Dipterocladia arabiensis sp. nov. (Dasyaceae, Rhodophyta) from the Sultanate of Oman

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Dipterocladia arabiensis sp. nov. is described on the basis of specimens collected from the Dhofar and Al Wusta regions of southern Oman. Observations are made on cystocarpic and tetrasporangiate specimens occurring from the shallow sublittoral to a depth of 17 m. The new species differs from the two previously known species of *Dipterocladia* by the much more robust size of the thalli, the higher order of branching, and the relatively smaller sizes of both the pseudolaterals and the tetrasporangia. In the new species all of the polysiphonous sympodial axes are indeterminate, unlike *D. pulchella*, in which there is a distinction between determinate and indeterminate sympodial axes, whereas *D. pinnatifolia* is intermediate with respect to this feature. Prior collections of this alga from Oman have been cited as '*Rhodoptilum plumosum* ?'.

Introduction

A red alga occurring on the southern and central coast of the Sultanate of Oman and belonging to the family Dasyaceae has been identified with a query as *Rhodoptilum plumosum* (Harvey *et* Bailey) Kylin (Barratt *et al.* 1984). This questionable determination has been repeated by Silva *et al.* (1996) in their catalogue of benthic marine algae of the Indian Ocean. *Rhodoptilum plumosum* is reported to have a distribution on both east and west sides of the North Pacific Ocean (Abbott and Hollenberg 1976, Scagel *et al.* 1989, Yoshida *et al.* 1995, Yoshida 1998). Its reported occurrence in the eastern Mediterranean Sea by Giaccone (1968, as *Dasyopsis plumosa* Schmitz) and its occurrence in Papua New Guinea by Ohba and Enomoto (1992) were discounted by Athanasiadis (1987) and Millar *et al.* (1999), respectively. Athanasiadis (1987) excluded the species on the basis that there was no evidence of its occurrence in the Mediterranean Sea. Millar *et al.* (1999) thought that the Ohba and Enomoto record 'most probably represents a *Dasya* or *Eupogodon* species' mainly because they regarded *Rhodoptilum plumosum* to be 'strictly endemic to the west coast' of North America. If this species were in fact to be present also in the northern Arabian Sea, this would represent an unusual instance of a disjunct distribution. Several collections of this dasyacean alga, including cystocarpic and tetrasporangiate specimens, have been examined and compared with genuine *Rhodoptilum plumosum* from the coast of Washington and California (U.S.A.). This study has led to the conclusion that the Omani alga represents an undescribed species of *Dipterocladia* Y. S. D. M. de Jong.

Materials and Methods

Most of the specimens of the new species have been deposited in the University of Michigan Herbarium (MICH), Ann Arbor. Some duplicates, as cited in the 'Collections Examined', have been deposited in the Natural History Museum, London (BM) and in the Natural History Museum of Oman, Muscat (ON). One collection has been deposited in the National Herbarium of The Netherlands, Leiden (L). Those collections made by various personnel of the Tropical Marine Research Unit of the University of York, U. K., are cited as 'TMRU'. Specimens of *Rhodoptilum plumosum* from California and Washington deposited in MICH were examined for purposes of comparison. Herbarium abbreviations are according to Holmgren *et al.* (1990).
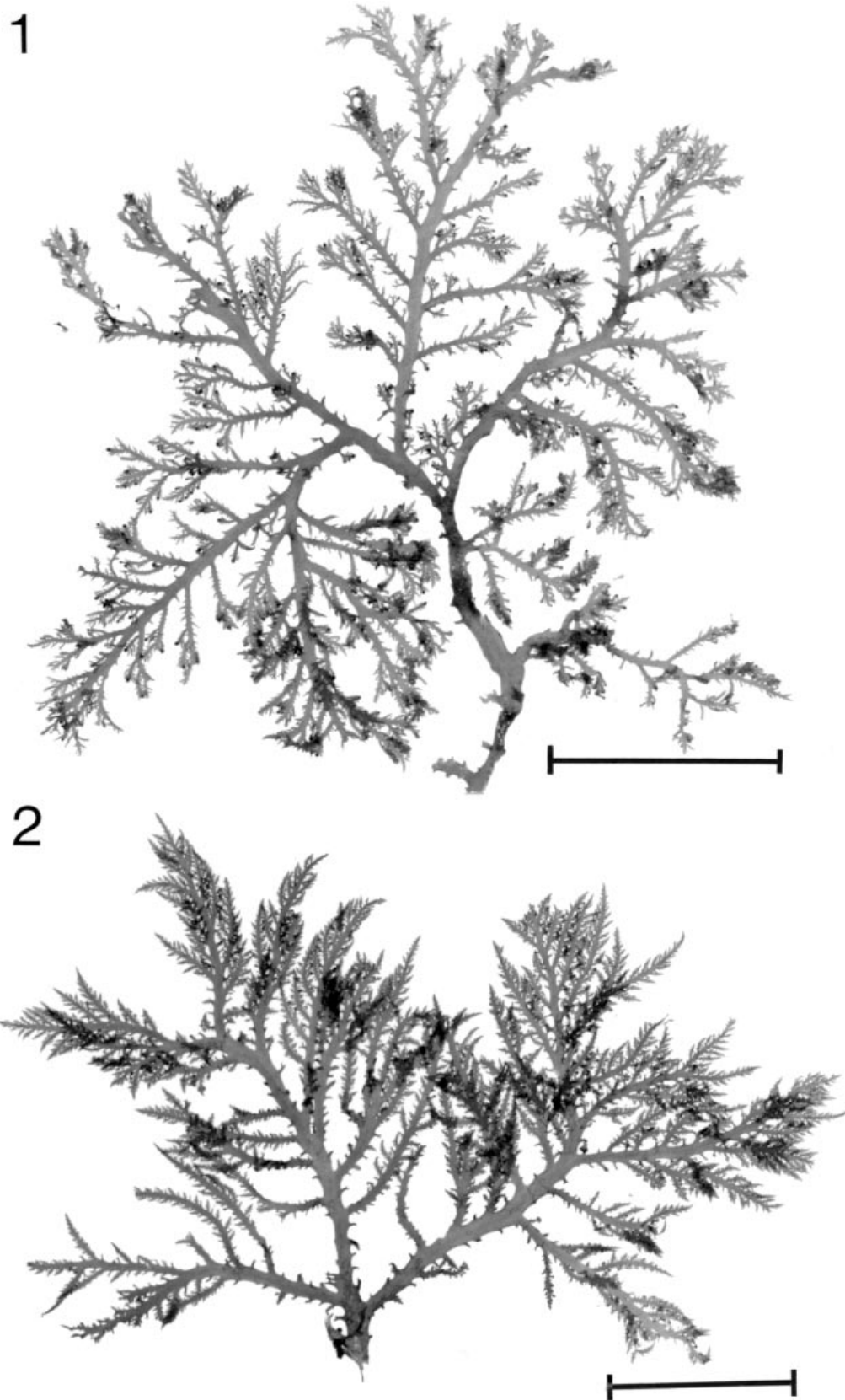
Dipterocladia arabiensis M. J. Wynne *et* Y. S. D. M. de Jong sp. nov.   Figs 1–14

