several species of *Dictyota* (and *Dilophus*) are characterised by surface proliferations. Such proliferations may either be compressed (e.g. *D. crispata* and *D. dumosa*) or terete (e.g. *D. intermedia* and *D. radicans*) and a multilayered medulla is often present. The presence of surface proliferations cannot unequivocally distinguish *Glossophora* from *Dictyota*. Therefore a re-examination of the type of *Glossophora* becomes a necessity.

## Acknowledgements

O. De Clerck is indebted to the Fund for Scientific Research-Flanders (FWO-Flanders) for a grant as postdoctoral researcher. Financial support was pro-

vided by FKFO projects 2.000.92 and G002496. We are grateful to the curators of the various herbaria who helped us out in retrieving the necessary specimens: Chantal Billard (CN), Jennifer Bryant (BM), Willem Prud'homme van Reine (L), Tim Entwisle (MEL), Michael Wynne (MICH), and Gerry Kraft and John West (MELU). Furthermore, we would like to thank Brian Womersley for kindly providing us with male specimens of *D. radicans*. Further thanks are expressed towards Dr Ngoile and Dr Julius, consecutive directors of the Institute of Marine Sciences, Zanzibar.

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## Appendix 1.

Selected specimens of *Dictyota naevosa* and *D. radicans* examined for morphological and anatomical studies

### *Dictyota naevosa*

Australia. Western Australia, Abrolhos, Pelsaert Group, Mostyns Lump (Kraft & Huisman, 14.x.1990, MELU K8590); Western Australia, Busselton (O'Brien, 8.i.1978, MELU K7113); Western Australia, Port Denison (Kraft, 14.xii.1971, MELU K3913); Western Australia, Rottneest Island, Point Clure (Kraft & Ricker, 2.xii.1980, MELU A35100). South Africa. Cape Agulhas, (Isaac, 27.ii.1952, BOL 29700); Cape of Good Hope, (Pappe, L 936.289-153) Holotype *D. grandis*; Diepwalle (Anderson, 27.xii.1989, BOL 62612); False Bay, Kalkbay (Pappe, MEL 537286) Holotype *D. pappeana*; Isipingo (Weber-van Bosse, L 936.289-142); Port Alfred [the Kowie] (Becker, 6.ii.1898, BOL 29674); Port Elizabeth, Algoa Bay (Ecklon Herb. Suhr, S s.n.) Lectotype *D. naevosa*; St. Lucia (Coppéjans, 23.xi.1995, HEC 11000); Umtentweni, (Isaac, 16.vii.1953, BOL 29695)

### *Dictyota radicans*

Australia. Western Australia, Fremantle, Rottneest Island, (Harvey, 1854, TCD 69A) Lectotype of *D. radicans*; Western Australia, Garden Island, (Clifford, BM 184); South Australia, Yorke Peninsula, Chinaman's Hat Island Bay (Woelkerling, 17.i.1968, MEL 699543); South Australia, Yorke Peninsula, Corny Point: drift, Lighthouse bay (Woelkerling, 11.iii.1967, MEL 699544). Victoria, Cape Woolamai: 15–18 m deep, (Goldsworthy & Berthold, 16.ii.1990, L 986.107-190). Victoria, Phillip Island, (Mueller, 1863, MEL 16995); Victoria, Port Phillip Bay, (Wilson, 24.xii.1889, MEL 16991)