A morphological study and taxonomic revision of *Euptilota* (Ceramiaceae, Rhodophyta)

MAX H. HOMMERSAND[1], OLIVIER DE CLERCK[2] AND ERIC COPPEJANS[2]

[1]*Department of Biology, Coker Hall, University of North Carolina, Chapel Hill, NC 27599-3280, USA*
[2]*Research Group Phycology, Biology Department, Ghent University, Krijgslaan 281 S8, 9000 Ghent, Belgium*

A reassessment of the genus *Euptilota* reveals that it presently contains four validly published species: *E. formosissima* (Montagne) Kützing from New Zealand and the islands of the Campbell Plateau, *E. articulata* (J. Agardh) Schmitz from Australia, India, South Africa and Japan, *E. fergusonii* Cotton from the Indian Ocean, and *E. molle* (Wollaston) comb. nov., from the eastern part of South Africa. *Euptilota pappeana* Kützing from the Western Cape Province, South Africa, and *E. mooreana* Lindauer from New Zealand are excluded from the genus. *Euptilota* is characterized by: alternate-distichous branching at the apex, a prominent central axis covered by a small-celled outer cortex and with internal rhizoidal filaments, spermatangia with a terminal nucleus subtended by a single mucilage-containing vesicle, and fertile female periaxial cells borne in the plane of lateral branching. The carpogonium does not divide after fertilization and produces two tubular protuberances that are cut off as connecting cells. Traditionally placed in the tribe Ptiloteae, *Euptilota* appears to be more closely related to the Callithamnieae. As in the Callithamnieae, periaxial cells are cut off longitudinally in pairs from the fertile axial cell. One of each pair bears a horizontally oriented four-celled carpogonial branch and both cut off auxiliary cells after fertilization. Sterile group cells are absent. Connecting cells mediate transfer of the derivatives of the fertilization nucleus to the auxiliary cells. A diploid nucleus divides at the surface of an auxiliary cell and one daughter nucleus moves to its centre while the other is extruded into a residual cell. The haploid auxiliary cell nucleus is cut off into a foot cell. It is proposed that the closest relatives of *Euptilota* are *Seirospora* and *Sciurothamnion*.

Key words: algae, Ceramiaceae, *Euptilota*, *Euptilota molle* comb. nov., morphology, Rhodophyta, systematics, taxonomy

Introduction

Euptilota is a small genus with six currently accepted species that are widely distributed in temperate and tropical waters of the Indo-West Pacific Ocean. Despite the small number of species, *Euptilota* exhibits an unusually wide range of morphological forms, so much so that the generic placement of some species has come into question. The type species, *Euptilota formosissima* (Montagne) Kützing (1849) from New Zealand and the Auckland Islands is robust with fully corticated axes and lateral pinnae. *Euptilota articulata* (J. Agardh) Schmitz (1896) [including *E. coralloidea* (J. Agardh) Kützing (1849)] from Australia, India, South Africa and Japan is another robust species with variable amounts of cortication of the pinnae. *Euptilota pappeana* Kützing (1849) from the West Coast of South Africa is an epilithic subtidal species known only from vegetative and tetrasporangial material (Stegenga *et al.*, 1997). *Euptilota*

fergusonii Cotton (1907) is a callithamnioid species from the Indian Ocean in which the central axis is surrounded by a single-layered cortex and a bundle of rhizoidal filaments. *Euptilota mooreana* Lindauer (1949) from New Zealand is a gracile epiphyte on *Pterocladia lucida* (Turner) J. Agardh. *Euptilota krusadiensis* Krishnamurthy *nom. illeg.* (in Desikachary *et al.*, 1998) from India is a recent species segregated from *E. fergusonii* by the absence of hooked spines at the tips of determinate laterals and the presence of polysporangia with eight spores in place of tetrasporangia.

Euptilota has traditionally been placed in the Ptiloteae; However, Hommersand & Fredericq (2001) suggested that it belongs in a separate tribe related to the Callithamnieae. The generic concept of *Euptilota* has been based almost entirely on vegetative characters. In this paper we will show that the development of the male and female reproductive systems is also important taxonomically. In particular, the organization of the carpogonial branch and associated cells in the fertile axis before fertilization and the mechanism by which derivatives of the fertilization nucleus are

Correspondence to: Max. H. Hommersand.
E-mail: hommersand@bio.unc.edu

transferred to the auxiliary cells, coupled with the early development of the gonimoblasts, provide diagnostic characters. It will be shown that *Euptilota* is most closely related to *Seirospora* and *Sciurothamnion* and more distantly related to members of the Callithamnieae. Based on the studies reported here, we will recognize four species in *Euptilota*: *E. formosissima*, *E. articulata*, *E. fergusonii*, and *E. molle* (Wollaston) comb. nov.

Materials and methods

Observations were made on specimens preserved in 5% formalin-seawater. Whole-mount and sectioned material was stained either with aniline blue and mounted in Karo® syrup or stained with Wittmann's aceto-iron-haematoxylin-chloral-hydrate and mounted in Hoyer's medium as described in Hommersand *et al.* (1992). Drawings were made with a camera lucida and photographs were taken with a Zeiss Photomicroscope III using Kodak® T-Max film or with an Olympus DP50 digital camera mounted on a Leitz Diaplan compound microscope or Leica Wild M10 stereo microscope. Herbarium abbreviations follow Holmgren *et al.* (1990). Specimens of *Euptilota formosissima* and *E. articulata* are housed at the herbarium of the University of North Carolina (NCU) and those of *E. fergusonii* and *E. molle* are in the herbarium of the Ghent University (GENT) unless otherwise indicated.

Observations

Euptilota Kützing (1849: 671)

Description

Plants erect from a discoid holdfast, cylindrical or compressed, with a prominent central axis and a surface layer of small, irregularly rectangular cells; lateral initials produced singly and alternately in a plane from the high sides of successive segments just below the apex with each initial forming a determinate lateral branch; indeterminate branches produced or transformed from the tips of the determinate laterals, less often from adventitious branchlets; cortical filaments issuing from the lower sides (sometimes also the upper sides) of the proximal cells of determinate laterals and growing downward (sometimes also upward) across the face of the axis for an average distance of two segments and forming a surface and internal cortex or only a surface cortical layer; internal rhizoids present, formed from surface or subsurface cortical cells and either conspicuous or obscure. Spermatangia in dense clusters borne terminally or laterally on determinate laterals, or produced from surface cortical cells and then solitary or borne in pairs. Each spermatangium with the nucleus terminal,

subtended by a single mucilage-containing vesicle. Procarps solitary or in series, formed near the apices on short to long modified indeterminate branches; supporting cell of the carpogonial branch cut off either directly beneath or on the opposite side of a vegetative lateral in the plane of branching and with a second periaxial cell cut off on the side opposite the first; carpogonial branch horizontal, the first three cells cut off by longitudinal divisions with the carpogonium cut off by a transverse division, or sometimes zigzag with the cells cut off by oblique divisions; sterile cells absent. Auxiliary cells cut off from the supporting cell and the opposite periaxial cell after fertilization, the carpogonium expanding horizontally and forming protrusions directed toward the two auxiliary cells and cutting off connecting cells that fuse toward the base of the auxiliary cells; the diploid nucleus dividing at the surface of the auxiliary cell with one nucleus entering and moving to the centre of the auxiliary cell and the other extruded to the outside in a residual cell; the auxiliary cell cleaving at the time of diploidization into a foot cell containing the original haploid nucleus which may divide; the two gonimoblast initials each cutting off a terminal gonimolobe initial that produces the gonimoblasts; secondary gonimolobes sometimes initiated but not developing further; the gonimoblasts from the two gonimolobes typically fusing to form a single carpospore mass or sometimes remaining distinct; gonimolobe stalks absent; involucral branches initiated from the hypogynous cell and sometimes also from neighbouring cells below and above the gonimoblasts and forming a loose to compact involucre surrounding the cystocarp. Tetrasporangia formed from terminal or lateral initials on determinate lateral branches, or borne adventitiously on cortical filaments or superficial cortical cells, loose to compact and stalked or sessile; tetrasporangia ovoid, dividing simultaneously to form tetrahedrally arranged tetraspores, or by two successive divisions with the four tetraspores irregularly tetrahedral or cruciate.

Type species

Euptilota formosissima (Montagne) Kützing 1849: 671 (*Ptilota formosissima* Montagne 1842: 8)

Nomenclatural history

Euptilota was initially proposed as a section or subgenus of *Rhodocallis* by Kützing (1847: 36) where it was separated from *Ptilota* on the basis that rhizoidal filaments rather than subspherical cells surrounded the central axis. Whereas *Rhodocallis* possesses a single longitudinal central axis, *Euptilota* was said to have three parallel longitudinal axes. Two species were included in *Rhodocallis*

subg. *Euptilota* by Kützing: *R. formosissima* (Montagne) Kützing from the Auckland Islands and *R. harveyi* (J.D. Hooker) Kützing from Cape Horn. When Kützing (1849: 671) elevated *Euptilota* to generic rank it contained these two species plus *E. pappeana* Kützing from the Cape of Good Hope, South Africa, and *E. coralloidea* (J. Agardh) Kützing from Australia. J. Agardh (1851, 1876) did not recognize *Rhodocallis* or *Euptilota* and returned all of Kützing's species to *Ptilota*. Agardh (1876) identified four groups in *Ptilota* based on branching pattern: I, with similar opposite pinnae; II, with dissimilar opposite pinnae; III, with strictly alternate pinnae, and IV, with sloping alternate and subopposite pinnae. Most species of *Euptilota* Kützing were placed in the third group. Schmitz (1896) reinstated Kützing's genera *Rhodocallis* and *Euptilota* and established a new genus, *Psilothalia*, to receive other species in Agardh's Group III. Later, Kylin (1956) established a new genus, *Diapse*, to contain the single species in Agardh's Group IV. Three species were added to *Euptilota* in the twentieth century: *E. fergusonii* Cotton (1907) from Ceylon (Sri Lanka), *E. mooreana* Lindauer (1949) from New Zealand) and *E. krusadiensis* Krishnamurthy (in Desikachary *et al.* 1998) *nom illeg.* from India. The taxonomic histories of each of these species are summarized in Table 1.

Euptilota formosissima (Montagne) Kützing

Kützing 1849: 671; Adams 1994: 254 – 255, pl. 95. *Ptilota formosissima* Montagne 1842: 8; 1845: 97 – 99, pl. 9, fig. 3 a-i [plate 9 first published in 1843]; Harvey & Hooker 1845: 190 – 191, pl. 17, Figs 1 – 4.

Lectotype

A specimen identified by Bruno de Reviers in the Montagne Herbarium at the Muséum National d'Histoire Naturelle, Paris (PC) numbered MA 6380 and labelled in Montagne's handwriting: 'Ptilota formosissima/Montag./Auckland'. The left upper branch resembles the reverse image seen in the Atlas (Montagne, 1845: pl. 9, Fig. 3a).

Habitat

Widely distributed throughout New Zealand and the Islands of the Campbell Plateau. Intertidal on wave-swept shores in southern localities; otherwise subtidal to depths of 40 m or more (Adams, 1994).

Specimens examined

New Zealand: Sandy Bay, Enderby Island, Auckland Is. (John C. Yaldwyn, i.1975, NCU); attached, pool in *Durvillea* zone, Snares Island (2.i.1961, G.A. Knox, NCU); drift, Ringaringa, Paterson Inlet, Stewart I. (3.xii.1974, M. H. Hommersand, NCU); attached, Evening Cove, Paterson Inlet, Stewart I (6.xii.1974, M.H. Hommersand, NCU); attached, Lonnekers Nggett, Halfmoon Bay, Stewart I. (2.xii.1974, M.H. Hommersand, NCU); drift, Moeraki, South I. (8.viii.1988, M.H. Hommersand, NCU); drift, Wairepo Flats, Kaikoura Peninsula,

Table 1. Taxa historically associated with *Euptilota* indicating their present taxonomic placement

Kützing (1849) *Euptilota/Ptilota*	Agardh (1876) *Ptilota* section III	Schmitz (1896) reinstatement of *Euptilota*	20th century	This treatment
Species included in *Euptilota*				
E. formosissima	*P. formosissima*	*E. formosissima*	*E. formosissima*	*E. formosissima*
P. articulata	*P. articulata*	*E. articulata*	*E. articulata*	*E. articulata*
E. coralloidea	*P. coralloidea*	*E. coralloidea*	*E. coralloidea*	*E. articulata*[6]
			E. fergusonii	*E. fergusonii*
			Thamnocarpus molle	*E. molle*[7]
Species excluded here from *Euptilota*				
E. pappeana	*P. pappeana*	*E. pappeana*	*E. pappeana*	*E. pappeana*[8]
			E. mooreana	*E. mooreana*[8]
			E. krusadiensis	*E. krusadiensis*[9]
Rhodocallis elegans	*P. rhodocallis*	*R. elegans*[2]	*R. elegans*	
	P. siliculosa	*Psilothalia siliculosa*[3]	*Ps. siliculosa*	
	P. striata	*Psilothalia striata*[3]	*Ps. striata*	
Carpothamnion ptilota	*P. jeannerettii*	*E. jeannerettii*	*Diapse ptilota*[4]	
E. harveyi	*P. harveyi*[1]		*Falklandiella harveyi*[5]	