Diagnosis: *Aliis speciebus in genere multum robustiore statura thalli (5–23 cm alt. et axes usque ad 10 mm lat.), ordine altiore ramificationis (ad 6 vel etiam 7), et relative parvioribus staturis duo pseudolateralium (300–350 µm long) et tetrasporangiorum (tantum 16–28 µm in diam.) distincta; stichidia tetrasporangifera sessilia, asymmetrica (arcuata), interdum bifurcata, 8–12 (et plus etiam) segmentis fertilibus per stichidium, 8 (–9) sporangiis per segmento fertili formatis; stichidia matura 290–365 µm long. et 126–145 (–176) µm lat.; cystocarpia ad extremum ramorum lateralium determinatorum evoluta, urceolata, 0.6–1.5 µm in diam. et 0.8–1.4 (–1.7) mm long; plantae masculae ignotae.*

Holotypus: Sultanate of Oman. Ras Abana (20.46° N, 58.07° E), on the west shore of Ghubat Hashish, Al Wusta: 31.x.1986, *leg. TMRU,* rock/sand, 9 m depth, south edge; in MICH.

Thallus flattened, branched to 6 (–7) orders, 5–23 cm in height, individual axes 3–7 (–10) mm in width; axes cellulosympodially developed with primary bilateral organization; four periaxial cells being cut off in an

