Eur. J. Phycol., (2012), **47(4)**: 366–383

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Molecular phylogeny and developmental studies of *Apoglossum* and *Paraglossum* (Delesseriaceae, Rhodophyta) with a description of Apoglosseae *trib. nov.*

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(Received 22 December 2011; revised 2 May 2012; accepted 11 May 2012)

Our morphological and molecular studies indicate that species from the southern hemisphere previously placed in *Delesseria* belong in *Paraglossum* and that *Paraglossum* and *Apoglossum* comprise a separate tribe, the Apoglosseae, S.-W. Lin, Fredericq & Hommersand, *trib. nov.*, within the family Delesseriaceae. From a vegetative perspective the Apoglosseae is readily recognized because some or all fourth-order cell rows are formed on the inner sides of third-order cell rows. All fourth-order cell rows grow adaxially in *Apoglossum*, whereas both adaxial and abaxial cell rows are present in *Paraglossum*. Periaxial cells do not divide in *Apoglossum*, whereas they divide transversely in *Paraglossum* in the same way as in *Delesseria*. Major branches are formed mainly from the margins of midribs in the Apoglosseae. The procarp consists of a straight carpogonial branch and two sterile cells, with the second formed on the same side as the first. The carpogonium cuts off two connecting cells in tandem from its apical end, the terminal cell being nonfunctional and the subterminal cell typically fusing with the auxiliary cell. Gonimoblast filaments radiate in all directions from the gonimoblast initials and produce carposporangia terminally in branched chains, with pit connections between the inner gonimoblast cells broadening and enlarging. The auxiliary cell, supporting cell, and sterile cells unite into a fusion cell, which remains small in *Apoglossum* but incorporates the branched inner gonimoblast filaments and cells in the floor of the cystocarp in *Paraglossum*. Elongated inner cortical cells seen in mature cystocarps in the Delesserieae are absent in the Apoglosseae. Phylogenetic studies based on *rbc*L (RuBisCO large subunit gene) sequence analyses strongly support the recognition of the Apoglosseae within the subfamily Delesserioideae of the Delesseriaceae, in agreement with our previous observations based primarily on analyses of large subunit ribosomal DNA (LSU).

Key words: Apoglosseae *trib. nov.*, *Apoglossum*, cystocarp development, *Delesseria*, Delesseriaceae, molecular phylogeny, *Paraglossum*, *rbc*L, red algae, systematics, taxonomy

Introduction

Agardh (1898) established the genus *Apoglossum* to include species he had previously treated under *Delesseria* section (subgenus) IX *Apoglossum* (Agardh, 1876). In the same work, he created the genus *Paraglossum* to include two species: *P. lancifolium* (Agardh, 1898, p. 217), based on *Delesseria lancifolia* (Agardh, 1872, p. 59; 1876, p. 496) from Cape Horn, and *P. epiglossum* (Agardh, 1898, p. 217), based on *Delesseria epiglossum* (Agardh, 1872, p. 59; 1876, p. 496) from the Falkland Islands. *Paraglossum lancifolium* was collected during the Antarctic voyage of H.M. Discovery Ships Erebus and Terror and was originally referred to as *Delesseria sanguinea* var. *lancifolia* (Hooker, 1847, p. 470). Agardh stated that he never saw the original Harvey material and that the samples he examined came from the Gray (J.E. Gray) Herbarium at the British Museum. The holotype (Agardh Herbarium 31749) of *Delesseria lancifolia* from Cape Horn was collected at St. Martins Cove, Hermite Island by Lieut. Smith in 1842, and the lectotype of *Delesseria epiglossum*, selected by Skottsberg (1923, p. 24, Agardh Herbarium 31754), was collected by Captain Abbott in 1859 in the Falkland Islands and sent to Agardh from the Gray Herbarium. Agardh elevated his subgenus *Paraglossum* of 1872 to genus level in 1898. Most authors have followed Kylin & Skottsberg (1919) and Skottsberg (1923) in placing the southern hemisphere delesserioid species under *Delesseria*, sometimes putting *Paraglossum* in parentheses; for

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ISSN 0967-0262 print/ISSN 1469-4433 online/12/00000366–383 © 2012 British Phycological Society
http://dx.doi.org/10.1080/09670262.2012.719164

example, Kylin & Skottsberg (1919) refer to *D.* (*Paraglossum*) *lancifolia* and *D.* (*Paraglossum*?) *larsenii*. Cotton (1915) referred to both species under *Paraglossum* in his cryptogamic flora of the Falkland Islands. Papenfuss (1964), on the other hand, placed both taxa under *Delesseria*. More recently, Lin *et al.* (2001) recognized the tribe Apoglosseae informally, based on combined LSU rDNA and *rbc*L analyses, to include two genera: *Apoglossum* and *Paraglossum*.

In the present study we reinvestigate the developmental morphology of the lectotype species of *Apoglossum*, *A. ruscifolium*, selected by Kylin (1924), and examine the developmental morphology of *Paraglossum*, based primarily on material of *P. lancifolium* and *P. epiglossum* that we collected in the Falkland Islands in December 1997 and January 1998. Our phylogenetic studies include all other species presently available to us and were designed to establish the relationship between *Apoglossum* and *Paraglossum* and their relationship to other Delesseriaceae, based on *rbc*L sequence analyses and morphological comparisons between these two genera and other members of the Delesserioideae.