[1]Transferred to a different section of *Ptilota* by J. Agardh (1851), currently placed in *Dasyptilon*. [2]See Hommersand *et al.* (1998) for a detailed treatment on the nomenclatural history of *R. elegans*. [3]Removed to *Psilothalia* by Schmitz (1896) and De Toni (1903) respectively (see Womersley, 1998). [4]Removed to *Diapse* by Kylin (1956). [5]Removed to *Falklandiella* by Kylin (1956) and transferred to *Dasyptilon* by Papenfuss (1958). For a discussion of the status of *Falklandiella*, see Silva (1993). [6]*Euptilota coralloidea* is treated as a synonym of *E. articulata* on the authority of Womersley (1998). [7]Present study. [8]*E. pappeana* and *E. mooreana* are incorrectly placed in *Euptilota* based on their reproductive morphology and *rbc*L and SSU rDNA sequence analyses (W. Freshwater and S. Fredericq, personal communication). [9]Invalidly described and not treated in the present study because material was not available for detailed observations.
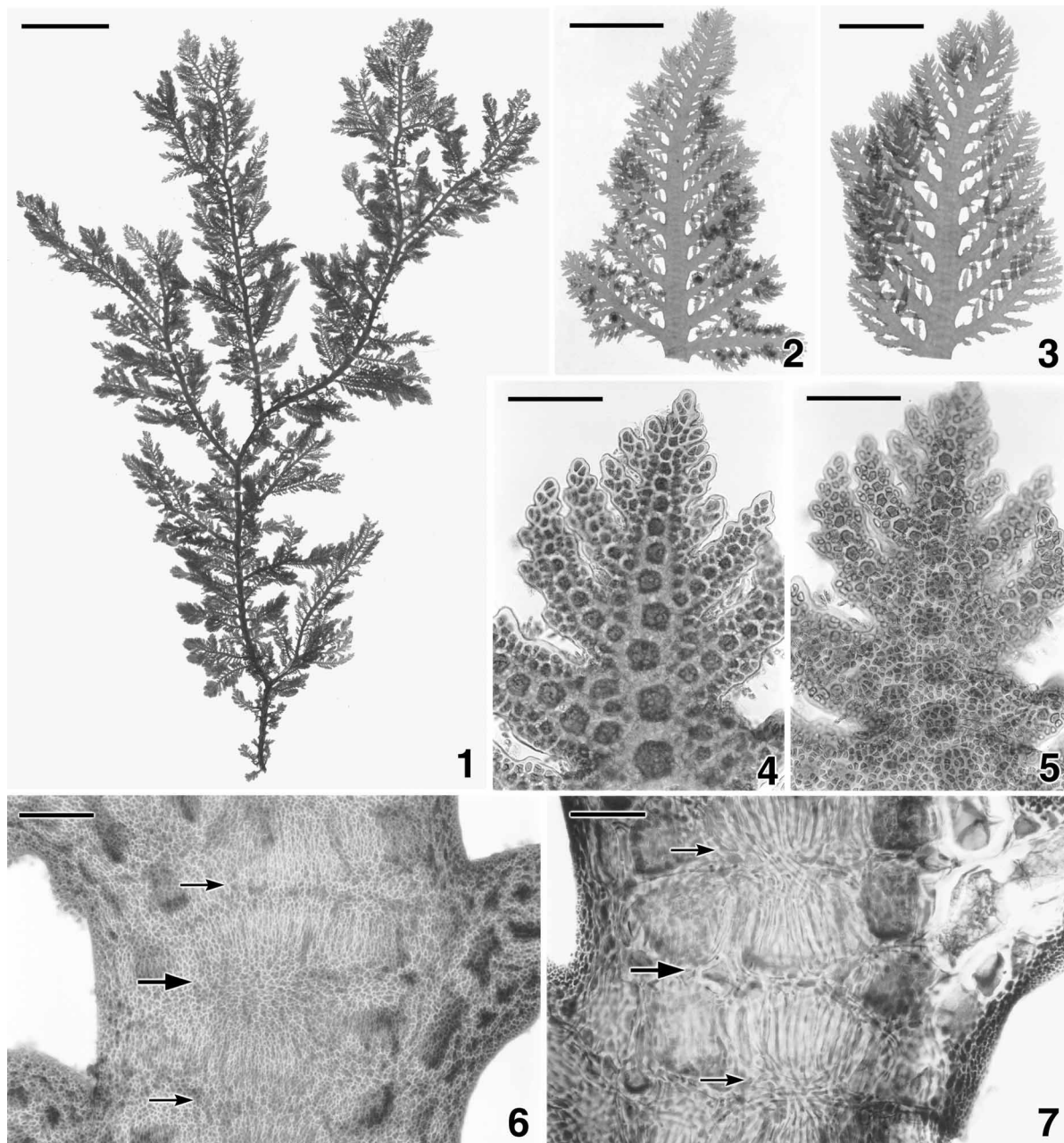
Figs 1–7. *Euptilota formosissima*. Habit and vegetative morphology. Fig. 1. Habit of a plant from Stewart Island, 6.i.1946, distributed by Victor W. Lindauer, Algae Nova-zelandicae Exsiccatae, No. 174. Figs 2–7. Vegetative morphology, plants from Sandy Bay, Enderby I., Auckland Is., 19.i.1975, leg. John C. Yaldwyn, lightly stained with aniline blue. Fig. 2. Tip of a female plant. Fig. 3. Tip of a tetrasporangial plant. Fig. 4. Median optical section of tip. Fig. 5. Surface view of tip in Fig. 4 focused on outer cortex. Fig. 6. Mature axis and side branches seen in surface view. Coarse arrow points to node between axial cells, fine arrowheads point to juncture between descending and ascending cortical filaments. Fig. 7. Mature axis and side branch from another plant seen at same magnification as in Fig. 6 from inside of cortex looking out. Coarse and fine arrows as in Fig. 6. Scale bars represent: Fig. 1, 2 cm; Figs 2–3, 500 μm; Figs 4–5, 100 μm; Figs 6–7, 200 μm.

South I. (11.x.1974, M.H. Hommersand, NCU); drift, Atia Point & Mudstone Bay, Kaikoura Peninsula, South I. (12.x.1974, M.H. Hommersand, NCU); Kean Point, Kaikoura Peninsula, South I. (11.viii.1988, M.H. Hommersand, NCU), drift, Muritai, Port Nicholson, North I. (23.ix.1974, M.H. Hommersand, NCU); drift, Island Bay, (M.H. Hommersand, 20.x.1974, NCU); attached, Lyall Bay, Wellington, North I. (19.ix.1974, M.H. Hommersand, NCU).

Habit and vegetative morphology

Thallus medium to dark red, often with a bluish tinge, arising from a discoid or conical holdfast (or several plants issuing from fused holdfasts) and growing to a height of 15–20 cm (–30 cm), pinnately or pectinately branched in one plane to four or five orders (Fig. 1). Holdfast spreading in older thalli, reinforced by descending rhizoids. Lower axis cartilaginous and terete to compressed, usually under 1 mm in diameter. Main axes

compressed, 1–2 mm wide by 0.5 to 1 mm thick. Branching alternate-distichous with the branches becoming rapidly corticated close to the apex (Figs 2 and 3). Axial cells initially isodiametric (Figs 4 and 5), becoming two-times longer than broad in older parts, flanked by two to four rows of enlarged, elongate inner cortical cells on either side interspersed by rhizoidal filaments (Fig. 14) and covered by a cortex three to four cell layers thick (Figs 8–10). Surface cells densely packed, irregularly angular, about as broad as long and with dimensions 10–15 μm (Figs 5, 17).

Growth of an indeterminate axis takes place by oblique division of the apical cell with the high side of successive axial cells alternating in a plane (1/2 divergence). Initials of lateral branches are cut off obliquely 1–2 cells below the apex and form side branches at approximately 45° angles (Figs 18 and 19). Laterals are alternate-distichously branched in the same manner as in the main axis but with the basal segments cutting off initials above and below that form ascending and descending files approximately two segments long. These form cortical filaments that grow in the plane of branching parallel to the lateral edges of the axial cells above and below (Fig. 18). Branches of the ascending and descending filaments spread across the axial cells and also divide periclinally to form a cortex several layers thick. The cortical filaments continue to grow, filling the spaces between neighbouring cells and converge from all directions toward the centre of each axial cell to form a smooth surface composed of small rectangular cells without gaps (Figs 5, 18 and 19). At maturity the cortex is two to four cell layers thick, being thicker over the spaces between axial cells and thinner over their surfaces (Figs 8–10). Axial cells initially expand isodiametrically, becoming rectangular in shape just below the apex as seen in surface view (Fig. 4). Below, the axial cells elongate becoming two times longer than broad and the basal-most cells of the ascending and descending filaments flanking the axial cell on either side enlarge and become highly vacuolate. Typically, 2–3 enlarged inner cortical cells border an axial cell on either side (Fig. 14). Additional cells lateral to the axial cell may also enlarge and the central region of vacuolate cells may be five or more cells broad as seen in cross section (Fig. 9). It is sometimes possible to see the denser cortex overlying the spaces between axial cells (Fig. 6, large arrow) and the line due to the juxtaposition of ascending and descending cortical filaments in the mid-regions of axial cells (Figs 6, small arrows). Narrow rhizoidal filaments issue from subsurface cortical cells and grow parallel to one another over and between the expanding axial cells and flanking cortical cells (Figs 8, 12). In regions adjacent to the expanded central cells the parallel rhizoidal filaments are typically only one cell layer thick (Figs 13, 14). Those that issue from ascending cortical filaments grow upwards and those that issue from descending cortical filaments grow downwards. They cross over to the opposite side of an axial cell and meet at its mid-region (Fig. 7). Rhizoidal filaments do not appear to extend beyond the length of an axial cell in the mid-region of the thallus; however additional rhizoidal filaments are produced that strengthen the stipe and holdfast at its base.

Individual plants consist of three to four orders of indeterminate axes and up to three orders of determinate laterals, which are sometimes called pinnae. The antepenultimate order of determinate laterals is usually less than 40 segments long; the penultimate order less than 20 segments long, and the ultimate order is tooth-like and less than 10 segments long. Branching of the determinate orders is typically more regular and hierarchical in tetrasporangial than in female plants (Figs 3 and 4). All orders of branches arise from the terminal growth of ordinary filaments and none are produced adventitiously. Thalli with a pyramidal outline do not have a sharp boundary between indeterminate and determinate branches, whereas the boundary is clearer in thalli with irregular or pectinate branching.

Reproductive morphology

Gametophytes are dioecious. Spermatangial parent cells are elongate and are borne in clusters of 2–3 at the tips of surface cells along the margins and over the surfaces of the determinate branchlets. Each spermatangial parent cell produces a single spermatangium at any one time (Fig. 16). Mature spermatangia are ovoid and measure 3–5 × 5–8 μm. Each contains a single apical nucleus subtended by a prominent proximal vacuole.

Procarps are borne on the ultimate order of lateral branchlets. A fertile branchlet is typically 5 to 8 cells long and bears only a single carpogonial branch. The basal segment and occasionally other lower segments are sterile. A procarp lies in the same plane as the vegetative determinate laterals. The first periaxial cell functions as the supporting cell of the carpogonial branch. It is cut off by a concavo-convex division either directly under the vegetative lateral or on the opposite side. The first three cells of the carpogonial branch are cut out by vertical septa and are directed horizontally across the face of the axial cell on one side of the axis. The carpogonium, cut off by a horizontal division, is directed toward the apex of the fertile branchlet and bears a trichogyne that emerges to one side. A second periaxial cell is cut off in the plane of branching opposite the supporting cell (Fig. 20).
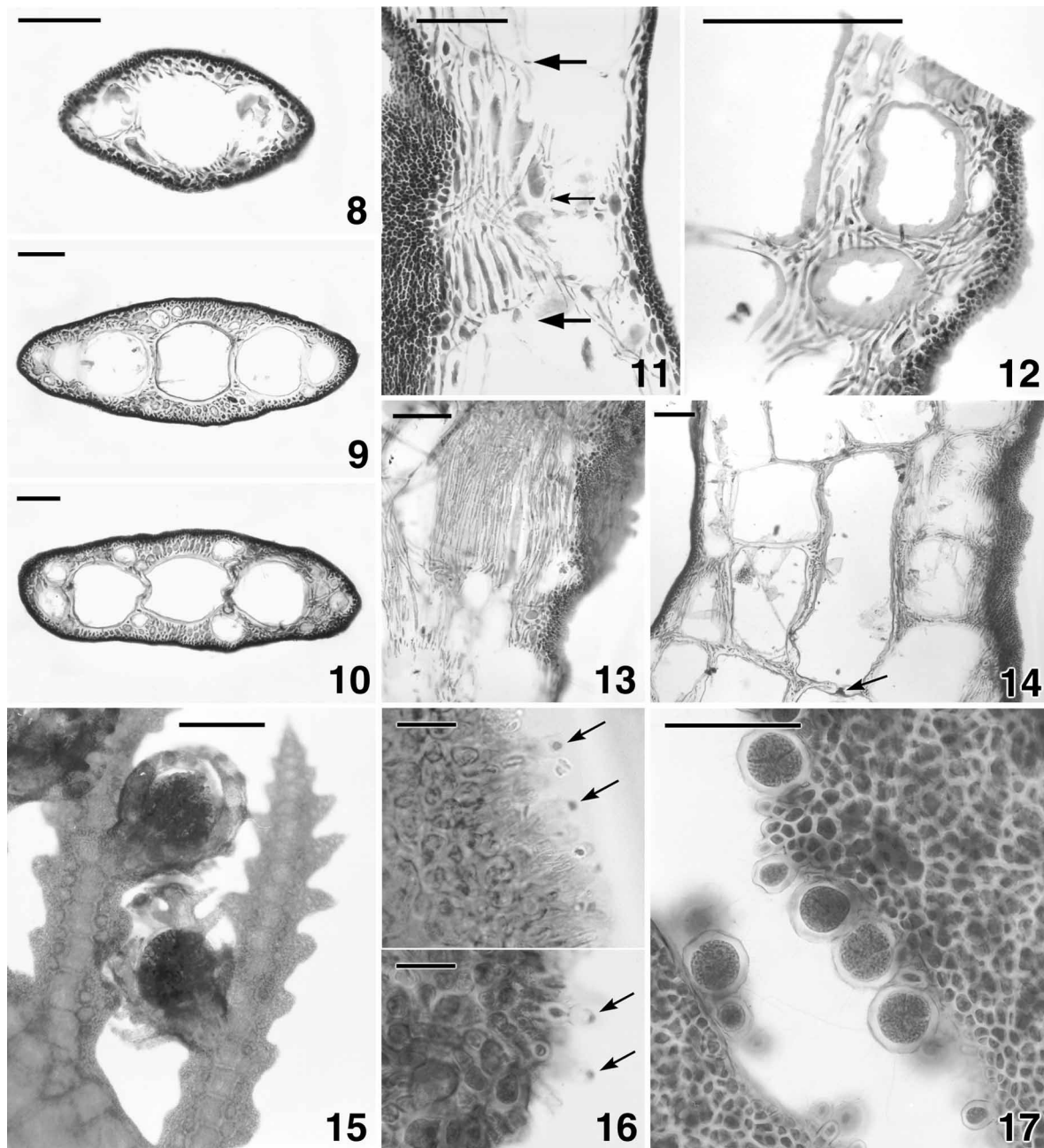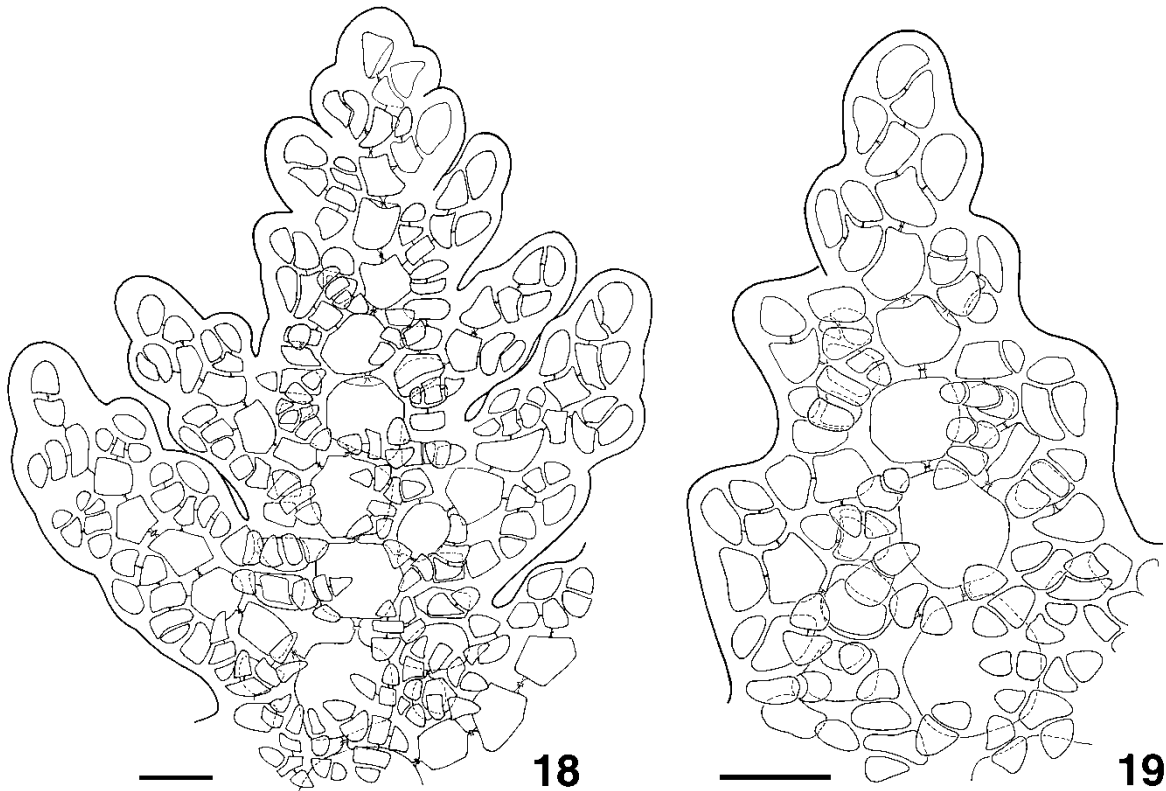
Figs 8–17. *Euptilota formosissima.* Vegetative and reproductive morphology. Material from Enderby I. (See Figs 2–7). Figs 8–14. Vegetative morphology. Fig. 8. Cross section of axis about 3 cm below tip. Fig. 9. Cross section axis in middle of plant. Fig. 10. Cross section of axis lower down. Fig. 11. Grazed longitudinal section of axis showing elongated inner cortical cells interspersed with rhizoidal filaments. Coarse arrows indicate node, fine arrow indicates juncture between descending and ascending inner cortical filaments. Fig. 12. Median section showing rhizoidal filaments issuing from subsurface cortical cells and growing mostly downward in the intercellular layer. Fig. 13. Grazed section showing a few elongated cortical cells and numerous parallel rhizoidal filaments. Fig. 14. Median longitudinal section of mature axis showing rhizoidal filaments within the intercellular layers. Fine arrow points to pit plug between axial cells. Fig. 15. Mature cystocarps with gonimolobes surrounded by involucral branchlets. Fig. 16. Surface cortical cells bearing spermatangial parent cells and spermatangia (arrows). (Marginal and surface view above, median marginal view below). Fig. 17. Margin of branchlets bearing developing and mature tetrasporangia. Scale bars represent: Figs 8–14, 200 μm; Fig. 15, 500 μm; Fig. 16, 20 μm; Fig. 17, 100 μm.