Figs 1 and 2. *Dipterocladia arabiensis* M. J. Wynne *et* Y. S. D. M de Jong sp. nov.
Fig. 1. Holotype (in MICH). Cystocarpic phase. Fig. 2. Isotype (in BM). Tetrasporangiate thallus. Scale bars: 5 cm in Fig. 1; 3 cm in Fig. 2.
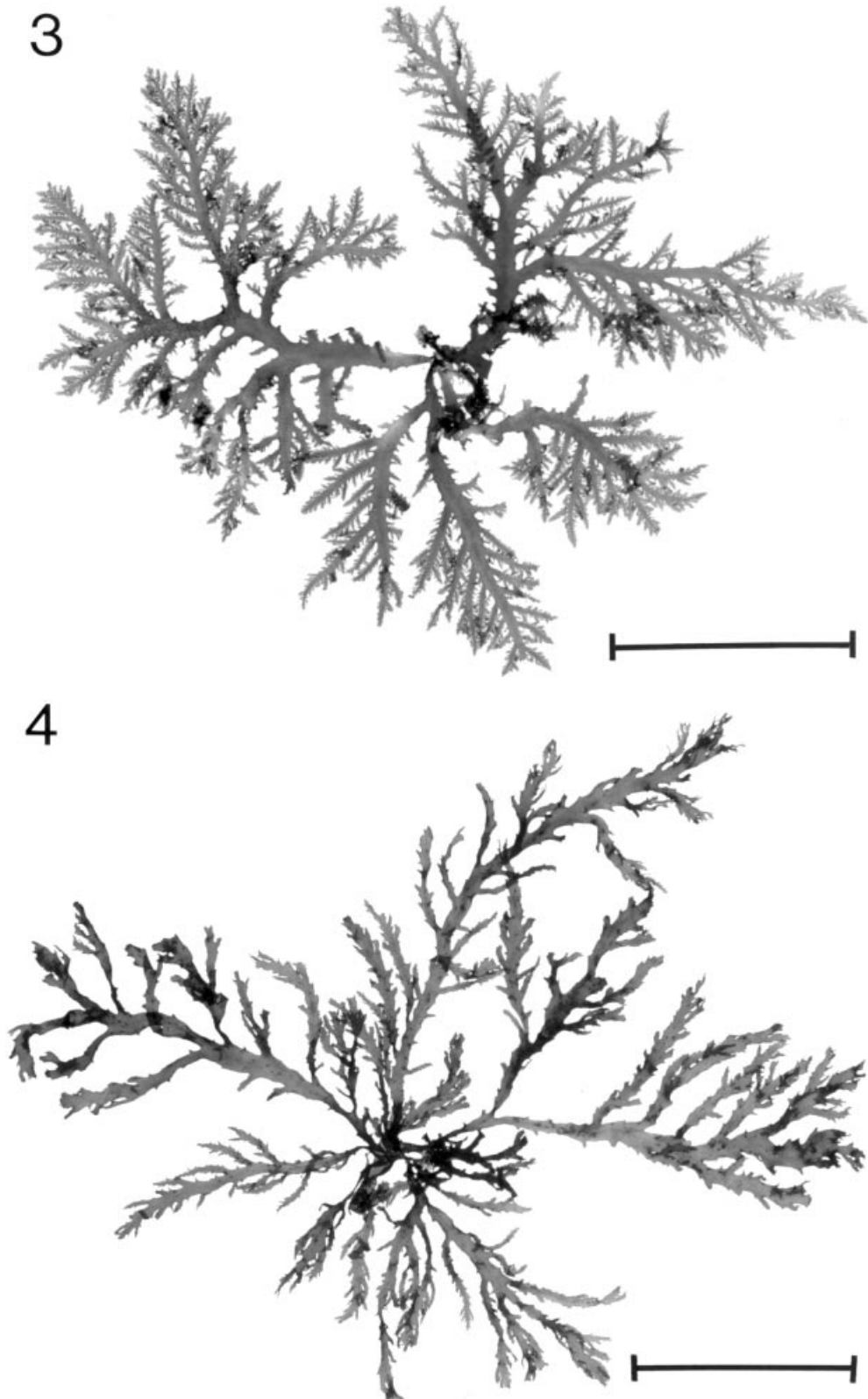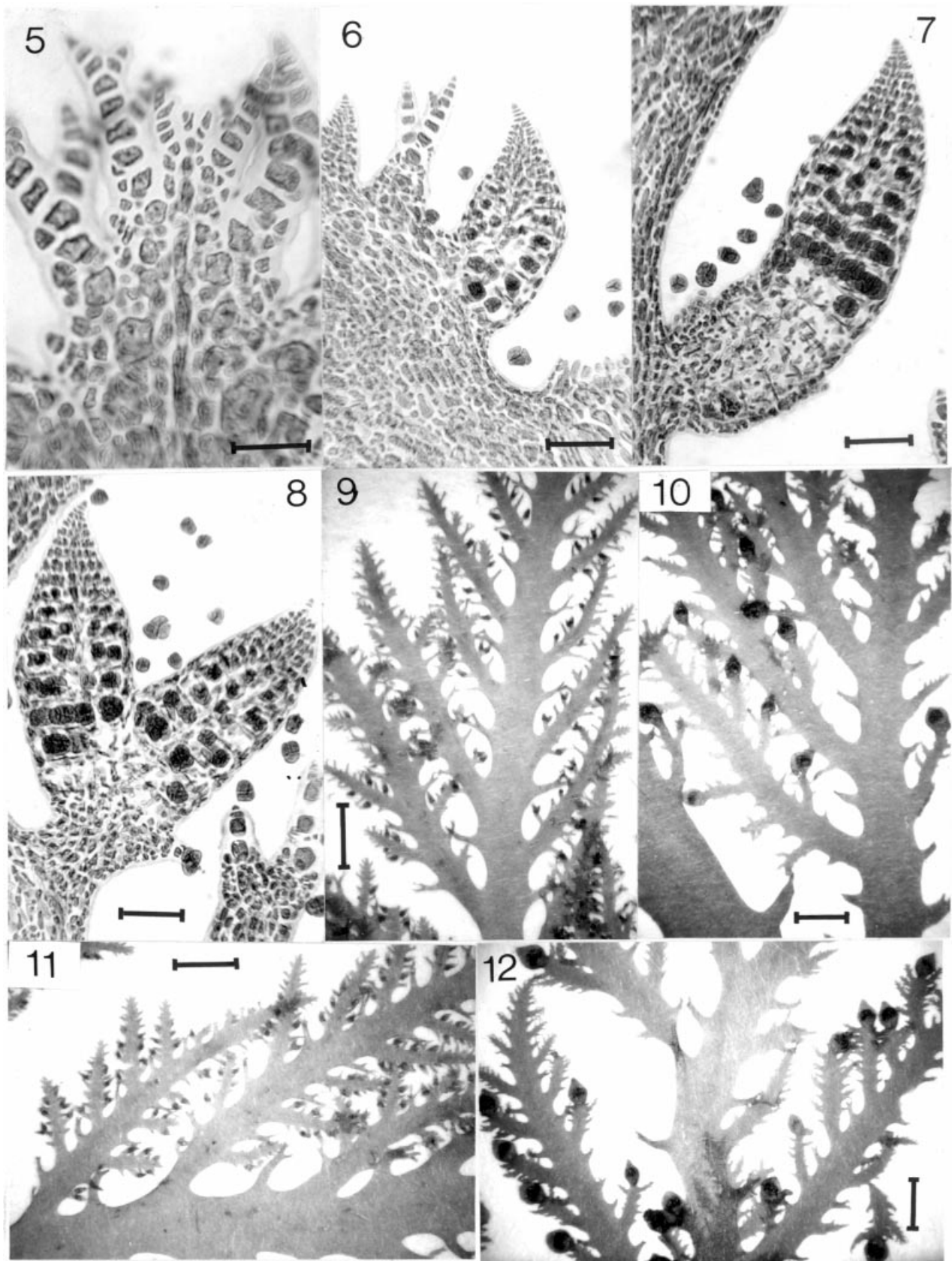
Figs 3 and 4. *Dipterocladia arabiensis* M. J. Wynne *et* Y. S. D. M de Jong sp. nov.
Fig. 3. Well developed but sterile specimen bearing pseudolaterals (no. 25999–02–06 in MICH). Fig. 4. Older specimen lacking most of the pseudolaterals (no. 29999–05–07 in BM). Scale bars: 5 cm in Fig. 3; 8 cm in Fig. 4.