Cytoplasm within the trichogyne is constricted below the point of emergence and expands immediately above it. Trichogynes were seen with one spermatium attached.

After presumed fertilization the base of the carpogonium distends, becomes lobed, and the nucleus enlarges (Fig. 21). The carpogonium continues to expand as the trichogyne withers and disappears. At the same time the supporting cell and the opposite periaxial cell cut off auxiliary cells in the plane of branching (Fig. 22). The trichogyne withers and the place where it emerged

Figs 18–19. *Euptilota formosissima*. Vegetative morphology. Material from Enderby Island. Fig. 18. Axis bearing alternate lateral branchlets and developing cortical filaments. Fig. 19. Enlarged view of a lateral. Scale bars represent 20 μm.

from the cuticular envelope remains evident as a refractive ring (Figs 20–24). The carpogonium forms protrusions on opposite sides that extend inwardly toward the auxiliary cells (Fig. 23). The diploid nucleus inside the carpogonium divides twice to produce either three or four daughter nuclei. In one scenario two of the diploid nuclei move above (Fig. 24) and then into (Fig. 25) the tubular protrusions. After cleavage two of the nuclei are cut off inside connecting cells and two are seen inside the carpogonium (Fig. 26). Alternatively, a nucleus is cut off inside each connecting cell and a third nucleus is seen in the carpogonium (Fig. 27). The two auxiliary cells elongate at their tips and each contains a basal haploid nucleus (Fig. 27). A connecting cell attaches to the surface of the auxiliary cell initiating fusion (Fig. 27, arrowhead), after which the diploid nucleus divides and one of the daughter nuclei moves into the auxiliary cell (Fig. 28, left side, dn) while the other is extruded (Fig. 28 left side, arrow) and cut off to the outside as a residual cell (Fig. 28, right side, arrow). The auxiliary cell next divides into a primary gonimoblast cell and a foot cell containing the haploid nucleus, which may undergo mitosis. By this stage the cells of the carpogonial branch have fused completely and are in the process of disintegrating (Fig. 28). Figure 29 illustrates a stage in which the supporting cell and the second fertile periaxial cell

each bear a foot cell (ft) containing two haploid nuclei (hn), a primary gonimoblast cell (pg), a residual cell containing an extruded diploid nucleus (arrows), and a gonimolobe initial (gonl). The diploid nucleus in the primary gonimoblast cell has divided and protrusions have formed that may potentially produce additional gonimolobes (Fig. 29, right side). The cell below the fertile axial cell produces four filaments at 45° angles with respect to the plane of branching, two on either side, which will form the involucre (Fig. 26). These grow and branch in a manner similar to a determinate branchlet and clasp the gonimoblasts (Fig. 30). The mature cystocarp consists of a single globular mass of carpospores surrounded by four involucral branches (Fig. 15). Only occasionally can one see that the mass consists of two gonimoblasts. The secondary gonimolobes seen in early stages apparently never develop and secondary gonimolobes were not seen in old cystocarps that had released their carpospores. The appearance of the globular mass of carpospores surrounded by the four involucral branches was well illustrated by Harvey & Hooker (1845, pl. 77, Figs 2 and 4).

Tetrasporangia are initially formed along the margins of determinate branches (Fig. 17) and later spread over their surfaces near the margins. They may be sessile or borne on one-celled stalks (Fig. 17) or at the ends of short unbranched filaments (Harvey
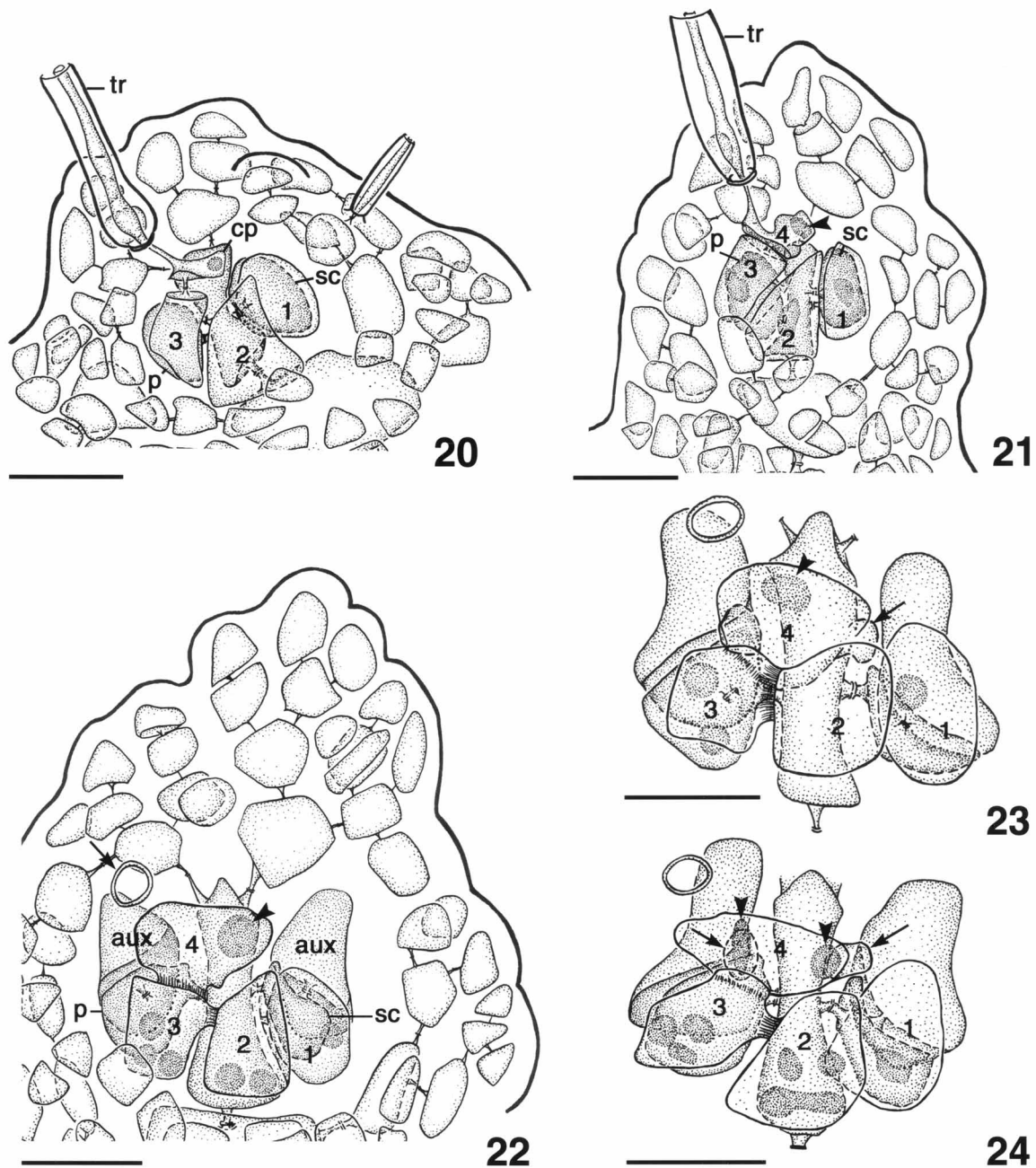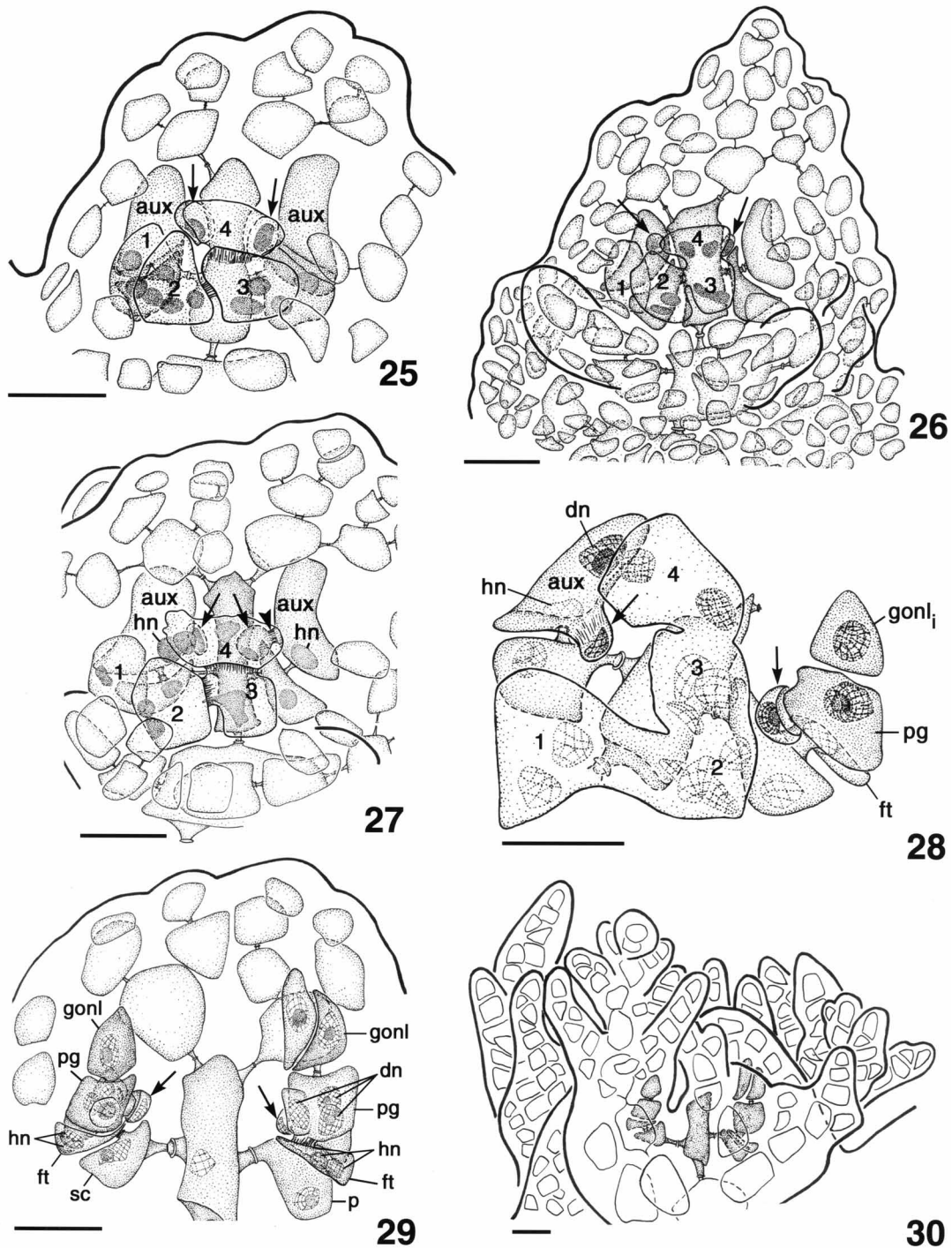
Figs 20–24. *Euptilota formosissima*. Development of female reproductive system. Material from Wairarapa Flat, Kaikoura, South I., 11.x.1974, leg. M.H. Hommersand, stained with aniline blue. Fig. 20. Unfertilized procarp with supporting cell (sc) bearing a four-celled carpogonial branch (1–3) including carpogonium (cp) and trichogyne (tr) and opposite fertile periaxial cell (p). Fig. 21. Fertilized procarp with distended carpogonium (4) containing a putative diploid fertilization nucleus (arrowhead). Fig. 22. Stage showing expanded carpogonium and diploid nucleus (arrowhead) after the supporting cell (sc) and opposite pericentral cell (p) have cut off auxiliary cells (aux). Arrow denotes refractive ring in wall where trichogyne had emerged. Fig. 23. The carpogonium (4) containing the diploid nucleus (arrowhead) has formed protuberances (arrow) extending toward the two auxiliary cells. Fig. 24. The diploid nucleus inside the carpogonium has divided into two nuclei (arrowheads) situated above the protuberances (arrows) inside the carpogonium (4). Nuclei inside cells 2 and 3 of the carpogonial branch have divided and cells of the carpogonial branch have begun to fuse. Scale bars represent 20 μm.

& Hooker, 1845, pl. 77, Fig. 3), or rarely on branched filaments. The tetrasporangia normally divide successively to form four irregularly cruciately arranged tetraspores. In some instances the arrangement of the tetraspores appears to be tetrahedral, but evidence of simultaneous cleavage was not seen.

***Euptilota fergusonii* Cotton**

Cotton, 1907: 262–264, Figs 1–6; Børgesen, 1936: 88–90, Figs 9, 10. (For additional references see: Silva *et al.*, 1996).

Figs 25–30. *Euptilota formosissima.* Development of female reproductive system. Material for Figs 25–27 from Kaikoura, South Island, stained with aniline blue; material for Figs 28–30 from Ringaringa, Stewart I., 3.xii.l974, leg. M.H. Hommersand, stained with hematoxylin. Fig 25. Two derivative diploid nuclei have entered the carpogonial protuberances (arrows) adjacent to the auxiliary cells (aux). Fig. 26. The diploid nuclei inside the protuberances have apparently been cut off as connecting cells (arrows) and two additional nuclei are seen inside the carpogonium (4). Involucral branches have issued from the cell below the fertile axial cell. Fig. 27. Of the two connecting cells (arrows) the one on the right has fused with the auxiliary cell (arrowhead). At this stage the two auxiliary cells (aux) each contain a basal haploid nucleus (hn). Fig. 28. The diploid nuclei have entered the auxiliary cell and divided. In the stage seen on the left, one of the daughter diploid nuclei lies inside the fused connecting cell (arrow) and the other has entered the auxiliary cell (dn, aux). In the stage on the right, the extruded nucleus has been cut off in a residual cell (arrow), the auxiliary cell has divided into a foot cell (ft) and a primary gonimoblast cell (pg) bearing a terminal gonimolobe initial (gonl_i). The cells of the carpogonial branch (1–4) have fused. Fig. 29. The supporting cell (sc) and opposite periaxial cell (p) each bear a foot cell (ft) containing two haploid nuclei (hn), a primary gonimoblast cell (pg), and a terminal gonimolobe (gonl). Residual cells (arrows) extruded from the primary gonimoblast cell each contain a diploid nucleus. The nucleus in the primary gonimoblast cell (pg) on the right has divided twice and two of the three diploid nuclei (dn) have begun to initiate lateral gonimolobes. Fig. 30. Stage seen in Fig. 29 showing the early development of four involucral branches issued from the cell below the fertile axial cell. Scale bars represent 20 μm.

Holotype

'Pantura' [Panadura?], Sri Lanka, Ferguson, No. 20, 1868, BM 000610842 (Fig. 31).

Habitat

Found predominantly in the subtidal, − 2 m to − 20 m, where it occurs on vertical walls and overhangs. Less commonly collected in deep rock pools of the lower intertidal and infralittoral fringe.

Selected specimens examined

Kenya: Mombasa, McKenzie Point (Coppejans, 1.vii.1985, HEC 5535); Kanamai (Coppejans & Beeckman, 29.i.1986, HEC 6051); Shimoni (Coppejans, 10.iii.1988, HEC 7295); Gazi, Chale Island (Coppejans, Vackier & Verstraete, 14.ix.1992, HEC 9451).

Madagascar: Tuléar (Coppejans, Douterlungne & Razanakoto, 20.viii.2003, HEC 15116). Oman: Masirah (Schils, 3.xi.1999, MAS 019); Masirah (Schils, 17.11.1999, MAS 219).

Seychelles: Mahé, L'Islette (Coppejans, Kooistra & Audifred, 10.i.1993, SEY 808); Mahé, L'Ile Sourie, Pointe du Sel (Coppejans, Kooistra & Audifred, 10.xii.1992, SEY 359).

South Africa: Sodwana Bay, Two Mile Reef (Coppejans et al., 9.viii.1999, KZN 324).

Sri Lanka: 'Pantura' (Ferguson, 1868, Coll. No. 20, BM 000610842) holotype; Weligama, Yala Rock (Coppejans, 6.i.1997, HEC 11566); Hikkaduwa (Coppejans, 16.i.1997, HEC 11726); Galle, Unawatuna (Coppejans, 7.i.2000, HEC 12654).

Tanzania: Dar es Salaam, Kunduchi (Coppejans & De Clerck, 5.i.1996, HEC 11082); Zanzibar, Nungwi (Coppejans & De Clerck, 23.viii.1994, HEC 10554); Pemba, Vitongoji (Coppejans & De Clerck, 23.i.1996, HEC 11416); Mtwara, Mnazi Bay (Coppejans, Dargent & Bel, 22.vii.2000, HEC 12817).

Yemen: Socotra, 2 km North of Rhiyi Diqatanhin (Leliaert, 3.iii.1999, SOC 257); Socotra (Schils, 4.iv.2000, SMM150).

Habit and vegetative morphology

Thalli grow from a felt-like, rhizoidal, discoid holdfast (Fig. 40), from which several erect axes arise and reach lengths of 5–17 cm. When freshly collected the plants are red in colour and mostly exhibit a bluish iridescence *in situ*. Indeterminate axes are repeatedly and irregularly dichotomously branched in a single plane and are densely beset with distichously arranged determinate laterals (Figs 31–33). Apical parts of the axes are corymbose and slightly flexuous (Figs 33 and 34).

Growth of an indeterminate axis takes place by oblique division of the apical cell, with the high sides of successive axial cells alternately offset in a 1/2 divergence to form the initials of the determinate laterals. The resulting axial cells exhibit a clear zigzag arrangement near the apex, are isodiametric, and measure 60–80 μm in width by 70–95 μm in length (L/B: 1–1.2) (Figs 42, 48). At maturity the axial cells are broader than long (160–
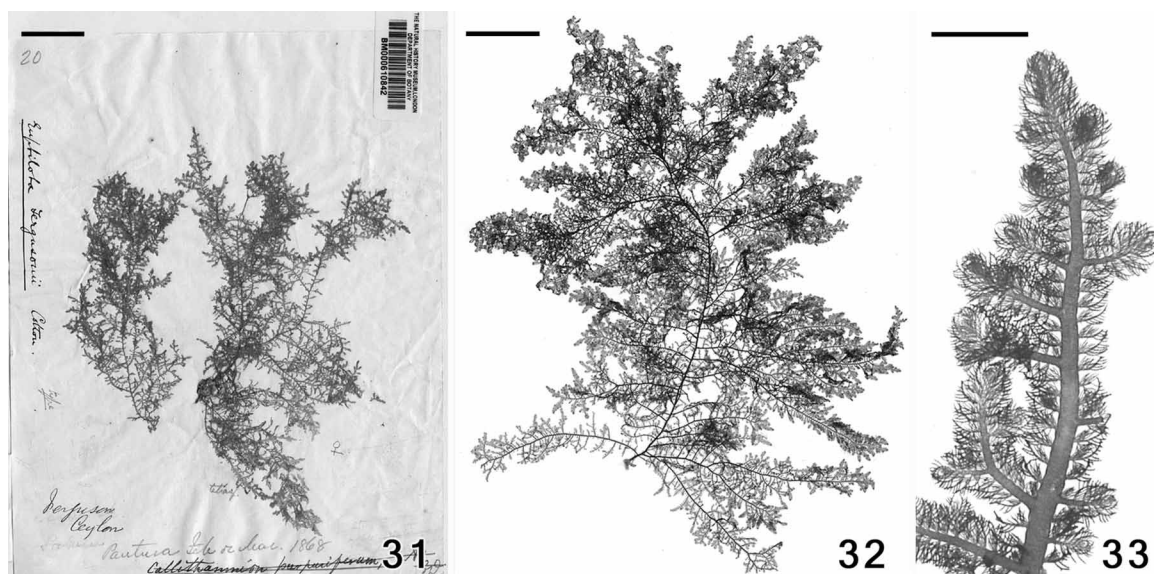
Figs 31–33. *Euptilota fergusonii*. Habit. Fig. 31. Holotype of *E. fergusonii* Cotton. BM 000610842, 'Pantura', Sri Lanka, (Ferguson, coll. No. 20, 1868). Fig. 32. Habit of a herbarium specimen of *E. fergusonii* (HEC 12817). Figs 33. Portion of apical part of an axis bearing alternate-distichous determinate laterals and irregularly spaced indeterminate lateral branches. Scale bars represent 1 mm.

180 μm × 80–125 μm; L/B: 0.4–0.8), ultimately reaching up to 350 μm in diameter (Figs 38, 39). Young determinate laterals curve upwardly and overtop the apical cell (Figs 42, 48). Determinate laterals are aligned in an alternate-distichous manner (1/2 spiral) and remain completely un-
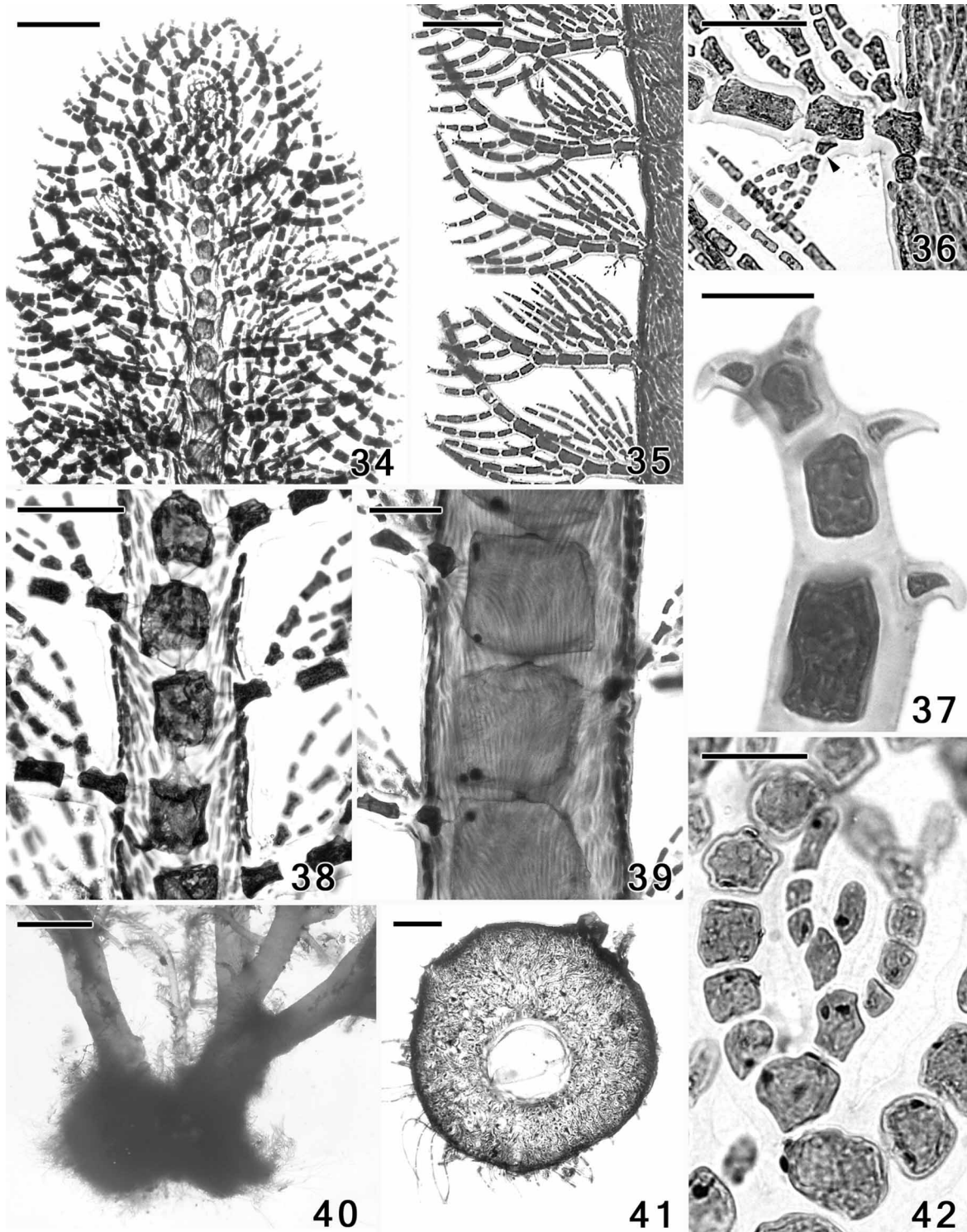
Figs 34–42. *Euptilota fergusonii*. Vegetative morphology. Fig. 34. Apical portion of the thallus. Fig. 35. Detail of an axis showing the branching pattern of the determinate laterals. Fig. 36. Detail of the proximal cells of a determinate lateral with an adventitious indeterminate branch forming on the abaxial side of the second-basal cell. Fig. 37. Apical and penultimate cells of a determinate lateral bearing hooked spinose cells. Figs. 38, 39. Portions of an axis in the mid-region of the thallus bearing distichously arranged alternating determinate laterals and showing the cortical filaments. Fig. 40. Rhizoidal base of thallus from which the main axes arise. Fig. 41. Transverse section of an axis near the base of the thallus showing rhizoids inside the cortex surrounding the axial cell. Fig. 42. Detail of an apex showing the zigzag arrangement of the axial cells in the upper part of the thallus. Scale bars represent: Figs 34–35 and 41, 250 μm; Figs 36 and 38–39, 100 μm; Fig. 37, 25 μm; Fig. 40, 2 mm.

corticated. They reach 9–12 cells (800–1100 μm) in length, are inserted perpendicularly to the parent axes and curve toward the apex (Fig. 34). The distal (3–) 4–9 cells of the determinate laterals each bear a single abaxial branch, which curves toward the apex in a manner similar to the main rachis of the determinate lateral (Fig. 35). Determinate laterals form abaxial branches while close to the apex. They have already been initiated by the third to the fifth segment, and soon after they are fully formed (Fig. 48). The proximal 3–4 cells are initially naked, but each later bears an adaxial lateral that branches subdichotomously (Fig. 35). Abaxial branches on the determinate laterals usually remain un-branched, but the larger proximal ones may branch once or twice. Adaxial branches develop from the ninth axial segment onwards. The apical cells of the main rachis and abaxial branches bear 2–4 slightly hooked spinose cells, the penultimate 2–3 of which may each bear one or two (rarely three) abaxial spines (Fig. 37). Growth of the determinate laterals proceeds through transverse or oblique divisions of their apical cells and elongation of the derivatives. Deciduous hairs terminating the ultimate cells were absent.

Indeterminate laterals form at irregular intervals along primary axes either by direct conversion of determinate laterals (Fig. 33), or by the develop-ment of an adventitious axis on the abaxial side of the proximal cells of the determinate laterals (Fig. 36). Primary and indeterminate axes are terete, heavily corticated to within a few cells of the apices, and reach diameters of 0.8–1.2 mm near the thallus base. Corticating filaments initially arise singly from the basal cells of determinate laterals approximately 16 to 20 cells below the apex. A second and third corticating filament issues from each of the basal cells a few segments below the site of cortex initiation. Cortical filaments branch irregularly and initially envelop the axial cells forming a single layer that extends over two axial segments below (Fig. 38). Rhizoidal filaments issue from the surface cortical cells and grow inward and downward progressively filling in the space be-tween the surface cortical layer and the axis and increasing thallus thickness from tip to base (Fig. 41). All vegetative cells are uninucleate.