alternating clockwise sequence (see Discussion for an explanation of this pattern); pigmented pseudolaterals cut off from every segment of indeterminate axes, in an alternating distichous manner; also at every segment,

Figs 5–12. *Dipterocladia arabiensis* M. J. Wynne *et* Y. S. D. M de Jong sp. nov.
Fig. 5. Apical region. Fig. 6. Typical sessile tetrasporangial stichidium. Fig. 7. Elongate mature tetrasporangial stichidium. Fig. 8. A bifurcate stichidium. Figs 9 and 11. Portions of tetrasporangiate specimen. Figs 10 and 12. Portions of cystocarpic specimen. Scale bars: 50 μm in Fig. 5; 100 μm in Figs 6–8; 2 mm in Figs 9–12.

below each pseudolateral, an indeterminate sympodial lateral developed from the second periaxial cell; pseudolaterals remaining monosiphonous throughout but becoming covered proximally with non-rhizoidal cortical cells; tetrasporangial stichidia sessile, asymmetric (arcuate), sometimes bifurcate, produced at the upper part of determinate laterals, 8–12 (and even more) fertile segments per stichidium, and 8 (–9) tetrasporangia borne per segment; 2 initial post-sporangial cells, dividing at later stages; cystocarps urceolate at the end of determinate laterals; spermatangia not seen.

Holotype: Sultanate of Oman. Ras Abana (20.46° N, 58.07° E) on the west shore of Ghubat Hashish, Al Wusta: 31.x.1986, *leg. TMRU,* rock/sand, 9 m depth, south edge; specimen deposited in MICH. Consistent with Articles 8.2 and 8.3 of the St. Louis Code (Greuter *et al*. 2000), the holotype comprises two different reproductive phases, cystocarpic (Fig. 1) and tetrasporangial, mounted on a single herbarium sheet, accompanied by microscope slides made from these two reproductive phases

Isotype: Tetrasporangial specimen (Fig. 2) deposited in BM.

Additional collections, all from Oman

1) Wadi Feshree, Dhofar (16.98333° N, 54.94444° E): 7.xi.1986, *leg. L. Barratt (Oman 303),* sandy bar, 9 m depth; tetrasporangiate (BM, MICH, ON).
2) Sadh, Dhofar (17.04366° N, 55.08050° E): 20.ix.1994, *leg. J. Stirn*, tetrasporangiate (MICH).
3) First cove east of Sadh (17.05755 ° N, 55.08544 ° E): 19.ix.2000, *leg. G. Richards 19092000–13–04* (MICH, ON); *leg. M. Wynne 19092000–13–34*, in drift (MICH).
4) Wadi Haart reef (17.07666° N, 55.11166° E), Sadh, Dhofar: 30.ix.1983, *leg. TMRU* (MICH); 7.x.1983, *leg TMRU*, 6 m depth (MICH).
5) Wadi Forh (16.95833° N, 54.73166° E), 6 km east of Mirbat, Dhofar: 8.viii.1985, *leg. L. Barratt (R64),* shallow sublittoral (BM).
6) Western side of Wadi Zead (= Hoon's Bay) (17.00517° N, 54.15339° E), east of Mirbat, Dhofar: 21.x.1983, *leg. TMRU*, in *Ecklonia* forest, 17 m depth (MICH). 12.ix.2000, *leg. G. Minton 12092000–05–11* (BM, MICH).
7) Raaha (=Alto) Bay (16.95116 ° N, 54.81650 ° E): 11.ix.2000, *leg. M. Wynne 11092000–04–06*, in drift (MICH), *leg. M. Wynne 11092000–04–23*, in drift (BM, L, MICH, ON), *leg. M. Wynne 11092000–04–36*, in drift (BM, MICH, ON).
8) Hatom Cove (16.96091 ° N, 54.82795 ° E), east of Mirbat, Dhofar: 24.ix.2000, *leg. T. Collins 24092000–17–02* (MICH, ON).
9) East/Northeast of a small rocky island off the coast of Dhofar, not far from Mirbat (16.95000° N, 54.74583° E): 25.ix.1999, *leg. Emma Dodsworth 25999–02–06,* 12 m depth (BM, MICH, and ON) (Fig. 3).
10) Northeast of Sadh Bay, Dhofar (17.043666° N; 55.08050° E): 29.ix.1999, *leg. Glenn Richards 29999–05–06* (BM, MICH, and ON), and *29999–05–07* (BM, MICH, and ON) (Fig. 4).

Results and Observations

Vegetative organization

Thalli are red to reddish-brown, complanate, spreading, 5–14 (–23) cm high (Figs 1–4). Branching is alternate, pinnate, to 6 (–7) orders, including 2 types of branches: regularly formed monosiphonous pseudolaterals and regularly formed side branches of unlimited growth (= indeterminate sympodial laterals). [Although the branches along indeterminate axes have a strictly distichous arrangement, the branching pattern of the individual pseudolaterals is radial, or spiral (Figs 5 and 13).] Periaxial cells are cut off in an alternating clockwise sequence, meaning that the position of the first periaxial cell switches on successive segments to the opposite (ventral to dorsal) part of the central axes, while the second periaxial cell always proceeds from a fixed position (left or right) with respect to the first periaxial cell.

Main axes are flattened, 3–7 (–10) mm in width. Older specimens have a very different appearance from younger, actively growing specimens (compare Fig. 3 with Fig. 4), in that older specimens become significantly broader and have shed most of the pseudolaterals and thus lack the delicate, fringed appearance of younger specimens. Pseudolaterals (Figs 14 and 15) are up to 3 times subdichotomously, divaricately branched, to 300–350 μm long, composed of up to 10–12 segments (cells). Segments near the base of pseudolaterals are 40–46 μm in width, 44–50 μm in length, tapering distally; cells in the mid-regions of pseudolaterals are 20–30 μm in width, 22–30 μm in length; cells in the distal regions of pseudolaterals are 12–20 μm in width, 6–10 μm in length, with pointed terminal cells. Cortical cells in surface view are round to elongate, often angular, (6–) 12–18 (–26) μm long and 6–9 μm wide (Fig. 18).

Reproductive structures

Tetrasporangial stichidia are produced from converted indeterminate sympodial laterals, such that the laterals become determinate (Figs 9 and 11). Stichidia are sessile, broad at the base, arcuate (curving adaxially) and asymmetric (Fig. 6). Sometimes stichidia are bifurcate (Fig. 8), near the base or close to the tip. Periaxial cells are cut off in an alternating sequence. Stichidia contain usually from 8 to 12 (but occasionally more; see Fig. 7) fertile segments, each segment with a whorl of 8 (–9) tetrasporangia (Fig. 16). Mature stichidia (Fig. 7) reach lengths of 290–365 μm and diameters of 126–145 (–176) μm. Tetrasporangia are tetrahedrally divided, reaching diameters of 16–28 μm. Each spor-
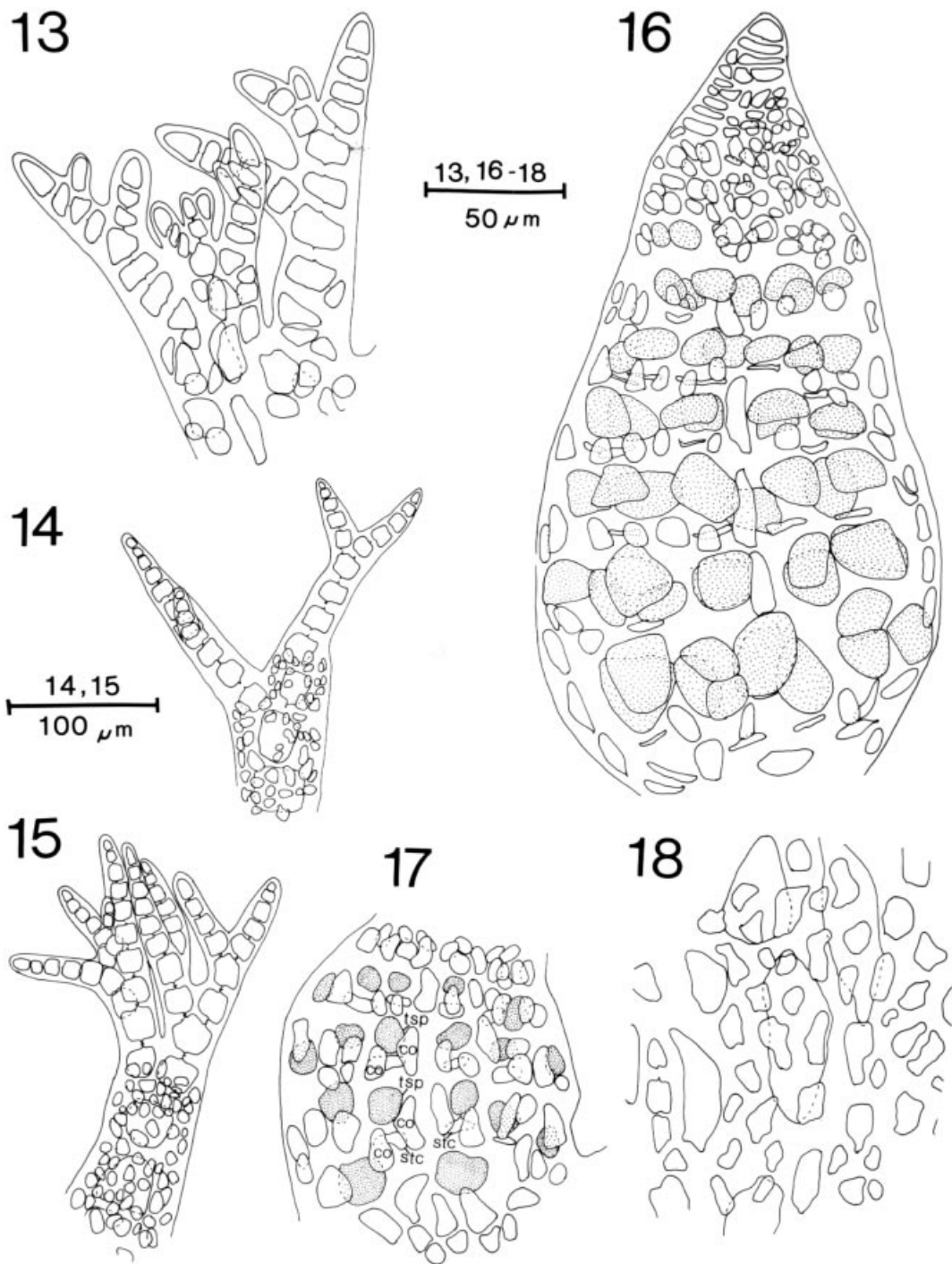
Figs 13–18. *Dipterocladia arabiensis* M. J. Wynne *et* Y. S. D. M de Jong sp. nov.
Fig. 13. Apical region. Figs 14 and 15. Examples of pseudolaterals. Fig. 16. Semi-schematic camera-lucida depiction of tetrasporangial stichidium, with 8 tetrasporangia per segment; most cover cells not included. Fig. 17. Portion of a tetrasporangial stichidium showing pairs of post-sporangial cover-cells and other features. co: cover cell; stc: stalk cell; tsp: tetrasporangium. Fig. 18. Surface view with cortical and subcortical cells.