Reproductive morphology

Gametophytes are dioecious. Spermatangia form on dwarf fertile axes that are borne singly at the distal ends and mostly adaxial sides of determinate laterals. The dwarf fertile axes are branched with the terminal cells acting as spermatangial mother cells. Each mature spermatangium, 3–4 × 5–7 μm, contains a single apical nucleus subtended by a proximal mucoid vesicle (Fig. 47).

Procarps and cystocarps are borne near the apices of short indeterminate axes transformed from the tips of determinate laterals (Fig. 43), or on adventitious abaxial branches such as the one illustrated in Fig. 36. Although several carpogonial branches may form along a single axis, only a single carposporophyte consisting of paired gonimoblasts matures. Procarps are situated in the middle of fertile axial cells in the same plane as the vegetative determinate laterals. The first periaxial cell func-tions as the supporting cell of the carpogonial branch. It is cut off by a concavo-convex long-itudinal division, either immediately beneath the determinate lateral, or on the opposite side (180°). A four-celled, L-shaped carpogonial branch forms progressively with the first and second cells ellipsoidal and the third cell angular in shape. The third cell divides transversely to cut off the carpogonium at a 90° angle to the plane of vegetative branching. A long trichogyne (to 700 μm) emerges from the carpogonium. At maturity, the second and third cells are usually binucleate, whereas the first cell and the carpogo-nium are uninucleate. In most instances the carpogonial branch is fully formed before a second fertile periaxial cell is cut off from the fertile axial cell opposite the supporting cell. No additional cells are produced by the procarp and sterile cell groups are absent.

Following presumed fertilization, the carpogo-nium expands laterally and the trichogyne breaks down completely. The place where the trichogyne emerged from the mucilaginous envelope remains clearly visible as a refractive ring in later stages. Following zygote formation the supporting cell and fertile periaxial cell each enlarge and divide by an unequal oblique cross-wall, cutting off a small basal cell and a large auxiliary cell (Fig. 49). The diploid nucleus in the carpogonium undergoes a single mitotic division unaccompa-nied by cytokinesis and two protrusions are formed on each side of the carpogonium adjacent to the auxiliary cells. Both carpogonial nuclei divide again and the division products migrate into the two protrusions which segregate into two large connecting cells that are not pit-connected to the carpogonium (Figs 44, 50). Concurrently, both auxiliary cells elongate and their haploid nuclei migrate toward the base. Diploidization of the auxiliary cells is followed by an immediate mitotic division of the diploid nucleus. One of the daughter nuclei migrates to the centre of the auxiliary cell while the other is extruded into a persistent residual cell. The original haploid nuclei, which at this stage are situated at the bases of the auxiliary cells, are cut off by a cleavage perpendicular to the longitudinal axes of the auxiliary cells to form a foot cell in which the
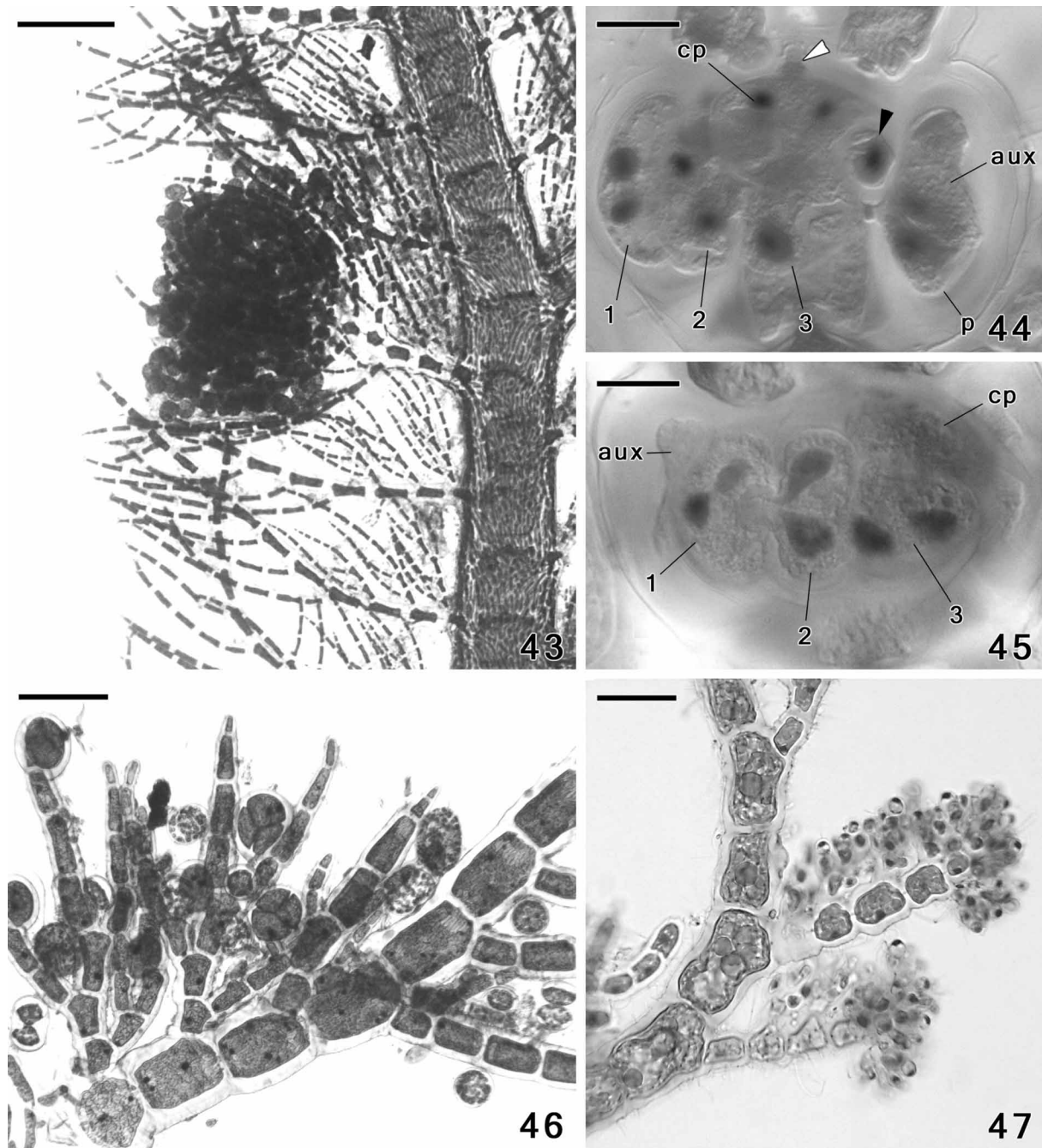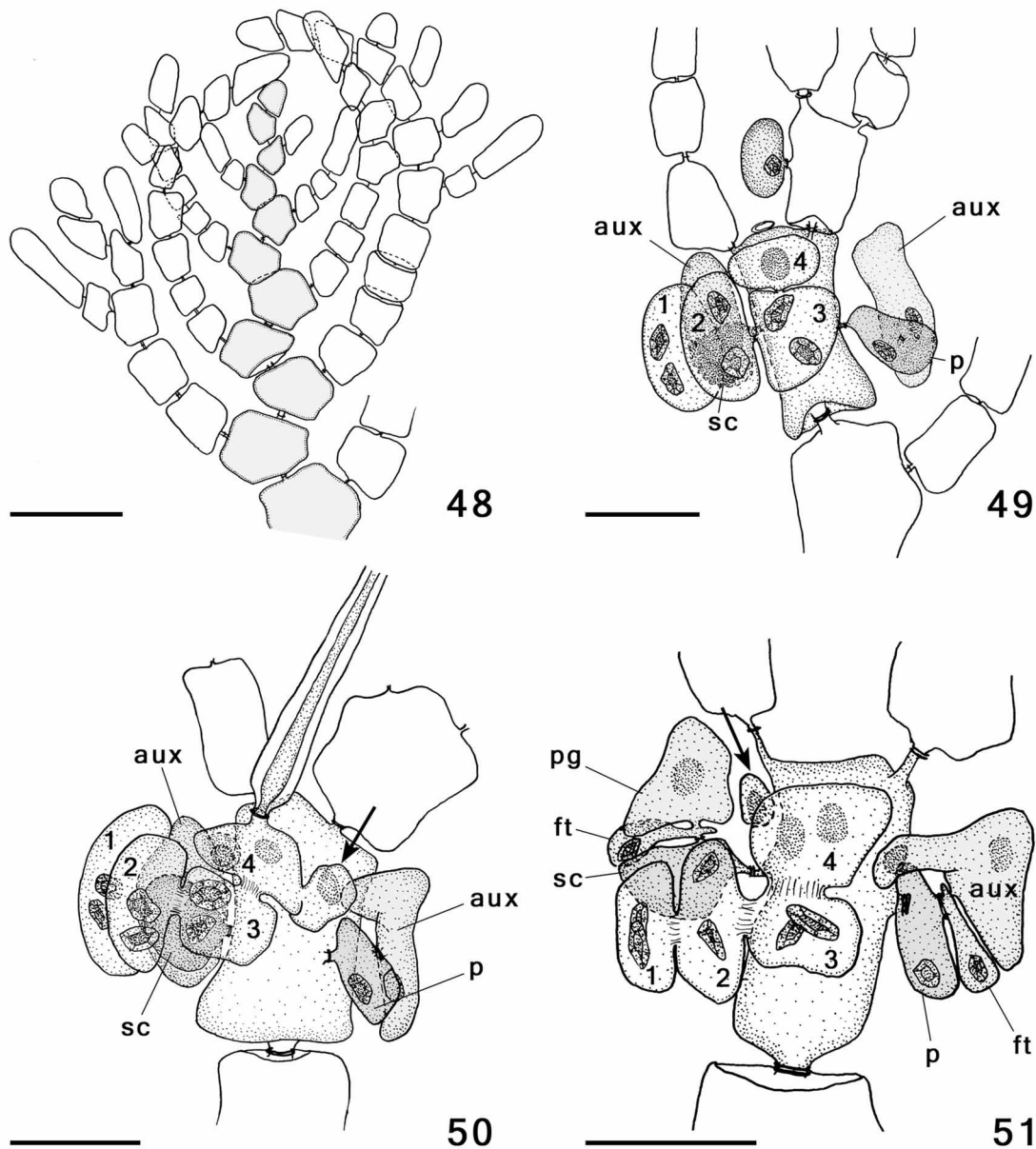
Figs 43–47. *Euptilota fergusonii.* Reproductive development. Fig. 43. A mature cystocarp surrounded by a dense involucrum and placed subterminally on a short indeterminate axis at the tip of a determinate branch. Fig 44. Detail of a procarp in which the carpogonium (cp) was presumably fertilized and has undergone two mitotic divisions with two nuclei still present in the carpogonium and two (only one visible) in large connecting cells (black arrowhead); cells of the carpogonial branch (1–3) have begun to fuse; the fertile periaxial cell has divided unequally resulting in a proximal basal cell (p) and a distal auxiliary cell (aux); the place where the trichogyne entered the mucilaginous matrix surrounding the procarp remains visible as a refractive ring (white arrowhead). Fig. 45. A disintegrating carpogonial branch (1–3 and cp) after presumed fertilization. Fig. 46. Proximal part of a determinate lateral bearing numerous tetrahedrally divided tetrasporangia. Fig. 47. Fertile determinate lateral bearing clustered spermatangia on modified abaxial branches. Scale bars represent: Fig. 43, 250 μm; Figs 44–45, 10 μm; Fig. 46, 100 μm; Fig. 47, 25 μm.

haploid nucleus may divide once mitotically (Fig. 51). All cells of the carpogonial branch including the carpogonium have fused by this stage. As events proceed the entire carpogonial branch withers (Fig. 45).

The auxiliary cell, which acts as the gonimoblast initial after segregation and removal of its

haploid nucleus, divides apically to form the first gonimolobe initial, after which a second, lateral gonimolobe initial soon arises. Although difficult to observe due to the density of the young gonimoblasts, it appears as though only the distal gonimolobe initial produces gonimoblasts. All gonimolobe cells become carposporangia and

Figs 48–51. *Euptilota fergusonii*. Vegetative and reproductive development. Fig. 48. Apex of a thallus showing the zigzag appearance of the axial cells and the distichous arrangement of the determinate laterals. Figs 49–51. Early postfertilization stages. Fig. 49. Detail of a procarp with a laterally expanded carpogonium (4) containing the presumed fertilization nucleus. The supporting cell (sc) and fertile periaxial cell (p) have divided unevenly resulting in a small basal cell and a large auxiliary cell (aux). Cells of the carpogonial branch (1–3) each contain two nuclei except the carpogonium. Fig. 50. Carpogonium has formed two lateral protuberances, containing diploid nuclei which may be cut off to form connecting cells (arrow). The auxiliary cell (aux) on the right has produced a large beak-like protrusion directed toward the connecting cell. The haploid nucleus of the auxiliary cell has migrated toward the base of the cell. Fig. 51. Following diploidization of the auxiliary cell the haploid nucleus of the auxiliary cell has been cut off into a wedge-shaped foot cell (ft), situated between the basal cell and the auxiliary cell (aux). A residual cell (arrow) has been cut off on the left and is in process of formation on the right. Scale bars represent 10 µm.

there are no distinctive elongate stalk cells present. Mature carposporangia are irregularly contoured and 12–20 µm in diameter. Directly after fertilization the 2–3 axial cells proximal to and two axial cells distal to the fertile axial cell initiate involucral filaments. A fertile indeterminate branchlet ceases growth after initiation of the

gonimoblasts resulting in a subapical cystocarp borne on a stunted, heavily corticated lateral (Fig. 43).

Tetrasporangia are tetrahedrally divided, sessile, and formed singly at the distal ends of cells of the ultimate branches of determinate laterals. The tetrasporangia are mainly, though not exclusively,

formed on the proximal adaxial branchlets of determinate laterals (Fig. 46). When fully mature sporangia are ovoid and $45-55$ μm in width by $55-65$ μm in length.

Euptilota molle (Wollaston) De Clerck, *comb. nov.*

Thamnocarpus mollis Wollaston, pro parte, *Phycologia* 31(2): $143-145$, Figs $17-22$ (1992).

Carpothamnion molle (Wollaston) P. Silva (in Silva *et al.*, 1996: 387).

Holotype

Tetrasporangial specimen (Fig. 52) collected off Mtentu River, 20 km south of Port Edward, South Africa (C.J. Hannocks, 30.xi.1984; NAT 2515 (NU 009765)).

Note

The original account of *Carpothamnion molle* by Wollaston (1992 as *Thamnocarpus mollis*) is based on two separate species. Sexual plants from Tanzania correspond to the recently described genus and species *Sciurothamnion stegengae* De Clerck et Kraft (in De Clerck *et al.*, 2002), whereas the tetrasporic holotype from the Eastern Cape Province, South Africa, is shown here to belong in *Euptilota*.

Habitat

Collected only at depths of more than 35 m, where it forms elegant tufts on rocky ledges. Its distribution may be limited to the region from the northern Eastern Cape Province (former Transkei region) to southern Kwazulu-Natal.