angium is covered by 2 post-sporangial cover cells (Fig. 17), which may later divide.

A single cystocarpic plant (part of the Holotype) is known (Fig. 1), but the fact that it is a pressed specimen prevents an in-depth knowledge of some reproductive details. Cystocarps are developed at the end of determinate laterals (Figs 10 and 12), urceolate, 0.6–1.5 mm in diameter and 0.8–1.4 (–1.7) mm long. Carposporangia are borne in terminal clusters and are oblong, distally broad, (32–) 38–43 (–52) µm long and 12–20 µm wide. Male plants are not known.

Discussion

Two main types of periaxial cell formation are recognized within the Dasyaceae:

(1) In the first pattern periaxial cells are cut off in a circular sequence, meaning that in each segment the first periaxial cell is developed to the left (when clockwise) or to the right (when counter-clockwise) position of a pseudolateral, and subsequent periaxial cells proceed in an unidirectional order, the second periaxial cell developed at the opposite side of the pseudolateral, the third periaxial cell beside the second periaxial cell, and the last periaxial cell developed beside the first. Because the position of initiation of the pseudolaterals slightly shifts between successive axial segments, Dasyaceae with this circular sequence of periaxial cell formation show a primary radial organization and a spiral or alternating symmetry of branching (e.g. *Dasya*, *Eupogodon*, and *Rhodoptilum*) (de Jong *et al*. 1997).

(2) In the second pattern periaxial cells are cut off in an alternating sequence, meaning that in each segment the first periaxial cell is developed to a left or right position of a pseudolateral and subsequent periaxial cells proceed in an alternating order, the second periaxial cell developed at the opposite side of the pseudolateral, the third periaxial cell developed beside the first, the fourth periaxial cell developed beside the second periaxial cell, and the last periaxial cell opposite the first periaxial cell. Regarding the continuing position of the first periaxial cell, two subtypes of alternating periaxial cell formation are recognized:

(a) An alternating, switching sequence of periaxial cell formation, meaning that on successive segments the first periaxial cell always keeps the same central dorsal position on an axis, but switching its place on either sides of the pseudolateral, and consequently the pseudolateral apparently changes its arrangement. Dasyaceae with this alternating, switching sequence of periaxial cell formation show a primary dorsiventral organization and an alternately distichous symmetry of branching (e.g. *Colacodasya*, *Dasyella*, and *Heterosiphonia*) (de Jong *et al*. 1997).

(b) An alternating, clockwise (if the first periaxial cell is developed to the left of the pseudolateral) or counter-clockwise (if the first periaxial cell is developed to the right of the pseudolateral) sequence of periaxial cell formation, meaning that on successive segments the first periaxial cell regularly shifts its position to the opposite side of the axis. Dasyaceae with this alternating, (counter-)clockwise sequence of periaxial cell formation show a primary bilateral organization and an alternately distichous symmetry of branching (e.g. *Dictyurus*, *Dipterocladia*, and *Thuretia*) (de Jong *et al*. 1997, this paper).

The genus *Dipterocladia* was described by de Jong (in de Jong *et al*. 1997) on the basis of its unique formation of a pair of branches from each segment of indeterminate axes in a pairwise distichous manner.

Pseudolaterals are developed in a holoblastic manner. The first and second periaxial cells develop at opposite positions on both sides of a pseudolateral. Then a polysiphonous sympodial lateral is formed by the second periaxial cell of each segment. In *D. pulchella* (Weber-van Bosse) Y. S. D. M. de Jong, most of these polysiphonous laterals cease growing after about 2 mm (see figs 8 and 9 in de Jong *et al*. 1997) and thus were termed 'determinate sympodial laterals.' In an irregular pattern some of these polysiphonous laterals continued growth indefinitely, and these were called 'indeterminate sympodial axes.' In the new species, however, there are no 'determinate sympodial axes' in that all of the polysiphonous lateral axes develop indeterminately, that is, grow indefinitely. *Dipterocladia pinnatifolia* (Suhr) Y. S. D. M. de Jong represents an intermediate stage between these other two species in that it shows a tendency toward the production of determinate sympodial laterals (see figs 1–4 in de Jong *et al*. 1997).

Dipterocladia arabiensis can easily be separated from the two previously described species in the genus mainly by its much larger size and its higher orders of branching (Table I). Thalli of the South African *D. pinnatifolia* are pyramidal, to 5–9 cm tall, with main axes up to 5 mm wide and with up to 4 orders of branching. Thalli of *D. pulchella*, known from the Malaysian Archipelago and the Marshall Islands, are up to 7 cm tall, with main axes to 2 mm wide, and with 3 orders of branching. Thalli of *D. arabiensis* can be 14, or occasionally even to 23 cm tall. Main axes of mature thalli can be up to 10 mm broad, and there may be up to 6 or even 7 orders of branching. The pseudolaterals are only 300–350 µm in length, far shorter than those of the other two species.

The tetrasporangiate plants of *Dipterocladia arabiensis* can be compared with those in *D. pinnatifolia*; they are not known in *D. pulchella*. In both *D. pinnatifolia* and *D. arabiensis* the tetrasporangial stichidia replace polysiphonous sympodial laterals. In *D. pinnatifolia* they were described as lanceolate and occurring singly or in pairs, whereas in *D. arabiensis* they are sessile, arcuate, and borne singly but are sometimes bifurcate, the bifurcation occurring anywhere from the base to near the tip. There is a whorl of 8 sporangia produced per fertile segment in the new species, whereas only 6 are produced in *D. pinnatifolia*. The size of the tetrasporangia in the new species is much smaller than that reported for *D. pinnatifolia* (de Jong *et al*. 1997).

Generic boundaries in the Dasyaceae have been recently discussed and re-defined by both Millar (1996) and de Jong (1997). Millar (1996) proposed a more narrow circumscription of *Eupogodon* by restricting its membership to species that are primarily bilaterally organized, whereas de Jong (1997) proposed *Eupogodon* to include both (secondarily) bilateral and radial forms. The treatments by Millar (1996) and de Jong (1997) of the distinctions between the

Table I. Comparison of species in *Dipterocladia*.

Character	D. pinnatifolia	D. pulchella	D. arabiensis
Vegetative structures			
Length of thallus	5–9 cm	7 cm	5–14(–23 cm)
Color	brown-reddish	reddish	red to brown-reddish
General habit	pyramidal	small, erect	tall, spreading
Branching habit	alternately, pinnately	irregularly	alternately, pinnately
Branching order	4	3	6(–7)
Diameter of main axes	to 5 mm	to 2 mm	3–7(–10) mm
Shape of main axes	flattened	ellipsoid to flattened	flattend
Number of periaxial cells	4(–5)	5	4
Determinate sympodial axes (+ or –)	+/–	+	–
Length of pseudolaterals	to 1 mm	1–2 mm	300–350 µm
Number of free segments of pseudolaterals	to 20 cells	to 25 cells	10–12 cells
Texture of pseudolaterals	robust and flaccid	delicate and flaccid	delicate
Number of branchings of pseudolaterals	to 4	to 3	to 3
Diameter of pseudolateral cells (µm)	(10–)25–40(–60)	proximal: 25–35 distal: 15–30	proximal: 12–20 distal: 40–46
Length of pseudolateral cells (proximal) (µm)	25–50(–85)	15–35	6–10
Length of pseudolateral cells (distal) (µm)	(15–)25–75	35–100	44–50
Mean ratio pseudolateral cells	proximal: 1–1.5 distal: 1–2.5	proximal: 0.5–1.5 distal: 1.5–4.5	proximal: 0.5 distal: 1
Size of cortical cells 1:w (µm)	(5.5–)10–23(–52) x (2.5–)5–10.5(–16)	(15–)25–40(–75) x (5–)7–11(–20)	(6–)12–18(–26) × 6–9
Mean ratio of cortical cells	(0.5–)2–3(–8)	(2–)3–5(–6)	(1–)2(–3)
Shape of cortical cells	round to oblong or angled	oblong	round to elongate, often angular
Attachment to paper	strongly adherent	strongly adherent	strongly adherent
Female reproductive structures			
Cystocarp position on the axes	?	?	stalked on polysiphonous determinate laterals
Size of mature carposporangia 1:w (µm)	?	?	(32–)38–44(–52) × 12–20
Shape of mature cystocarps	?	?	urceolate
Size of mature cystocarps 1:w (mm)	?	?	0.8–1.4(–1.7) × 0.6–1.5
Tetrasporangial stichidia			
Development of tetrasporangial stichidia	determinate sympodial axis	?	sessile on determinate sympodial axis
Number of tetrasporangial stichidia in a cluster	1–2	–	1 (often bifurcate)
Number of pedicel cells	1–4	?	1
Number of fertile segments per stichidium	14–20	?	8–12 (or even more)
Size of tetrasporangial stichidia 1:w (µm)	(715–)430–255 × 145–170	?	(226–)290–365 × 126–145(–176)
Size of mature tetrasporangia (µm)	25–50	?	16–28
Maximal number of tetrasporangia in each whorl	6	?	8(–9)
Number of (postsporangial) cover cells	6	?	2, dividing at later stages
Size of cover cells 1:w (µm)	10–20 × 5–15	?	12–22 × 8–10

genera *Rhodoptilum* and *Eupogodon* are in substantial agreement. Both of these genera are secondarily bilateral in their development, with flattened thalli, although the flattening is more pronounced in *Rhodoptilum*. Also, every segment of the sympodium produces a single pseudobranch (= pseudolateral, or pseudopodium) (Kylin 1956). The main difference in the vegetative structures between these two genera is that the bases of the pseudolaterals become polysiphonous in *Eupogodon*, but they remain monosiphonous in *Rhodoptilum* (Rosenberg 1933). Also, adventitious filaments, often abundantly present in *Rhodoptilum*, are absent or rudimentary in *Eupogodon*. In addition to the basic distinction of having two laterals arising from every axial segment, *Dipterocladia* differs from *Rhodoptilum* in lacking the adventitious filaments that characterize the axes of *Rhodoptilum*. Parsons (1975) defined adventitious filaments as being produced from both periaxial cells and cortical cells but morphologically resembling the lateral organs (pseudolaterals or trichoblasts) formed at the apex. A second type of adventitious filament is formed from cortical cells from the lower portions of the axes.