Specimens examined

South Africa: Eastern Cape Province, Mtentu River, (Hannocks, 30.xi.1984, NU NAT 2515) holotype; Kwazulu-Natal, Protea Banks, Southern Pinnacle (De Clerck *et al.*, 4.ii.2001, KZN 1938); Kwazulu-Natal, Protea Banks, Northern Pinnacle (De Clerck *et al.*, 5.ii.2001, KZN 1987),

Habit and vegetative morphology

Plants grow from a small discoid holdfast from which a single axis arises reaching a height of $6-13$ cm (Figs $52-53$). When freshly collected they are pale and pinkish in colour with a faint bluish-grey iridescence. Thalli consist of repeatedly and irregularly dichotomously branched indeterminate axes that are moderately to sparsely beset with distichously arranged determinate laterals (Figs $53-55$). Laterals are readily shed and basal parts

of axes are nearly devoid of laterals. Thalli are exceedingly flaccid and supple, nearly gelatinous. Determinate laterals are aligned in an alternate-distichous manner (1/2 spiral) and remain completely uncorticated (Figs $54-56$). They reach $18-26$ cells ($1400-2000$ μm) in length and form distinctive tufts perpendicular to the parent axis. The basal $4-6$ cells of each determinate lateral branch subdichotomously with the branches becoming lax distally, with each branch separated by $2-5$ cells (Fig. 56). The distal unbranched parts of the laterals may consist of up to 14 cells. Branching of determinate laterals takes place through protrusions at the distal ends of cells. The first branches originate from the third to sixth cells when a determinate lateral has reached a length of $5-9$ cells at approximately $10-14$ segments below the apex (Fig. 57). Additional branches are produced acropetally as well as basipetally. Spines ornamenting the apical and subapical cells of the determinate laterals are lacking. Deciduous hairs were seen terminating the ultimate cells of determinate laterals, but only when they were close to the apex (Fig. 61).

Indeterminate branches form at irregular intervals along primary axes either by direct conversion of the tips of determinate laterals to indeterminate axes (Fig. 55) or (especially in female gametophytes) adventitiously on the proximal cells of existing determinate laterals. Growth of an indeterminate axis takes place by oblique division of the apical cell, with the high sides of successive axial cells alternately offset in a 1/2 divergence. This results in a zigzag arrangement of the axial cells in the apical parts of the thallus (Fig. 57). Young determinate laterals curve upwardly and may or may not overtop the apical cell. Axial cells in the distal parts of the thallus are isodiametric and measure $24-47$ μm in width by $26-55$ μm in length (L/B: $0.7-1.3$). Mature axial cells are rectangular in shape, slightly longer than broad ($85-110$ μm $\times$ $80-155$ μm; L/B: $1.0-1.4$) (Fig. 58). Lower down, the axial cells reach $300-480$ μm in diameter and are connected by short pit-connection (Fig. 59). An indeterminate axis is terete, heavily corticated to within a few millimetres of the apex, and reaches a diameter of approximately 1 mm near the base. Cortical filaments initially arise singly from the basal cells of determinate laterals, approximately $35-40$ cells below the apex (Fig. 58). A second and third cortical filament then issues from each of the basal cells a few segments lower down. Cortical filaments branch irregularly, initially enveloping the axial cells in a single layer, extending a distance of about two segments (Fig. 59). Once the axis is completely enveloped cortical filaments differentiate into inner cortical rhizoidal filaments and outer small angular cortical cells. The inner rhizoidal filaments branch frequently to give rise to additional rhizoidal filaments composed of cells $3-$
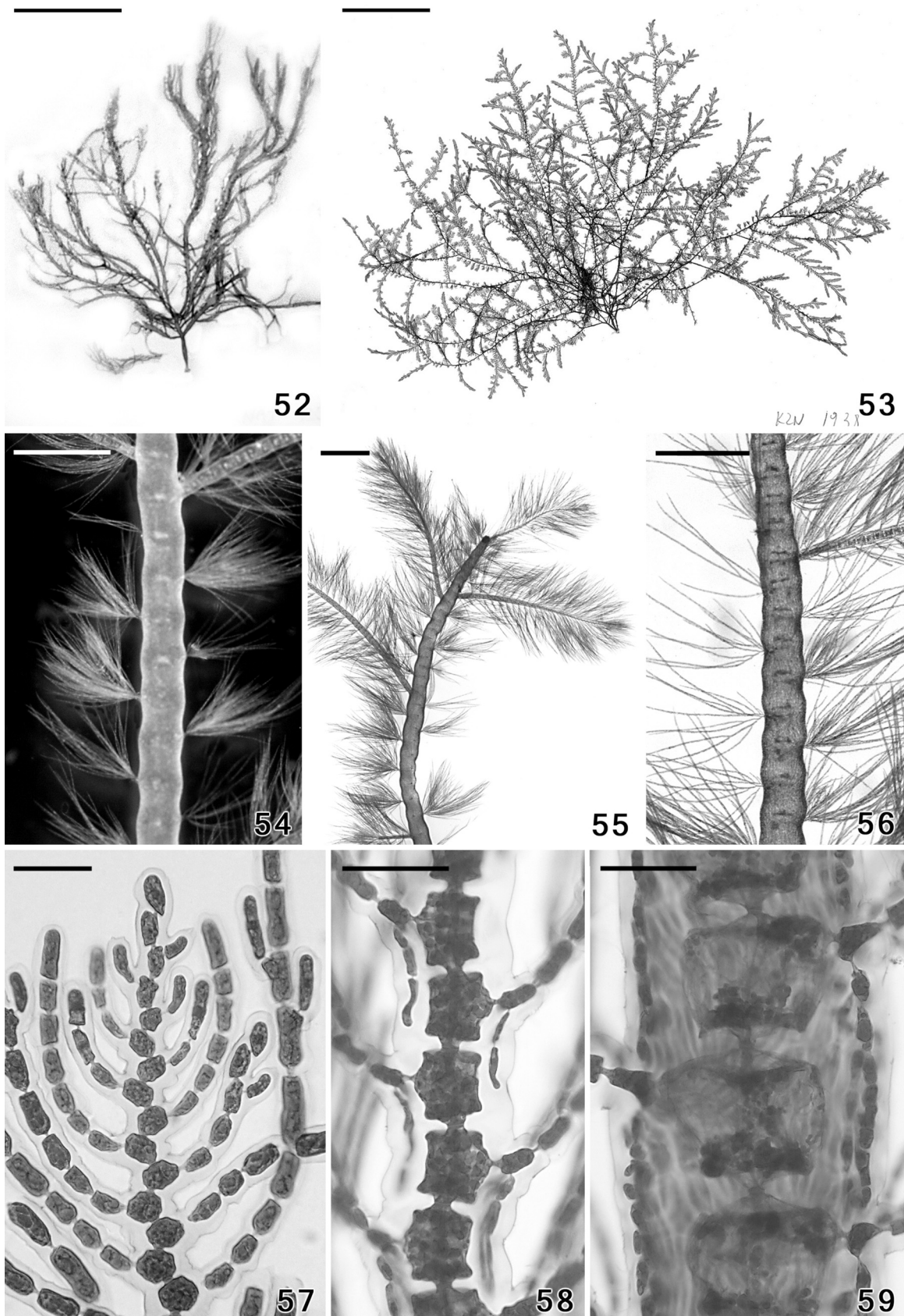
Figs 52–59. *Euptilota molle*. Habit and vegetative development. Fig. 52. Holotype of *C. molle* (NAT 2515). Fig. 53. Habit of a herbarium specimen of *C. molle* (KZN 1938). Figs 54–56. Portions of corticated axes in the middle parts of the thallus bearing alternate-distichous determinate and indeterminate lateral branches. Fig. 57. Detail of an apex showing the zigzag arrangement of the axial cells and the early development of determinate laterals. Fig. 58. An axis near the tip showing the initiation of cortical filaments from the proximal cells of the determinate laterals. Fig. 59. Median optical section of an axis in the mid-region of the thallus showing the outer cortex composed of small isodiametric cells and the internal rhizoids. Scale bars represent: Figs 52–53, 1 cm; Figs 54 and 56, 0.5 mm; Fig. 55, 1 mm; Figs 57–59, 50 *μ*m.

10 μm wide by 100–200 μm. Rhizoidal filaments also cut off smaller cells toward the periphery which will divide again to form the consolidated surface of small angular cortical cells (Fig. 60). All vegetative cells are uninucleate.

Reproductive morphology

Gametophytes are dioecious. Spermatangia are clustered on dwarf fertile axes borne on the branches of determinate laterals (Fig. 73). Terminal cells of the fertile branchlets function directly as spermatangial mother cells, with each producing 2–4 ovoid spermatangia 3–4 × 5–7 μm. Each spermatangium contains a distal nucleus subtended by a mucoid vesicle.

Procarps are borne near the apices of short, young indeterminate axes, which are formed either from the tips of determinate laterals, or adventitiously from one of the proximal cells of a determinate lateral. Although several carpogonial branches may form on a single axis, only one carposporophyte matures. A procarp arises by a concavo-convex division at the middle of the fertile axial cell. The first periaxial cell is cut off in the same plane as the vegetative determinate lateral and directly below it. It becomes the supporting cell of a four-celled carpogonial branch which is cut out in a zigzag pattern similar to the '*Callithamnion byssoides*-type' of Miranda (1934) or 'zigzag-type' of Harris (1962) (Figs 61, 69). The trichogyne is long (to 500 μm). The mature second and third cells of the carpogonial branch are usually binucleate, whereas the first cell and the carpogonium are uninucleate. In most instances the carpogonial branch is fully formed before a second fertile periaxial cell is cut off opposite the supporting cell (Fig. 63). No further cells are produced and sterile-cell groups are absent.

Following presumed fertilization, the carpogonium expands laterally and the trichogyne breaks down completely (Fig. 70). The place where the trichogyne emerged from the mucilaginous coat enveloping the procarp remains clearly visible as a refractive ring in later stages. The supporting cell and fertile pericentral cell both enlarge and soon divide by an oblique, unequal cross-wall into a small basal cell and a large auxiliary cell (Fig. 70). The diploid nucleus in the carpogonium undergoes a single mitotic division that is unaccompanied by cytokinesis and two protrusions are formed on each side of the carpogonium, adjacent to the auxiliary cells (Fig. 66), followed by a second division of both carpogonial nuclei. Both division products then migrate into the two large protrusions, which are segregated as two large connecting cells that are not pit-connected to the carpogonium. Concurrently,

both auxiliary cells elongate and their haploid nuclei migrate toward the base. An immediate mitotic division of the diploid nucleus follows diploidization of the auxiliary cells. One of the daughter nuclei migrates toward the centre of the auxiliary cell while the other is extruded in the form of a persistent residual cell (Figs 67 and 68, 71 and 72). This extrusion is accompanied by a second nuclear division leaving a nucleus in the auxiliary cell at the place where the residual cell was cut off. The original haploid nucleus, which at this stage is situated at the base of each auxiliary cell, is cut off by a cleavage perpendicular to the longitudinal axis of the auxiliary cell to form a foot cell and a gonimoblast initial (Fig. 72). The haploid nucleus inside each foot cell usually divides once mitotically. Division of the primary gonimoblast cell is oblique cutting off a terminal gonimolobe initial in a somewhat lateral position (Figs 67 and 72). All cells of the carpogonial branch, including the carpogonium, have fused by this stage. As events proceed the entire carpogonial branch withers. A second gonimolobe initial at the site where the residual cell was cut off may, however, not develop a gonimolobe. All gonimolobe cells become carposporangia and elongated stalk cells are not formed. Mature carposporangia are irregular in contour and 12–25 μm in diameter.

Directly after fertilization the 2–3 axial cells proximal to the fertile axial cell initiate involucral filaments from their distal poles (Figs 64 and 65). The two opposite gonimoblasts are readily visible at early stages (Figs 64 and 65) but are often difficult to distinguish at later stages. Elongation of the fertile axis ceases with initiation of the gonimoblasts, and cystocarps are borne on stunted, heavily corticated modified axes (Fig. 62).

Tetrasporangia are tetrahedrally divided, sessile, and formed singly at the distal ends of cells of the determinate laterals (Figs 74 and 75). When fully mature they are obovoid and 40–55 μm in width by 50–65 μm in length (Fig. 75).

Euptilota articulata (J. Agardh) Schmitz

Schmitz 1896: 7; Okamura 1921: 130, pl. 183, Figs 1–9; 1932: 52, pl. 277, Fig. 11; Itono 1977: 139–141, 206, 279–280, Fig. 21 A–C, Fig. 42 C–F, Fig. 63 A–G; Desikachary *et al*. 1998: 249, Fig. 67 C-H; Womersley 1998: 355–356, 358, Fig. 164 A–E.

Ptilota articulata J. Agardh 1841: 36, Kützing 1849: 670; 1862: 17, pl. 56d.

Euptilota coralloidea (J. Agardh) Kützing 1849: 672; De Toni & Forti 1923: 54, pl. 7, Figs 2,3; Lucas & Perrin 1947: 338, Fig. 165.