Smith (in Smith and Hollenberg 1943), followed by Dawson (1963), described what he regarded to be a second species of *Dasyopsis* on the Pacific coast of
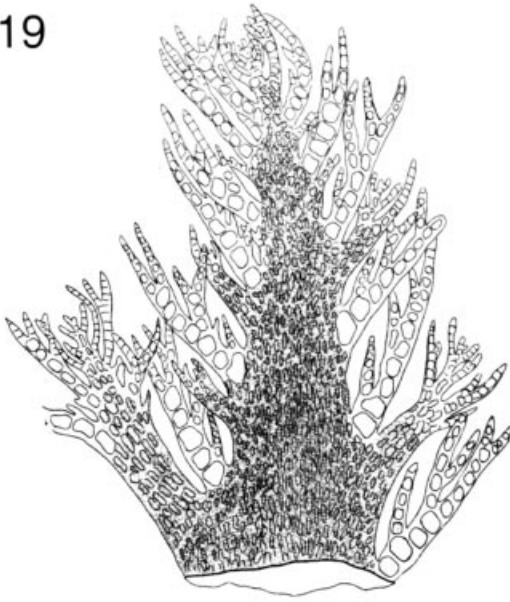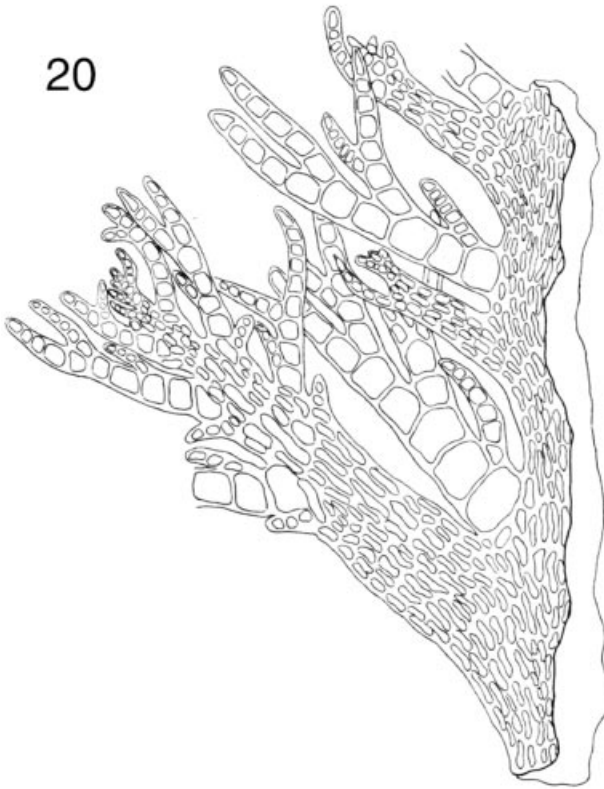
Figs 19 and 20. So-called *Rhodoptilum plumosum* from Japan.
Fig. 19. Surface view of terminal portion of branch.
Fig. 20. Portion of branch to show ramelli and ramuli (from Okamura, 1910, pl. 78, figs 5 and 7, as *Dasyopsis plumosa*).

North America. Smith distinguished *Dasyopsis densa* G. M. Smith, with a central Californian distribution and having pseudolaterals not over 1.0 mm in length and lying in a continuous fringe along the margins of the axes, from *Dasyopsis plumosa* (Harvey *et* Bailey) Schmitz, occurring in Puget Sound, Washington, and

having pseudolaterals usually 1.5–2.0 mm long and occurring in distinct tufts along the margins of the axes. Also, the Californian plants were smaller (to 30 cm tall), with proportionately smaller branches and a broader main axis. Hollenberg and Abbott (1966) thought that the degree of difference between these two species probably did not justify their being kept distinct, and later their conspecificity was proposed (Abbott and Hollenberg 1976). *Rhodoptilum* is currently viewed as a monotypic genus from warm-to-cold temperate areas, with a broad morphological plasticity regarding the sparseness of branches. The alleged occurrence of *Rhodoptilum plumosum* in Japan is based on a very small number of collections. We are struck by the strong resemblance of the figures in Okamura (1910, pl. 78, figs. 1–7, as *Dasyopsis plumosa*) to the Omani specimens of *Dipterocladia arabiensis*. Okamura's figs 5 and 7 are repeated here (figs 19 and 20). But not having sufficient material of the Japanese alga we are reluctant to identify it as *D. arabiensis*.

The benthic marine algal flora of the Sultanate of Oman is proving to be very rich and contains a number of both new taxa and new records for this region (Nizamuddin and Campbell 1995, Wynne 1998, 1999a, 1999b, 2000, 2001, Wynne and Jupp 1998, Wynne and Leliaert 2001).

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