(For additional references see Womersley, 1998)
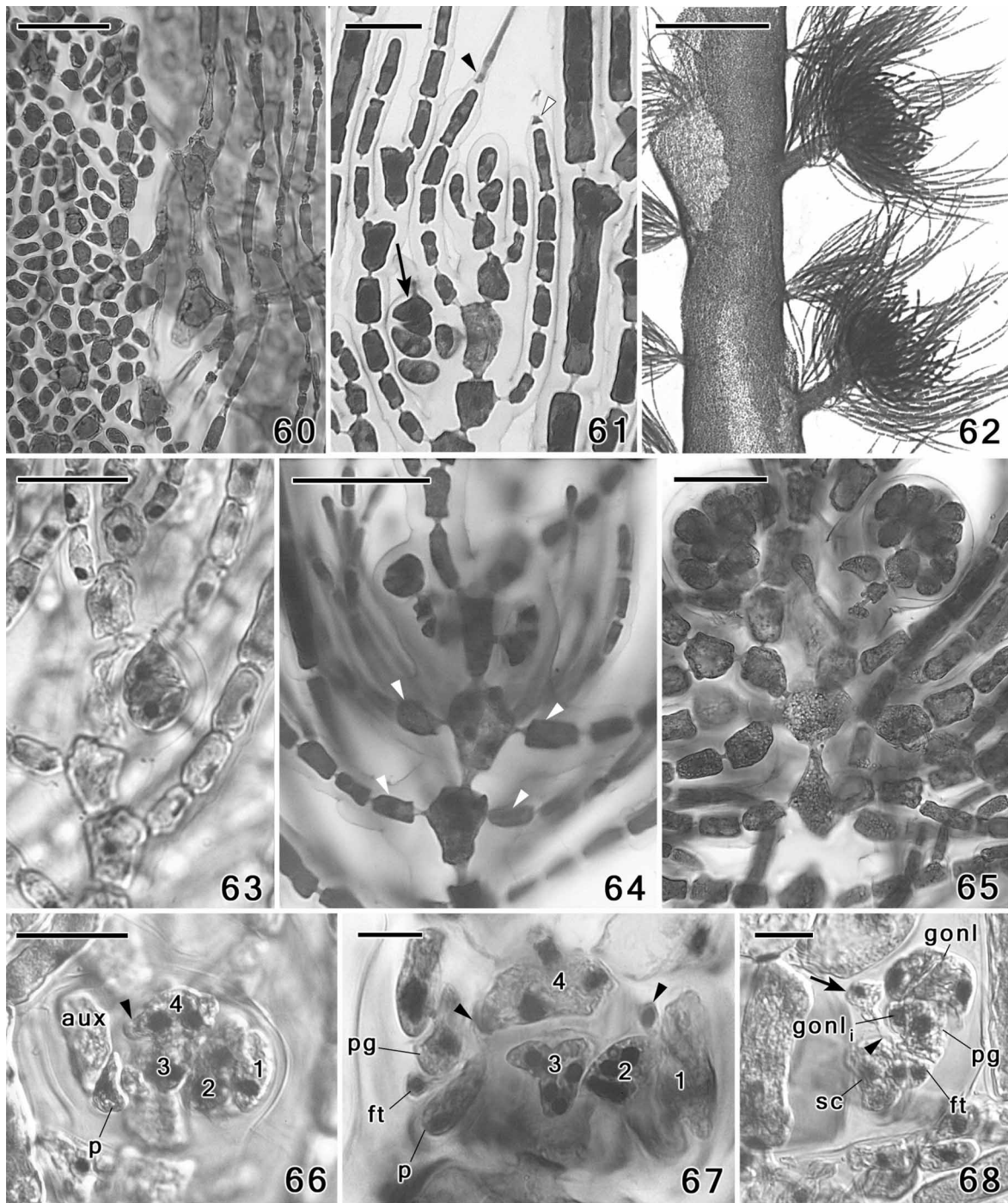
Figs 60–68. *Euptilota molle.* Vegetative and reproductive development. Fig. 60. Squash preparation of the cortex showing differentiation between the outer cortical layer composed of small isodiametric cells and the inner layer of elongate rhizoidal cells. Fig. 61. Detail of an apex with a determinate lateral bearing a hyaline hair (black arrowhead) and the condition below in which the hair has already been shed (white arrowhead). A carpogonial branch is seen on the left (arrow). Fig. 62. Two mature cystocarps, each surrounded by a dense covering of involucral filaments. Fig. 63. Young carpogonial branch with an incompletely developed trichogyne. Note the absence of the second periaxial cell at this stage. Fig. 64. Two opposite immature gonimoblasts with involucral branches developing from the segments below the fertile axial cell (white arrowheads). Fig. 65. Two maturing opposite gonimoblasts with distal gonimolobes. Figs 66–68. Early post-fertilization stages in the development of the procarp. Fig. 66. The diploid nucleus in the carpogonium (4) has divided and at least one protuberance has been initiated (arrowhead), the periaxial cell (p) has divided unevenly to produce a proximal basal cell and a large distal auxiliary cell. Fig. 67. Stage where the auxiliary cells have been diploidized. The original haploid nuclei of the auxiliary cell have been cut off in a foot cell (ft), two residual cells (arrowheads) have been cut off and the auxiliary cell has divided to form a primary gonimoblast cell (pg) and apical gonimolobe initial; cells of the carpogonial branch (1, 2, 3) are degenerating. Fig. 68. The residual cell (arrow) remains connected to the foot cell (ft) by a narrow cystoplasmic strand (arrow head); the primary gonimoblast cell (pg) has issued a terminal gonimolobe (gonl) and a lateral gonimolobe initial (gonl$_i$) is visible just to the left of the primary gonimoblast cell; the foot cell (ft) contains two nuclei. Scale bars represent: Fig. 60 and 64–65, 50 μm; Fig. 61, 63 and 66–68, 25 μm; Fig. 62, 500 μm.
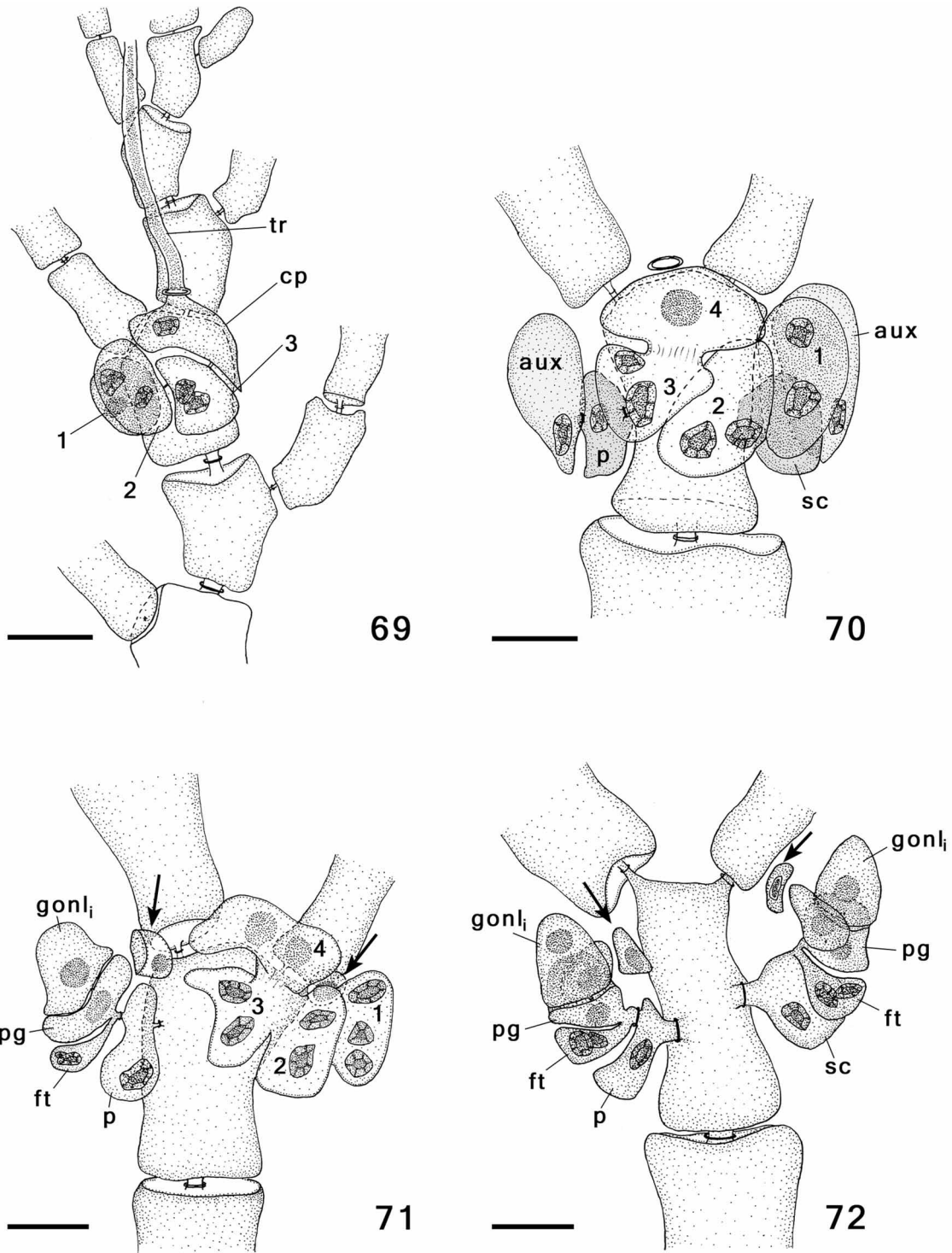
Figs 69–72. *Euptilota molle.* Female reproductive apparatus. Fig. 69. Procarp with a four-celled carpogonial branch (1–4) including carpogonium (cp) and trichogyne (tr). Fig. 70. Early post-fertilization stage showing a carpogonium (4) containing a diploid nucleus and two auxiliary cells (aux). Fig. 71. Post-fertilization stage showing a fused carpogonial branch (1–4), a carpogonium (4) with two nuclei, a periaxial cell (p) bearing a foot cell with two nuclei (ft), a primary gonimoblast cell (pg) and gonimolobe initial (gonl$_i$), and two residual cells (arrows). Fig. 72. Developing gonimoblasts showing a supporting cell (sc) and opposite periaxial cell (p), two foot cells (ft), two primary gonimoblast cells (pg), two gonimolobe initials (gonl$_i$), and two residual cells (arrows). Scale bars represent 10 μm.
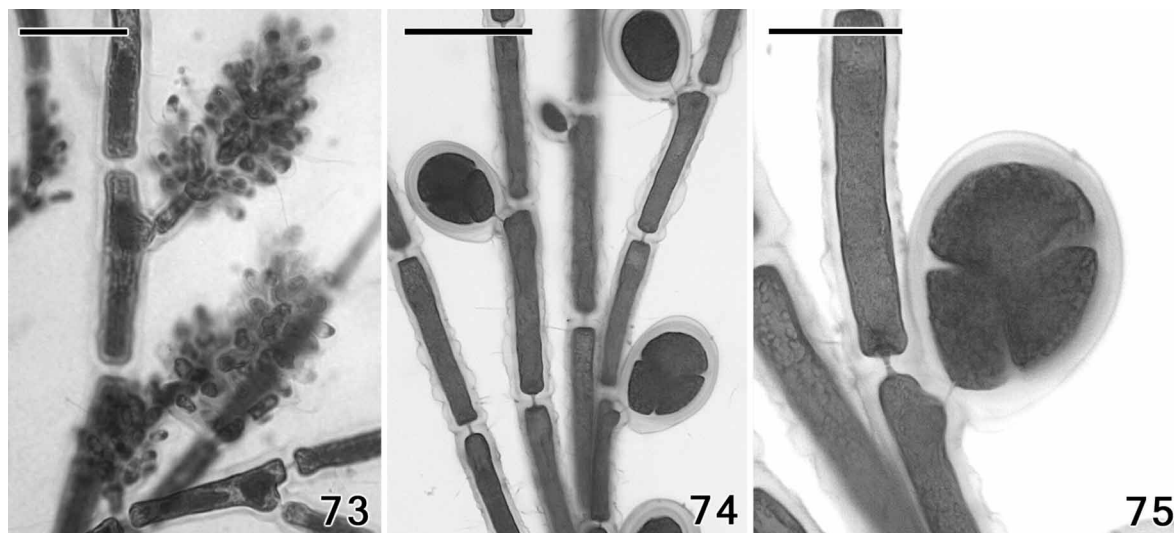
Figs 73–75. *Euptilota molle*. Spermatangia and tetrasporangia. Fig. 73. Determinate branch bearing dwarf fertile axes with spermatangia. Fig. 74. Determinate branch bearing several developing and mature tetrasporangia. Fig. 75. Detail of a mature, tetrahedrally divided tetrasporangium. Scale bars represent: Figs 73 and 75, 25 μm; Fig. 74, 50 μm.

nia (27.xii.1980, M.H. Hommersand, NCU); drift, Warrnambool, Victoria (13.vii.1995, M.H. Hommersand & G. Kraft, NCU); drift, Warrnambool, Victoria (17.viii.1995, M.H. & F.C. Hommersand, NCU); drift, Port MacDonnell, South Australia (11.xi.1995, M.H. & F.C. Hommersand, NCU).

Vegetative morphology

Growth of an indeterminate axis takes place by oblique division of the apical cell with the high side of each successive axial cell alternating in a plane (1/2 divergence). Initials of lateral branches are cut off obliquely from successive segments beginning 2–4 cells below the apex and form side branches at 35° to 45° angles. Lateral initials develop into determinate branchlets that are essentially uncorticated, except for short descending filaments that develop from the proximal two to three segments. The basal segments of each lateral cut off an initial from the lower side and also sometimes from the upper side. Additional lateral initials are also cut off on both sides of the proximal cell and all three initials form filaments that grow and branch downward over two segments and extend across the axial cell on both sides (Fig. 76). The adaxial initial, if present, does not develop further and there are no ascending cortical filaments. Descending cortical filaments initially form a one-layered cortex surrounding the axial cell. These, in turn divide periclinally and form an inner layer of larger cells and an outer layer of smaller cells, such that the cortex is typically two cell layers thick (Womersley, 1998, Fig. 164E). The proximal cells of the cortical filaments elongate and expand as the axial cell elongates producing flanking cells on both sides of
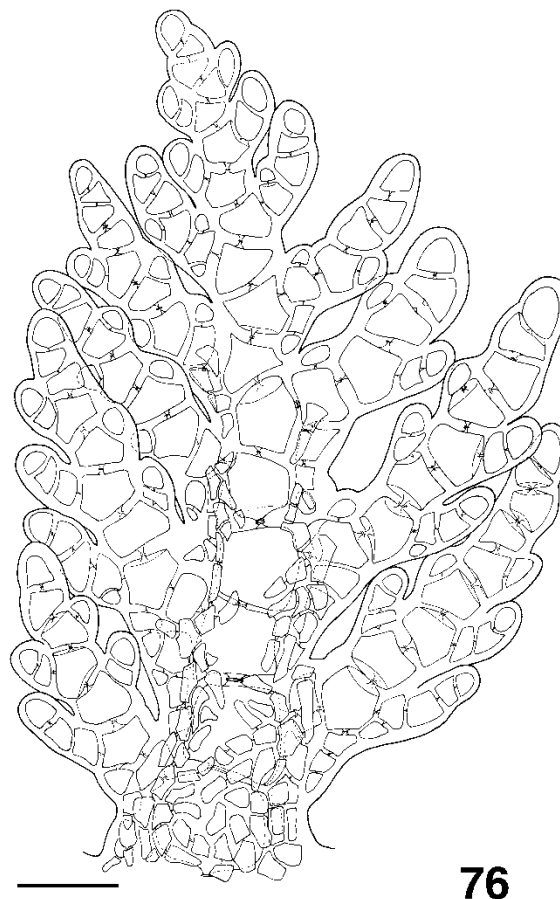

Fig. 76. *Euptilota articulata*. Vegetative morphology. Material from Currie River, north coast, Tasmania, i.1937, leg. F. Perrin, NCU, stained with aniline blue. Axis bearing alternate lateral branchlets and developing cortical filaments. Scale bar represents 50 μm.

the axis and are responsible for the compressed appearance of the axis in surface view and cross

sections. Rhizoidal filaments originate from subsurface cells and are weakly developed except in basal parts. They grow irregularly between the subcortical cells and between subcortical and axial cells.

Reproductive morphology

Each spermatangium possesses a terminal nucleus subtended by a mucoid vesicle (De Clerck, personal observation). See Table 2 for additional morphological characters found in Okamura (1921, 1932), Itono (1977) and Womersley (1998).

Discussion

In the revised classification of the Ceramiaceae proposed by Kylin (1956) the Ptilota-group was placed in an assemblage in which the procarps were subterminal on ordinary or special short lateral vegetative branches. The group was further characterized as having a pinnately branched central axis in which, with few exceptions, the thallus was thickly clothed by larger inner and smaller outer cortical cells. *Euptilota* was unique among members of the Ptilota-group in being alternately branched

Table 2. Morphological features of *Euptilota* species

Species Category	*E. formosissima*	*E. articulata*	*E. fergusonii*	*E. molle*
Branching at apex	Alternate-distichous, from successive segments	Alternate-distichous, from successive segments	Alternate-distichous, from successive segments	Alternate-distichous, from successive segments
Initial branching of the determinate laterals	Alternate-distichous, laterals resembling pinnae, straight or curved at 45° angle	Alternate-distichous, laterals resembling pinnae, straight at 45° angle	Curved, first 3–4 segments naked, distal 4–9 cells branching abaxially	Curved, perpendicular to axis, initial branching abaxial
Habit of the mature determinate laterals	Corticated, similar to indeterminate axes	Similar to indeterminate axes but largely uncorticated	Uncorticated, with distal abaxial and proximal adaxial branchlets	Uncorticated, sub-dichotomously branched readily deciduous tufts
Branching of basal cell of a lateral	Naked except for cortical initials	Naked except for cortical initials	Initially naked, later with an adaxial branch	Naked except for cortical initials
Secondary branching of the determinate laterals	No special secondary branching	No special secondary branching	Proximal segments produce adaxial branches	Additional branches interpolated acropetally and basipetally
Origin of the cortical filaments	Bidirectional, from an adaxial and an abaxial initial on basal cells of laterals	Undirectional, from abaxial initials on basal cells; adaxial initials rudimentary	Singly, from abaxial initials on basal cells followed by two lateral initials	Singly, from abaxial initials on basal cells followed by two lateral initials
Growth of the cellular cortex	Bidirectional and around axis covering two segments	Downwards and around axis covering two segments	Downwards and around axis covering two segments	Downwards and around axis covering two segments
Thickness of cortex	2–3 (–4) layered	2–3 (–4) layered	1–layered	1–layered
Rhizoidal cortication	Bidirectional, in thin layer between axial and cellular cortical cells	Unidirectional, irregularly branched between axial and cellular cortical cells	Downwards, filling space between 1–layered outer cortex and axis	Downwards inside, cellular cortex layer; interpolating secondary outer cortex
Origin of the indeterminate branches	From tips of determinate branches, none adventitiously	From tips of determinate branches, none adventitiously	From tips or adventitiously from proximal cells of determinate branches	From tips or adventitiously from proximal cells of determinate branches
Origin and structure of the spermatangia	On adventitious filaments from cortex; nuclei terminal	Clustered at tips of determinate laterals; nuclei terminal	In clusters on dwarf fertile axes; nuclei terminal	In clusters on dwarf fertile axes; nuclei terminal
Location of the procarps	Solitary, on dwarf indeterminate branchlets	1 to 3 on dwarf indeterminate branchlets	1–several on transformed tips of determinate laterals	In series on transformed tips of determinate laterals
Position and shape of procarps	Below or opposite determinate lateral; oriented horizontally	Below or opposite determinate lateral; oriented horizontally	Below or opposite determinate lateral; oriented horizontally	At right angles to determinate lateral; zigzag orientation
Structure of mature cystocarp and carpospores	Single cluster enclosed by four corticated involucral branchlets	Single cluster enclosed by many uncorticated involucral branchlets	Single cluster enclosed by loosely clustered involucral filaments	One or two clusters enclosed by loosely clustered involucral filaments
Position of the tetrasporangia	Terminal or sessile on adventitious cortical filaments	Terminal or sessile on branchlets of a determinate lateral	Terminal or sessile, mostly on adaxial determinate laterals	Sessile at distal ends of cells of determinate laterals

with a branch initial formed right and left from each successive axial segment and with opposite branching from the same segment absent. The most recent treatment of the Ceramiaceae (Womersley, 1998) retains *Euptilota* in the Ptiloteae. The latter has been considered to consititute an unnatural group by Hommersand (1990). Although several genera of the Ptilota-group require thorough investigations, *Euptilota* is clearly distinct based on vegetative as well as reproductive characters.

The pattern of apical cell division, cell enlargement and the behaviour of the derived segmental cells determine primary branching in the Ceramiaceae (Hommersand, 1963; Itono, 1977; Moe & Silva, 1979). Itono (1977) labelled the types of apical growth as 'transverse', 'oblique', 'oblique–alternate' and 'oblique–spiral'. Primary branching in *Euptilota* is 'oblique–alternate'. Apical cells divide obliquely and lateral initials are cut off from the high sides of segmental cells beginning 1–2 (–3) segments below the apex and give rise to lateral branches alternately in a 1/2 spiral from successive segments. A second lateral never issues opposite the primary lateral in the same segment in *Euptilota*.

The combination of a small-celled outer cortex and internal rhizoidal cortication is uncommon in the Ceramiaceae. Besides *Euptilota*, it is reported in the monospecific genera *Carpothamnion* Wollaston (1992, as *Thamnocarpus*), *Rhodocallis* (Hommersand *et al.*, 1998), *Sciurothamnion* (De Clerck *et al.*, 2002), *Diapse* (Womersley, 1998), and *Psilothalia* with three species (Womersley, 1998). The tribal affinities of these genera remain obscure, but they are probably dispersed among several evolutionary lines.

No one vegetative character is diagnostic for *Euptilota* and the recognition of the genus is validated by a combination of vegetative and reproductive characters. The range of vegetative morphologies is exceedingly broad for a genus containing so few species and characterization of the genus rests largely on a small number of highly conserved characters involving the male and female reproductive systems. Table 2 summarizes the vegetative and reproductive variation seen in the four species of *Euptilota* recognized here.

Reproductive development in *Euptilota* is best understood through comparisons with anatomical features found in *Aglaothamnion* or *Callithamnion* of the Callithamnieae. The nucleus is centrally located between terminal and proximal mucilage-containing vesicles in the spermatangia of *Aglaothamnion* and *Callithamnion* (McIvor *et al.*, 2002). A median nucleus and terminal and proximal mucilage-containing bodies are encountered in *Euptilota mooreana* (Hommersand, personal observation) and in *Crouania* and *Wrangelia* (Feldmann-Mazoyer, 1941). In contrast, the nuclei are

terminal in all four species of *Euptilota* subtended by a single mucoid vesicle. Elsewhere, terminal nuclei are encountered in spermatangia of *Sciurothamnion* (De Clerck *et al.*, 2002) and *Seirospora* (Feldmann-Mazoyer, 1941; Aponte & Ballantine, 1995; McIvor *et al.*, 2002) and is the most common condition in the Ceramiaceae. The position of the nucleus in spermatangia, whether median or terminal, may prove to be diagnostic at the tribal level in the Ceramiaceae.

There is a strong resemblance between the procarps of *Euptilota* and those of *Aglaothamnion* and other members of the Callithamnieae. In both, the fertile segment consists of an axial cell bearing a determinate vegetative lateral and two opposite fertile periaxial cells, one of which bears the carpogonial branch. Sterile group cells are absent. The supporting cell and opposite periaxial cells are cleaved by concavo-convex divisions from the mid-region of the fertile axial cell in both. Only their orientation relative to that of the vegetative lateral appears to be different. In *Aglaothamnion halliae* (Hommersand, 1997) and other Callithamnieae that have been investigated the pair of periaxial cells lie at a 90° angle from the vegetative lateral. This same relationship has been described in *Georgiella* (Moe & Silva, 1983), a genus presently placed in the Ptiloteae. In contrast, the supporting cell of the carpogonial branch is either cut off directly underneath the determinate lateral or on the opposite side (180°) in *Euptilota*. The first fertile periaxial cell functions as the supporting cell of the carpogonial branch and the second, opposite fertile periaxial cell is cut off only after the carpogonial branch has been initiated or after it is fully formed. Orientation of the fertile periaxial cells in the same plane as the vegetative lateral has been reported in *Seirospora* (Feldmann-Mazoyer, 1941; Maggs & Hommersand, 1993) but does not occur in *Sciurothamnion* (De Clerck *et al.*, 2002). The first three cells of the carpogonial branch extend horizontally across the face of the axial cell with the carpogonium cut off horizontally and oriented vertically in *Aglaothamnion* (Feldmann-Mazoyer, 1941; Hommersand, 1997) and most other Callithamnieae. The horizontal orientation is found in three of the four species in *Euptilota* and is also reported in *Seirospora* (Feldmann-Mazoyer, 1941; Kraft, 1988; Aponte & Ballantine, 1991) and in *Sciurothamnion* (De Clerck *et al.*, 2002). A zigzag arrangement of cells of the carpogonial branch was described in *Callithamnion corymbosum* (Miranda, 1934; Feldmann-Mazoyer, 1941) and some other species of *Callithamnion*, and is found in *Euptilota molle*.

Kylin (1956) stated that procarps were borne along the lengths of unmodified indeterminate axes (Langtriebe) in the Callithamnion group and were subterminal on main axes or side branches in the

Spermothamnion, Compsothamnion, Griffithsia, Dasyphila and Ptilota groups. Procarps occupy the same position in *Seirospora* as in *Callithamnion* (Maggs & Hommersand, 1993). They are borne on indeterminate axes transformed from the tips of determinate laterals in *Sciurothamnion* (De Clerck *et al.*, 2002). The same is true of *Euptilota molle* except that the fertile axes are shorter than those in *Sciurothamnion*. Fertile branchlets are shorter still with fewer procarps in *E. fergusonii* and *E. articulata* and are reduced to a single procarp per fertile branch in *E. formosissima*. The trend appears to be toward reduction, culminating in a single subterminal procarp in the last-mentioned species.

After fertilization an auxiliary cell is cut off from the supporting cell and the periaxial cell on the opposite side, and the carpogonium divides by a vertical septum into two cells in *Callithamnion corymbosum* (Oltmanns, 1898), *Aglaothamnion cordatum* (O'Kelly & Baca, 1984, as *Callithamnion cordatum*), and *Aglaothamnion halliae* (Hommersand, 1997). This behaviour appears to be widespread in the Callithamnieae. Each daughter cell then cuts off a minute connecting cell on the same side as the adjacent auxiliary cell. Contact and fusion of the connecting cell with the auxiliary cell take place as the auxiliary cell enlarges. In contrast, the carpogonium does not divide but enlarges horizontally and forms a pair of tubular protrusions directed inwardly toward each of the auxiliary cells in *Seirospora orientalis* (Kraft, 1988), *S. occidentalis* and *S. viridis* (Aponte & Ballantine, 1991, 1995), *Sciurothamnion stegengae* (De Clerck *et al.*, 2002), and *Euptilota*. The fertilization nucleus (diploid nucleus) inside the carpogonium divides twice and two derivative nuclei enter the tubes and are cut off terminally inside prominent connecting cells adjacent to the auxiliary cells. In general, each connecting cell fuses with its respective auxiliary cell and the diploid nucleus is deposited inside the auxiliary cell membrane where it undergoes mitosis. Rarely does only one auxiliary cell become diploidized. In *Aglaothamnion halliae* one of the daughter nuclei moves to the centre of the auxiliary cell and the other is extruded to the outside in a small cell that has been termed a 'residual cell' (Hommersand, 1997). The auxiliary cell undergoes incomplete transverse cleavage into a large terminal gonimoblast initial and a small basal foot cell that contains the haploid nucleus, which may divide. The same sequence of events takes place in *Euptilota* and in *Sciurothamnion*, except that in the latter the haploid nucleus is cut off to one side in what has been termed a 'disposal cell' (De Clerck *et al.*, 2002). In *Seirospora orientalis* (Kraft, 1988), *Seirospora occidentalis* (Aponte & Ballantine, 1991); *Spyridia filamentosa* (Hommersand, 1963); *Rhodocallis elegans* (Hom-

mersand *et al.*, 1998), and some other Ceramiaceae, the diploid nucleus enters the auxiliary cell at its base and the auxiliary cell divides into a gonimoblast initial containing a diploid nucleus and a foot cell containing one diploid and one or two haploid nuclei. The connecting cell remains attached at the proximal end of the foot cell. De Clerck *et al.* (2002) interpreted the three developmental patterns following diploidization of the auxiliary cell as manifestations of the same process.

Each of the two gonimoblast initials cuts off a primary terminal gonimolobe initial and secondary lateral gonimolobe initials in *Aglaothamnion, Callithamnion* and *Seirospora* (Maggs & Hommersand, 1993) and in *Sciurothamnion* (De Clerck *et al.*, 2002). Nuclear divisions that might initiate secondary gonimoblobe initials were seen in *Euptilota formosissima* and *E. molle*, but there was no evidence that any of them ever produced secondary gonimolobes. Because two gonimoblasts developed on opposite sides, one would expect to see at least two packets of carposporangia or a bilobed cystocarp. This was illustrated by Okamura (1932) for *E. articulata* but was not evident in most mature cystocarps in species of *Euptilota*. Instead, the two gonimoblasts unite into a sphere containing a single mass of carposporangia surrounded by an involucre. All the carpospores appeared to mature and be released at the same time, and mature cystocarps remained empty once the initial cluster of carpospores has been released. Mature cystocarps were illustrated previously for *Euptilota formosissima* (Harvey & Hooker, 1845; Adams, 1994), *E. articulata* (Okamura, 1932; Itono, 1977; Womersley, 1998), and *E. fergusonii* (Cotton, 1907). The photographs in this paper also illustrate a unitary cystocarp. This is in contrast to the separate gonimoblasts and bilobed cystocarps that have typically been illustrated for species of *Aglaothamnion* or *Callithamnion* (Feldmann-Mazoyer, 1941) and *Hirsutithallia* or *Carpothamnion* (Womersley & Wollaston, 1998) of the Callithamnieae. Two gonimoblasts with carposporangia in chains resembling seirospores are seen in *Seirospora* (Maggs & Hommersand, 1993) and paired gonimoblasts with stalked secondary gonimolobes characterize *Sciurothamnion* (De Clerck *et al.*, 2002). Two well-separated gonimoblasts, each with spreading gonimolobes, were seen in *Euptilota pappeana* and *E. mooreana* (Hommersand, personal observation). Mature cystocarps of *Euptilota* are surrounded by an involucre formed from the cell or cells below and above the fertile axial cell after fertilization (Table 2).

Tetrasporangia are either terminal or sessile and lateral in *Euptilota* on ordinary or adventitious filaments. They undergo simultaneous cleavage to produce four tetrahedrally arranged tetraspores in

E. fergusonii and *E. molle*; however, irregularities are reported for *E. articulata* (Itono, 1977) and the tetrasporangia of *E. formosissima* appear to undergo successive mitoses followed by cytokinesis, even when the spores appear to be arranged tetrahedrally. Perhaps tetraspore arrangement depends on whether the tetrasporangia undergo a typical meiosis or not.

The results and discussion presented here affirm a close relationship between *Euptilota* and *Seirospora* and *Sciurothamnion,* and a more distant relationship to the Callithamnieae. *Euptilota molle* and *E. fergusonii* are more similar to *Sciurothamnion* than are *E. articulata* and *E. formosissima*. The first two species can be regarded as ancestral and the latter two as advanced. If so, evolution has proceeded through the loss of a sharp differentiation between indeterminate and determinate branches, rather than the reverse. The first three species listed above are widely distributed in the Indo-West Pacific Ocean, whereas *E. formosissima* is restricted in its distribution to New Zealand and the islands of the Campbell Plateau. An origin in the southern Tethyan Ocean is implied by the suggested evolutionary relationships with the cool temperate *E. formosissima* having differentiated from the other species after tectonic separation and isolation in New Zealand.

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