Materials and methods

Specimens were collected intertidally or from the drift. Samples used in morphological studies were preserved in 5% formalin in seawater or pressed on herbarium sheets. Type and voucher specimens have been deposited in the herbaria of the University of Louisiana at Lafayette (LAF) and the University of North Carolina at Chapel Hill (NCU). Herbarium abbreviations follow Thiers (2012). Hand sections were stained with 1% aniline blue acidified with 1% HCl and mounted in 25–30% Karo® syrup (Englewood Cliffs, USA) or treated with Wittmann's aceto-iron-haematoxylin–chloral hydrate (Wittmann, 1965) and mounted in 50% Hoyer's mounting medium (Lin *et al.*, 2004). Photomicrographs were taken on an Olympus BX51 (Tokyo, Japan) microscope with a Q-imaging digital camera (Burnaby, BC, Canada), and habit views were reproduced with an Epson scanner (Tokyo, Japan) or a Microtek Scanmaker 9800XL (Microtek International, Hsinchu, Taiwan, R.O.C.).

DNA from silica gel-dried specimens was extracted using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA) following the manufacturer's instructions. DNA amplification and sequencing procedures were as described in Lin *et al.* (2001). New sequence data and those available from GenBank were compiled and aligned using Sequencher (Gene Codes, Ann Arbor, MI, USA). Seven *rbc*L sequences, including those of *Paraglossum lancifolium* from the Falkland Islands, *Delesseria nereifolium* from New Zealand, *Delesseria lancifolia* and *D. salicifolia* from the Antarctic Peninsula, and *Membranoptera alata* from France, were newly generated (Table 1). The generitypes of *Phycodrys* and *Cryptopleura* were selected as outgroups, based on Lin *et al.* (2001).

Maximum parsimony (MP) heuristic and maximum likelihood (ML) searches, and calculation of bootstrap percentage values (BP) were conducted as described in Lin *et al.* (2011). MP heuristic searches consisted of 500 random sequence additions, MULPARS (but holding five trees at each step), and tree–bisection–reconnection (TBR), whereas the MP bootstrap analysis was conducted by simple sequence addition. MP analyses and bootstrapping methods were performed using PAUP* v4.0 (Swofford, 2003), whereas ML was conducted using GARLI 1.0 (Zwickl, 2006). 1000 and 100 bootstrap replicates were completed for the MP and ML analyses, respectively. The model used for ML was the general time reversible method with gamma distributed rate heterogeneity ($GTR + \Gamma$) as the default in GARLI 1.0. A Bayesian analysis (BA) was performed in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) using a $GTR + I + \Gamma$ model, which allowed for rate variation among different codon positions. The analysis was applied in four chains of the Markov chain Monte Carlo (one hot and three cold). Each run started with a random tree and consisted of 10^6 generations with sampling every 100 generations. Stationarity was reached at generation 25 000, which was used as the 'burn-in' value. A 50% consensus tree (majority rule as implemented by PAUP* v4.0) was computed from the remaining $9750 + 1$ trees.

Results and discussion

Molecular analyses

The 34 *rbc*L sequences analysed in this study included the genera *Apoglossum*, *Delesseria*, *Paraglossum* and related genera in the subfamily Delesserioideae, with *Phycodrys rubens* and *Cryptopleura ramosa* serving as the outgroups (Table 1). The analysed data matrix included 1365 base pairs for *rbc*L, with 347 parsimony-informative sites.

The topologies of the ML, MP and BA trees were largely congruent, and only the MP tree is shown in Fig. 1. The genera bearing '*Delesseria*-type' apices clustered into three natural assemblages (see Clades I, II and III shown in Fig. 1). The species of *Apoglossum*, *Paraglossum* and *Delesseria* from the Falkland Islands, Tierra del Fuego, New Zealand and the Antarctic Peninsula formed a strongly supported assemblage (=Clade I) in the *rbc*L tree, whereas the generitype of *Delesseria*, *D. sanguinea* from Europe, together with *Delesseria decipiens* from Washington (USA) and two species of *Membranoptera*, *M. alata* (generitype) from France and *M. weeksiae* from Oregon (USA), formed a distinct clade, presently referred to as the Delesserieae (=Clade II), that is sister to the tribe Botryocarpeae (=Clade III) and

Table 1. List of the species and accessions of Delesseriaceae used in *rbc*L analyses.

Species	Collection information	GenBank accession number
Apoglossum oppositifolium (Harvey) J. Agardh	Coll. S. Wing & N. Goebel, 7.Oct.2000, Deep Cove North, Doubtful Sound, New Zealand (ASA 362)	JQ864358 (This study)
Apoglossum ruscifolium (Turner) J. Agardh 1898	Coll. Chris Maggs, 1999, France	AF254157[1]
Apoglossum ruscifolium (Turner) J. Agardh 1898	Coll. F. & M.H. Hommersand, 7.Apr.2000, Receira das Ilhas, Distr. Lisboa, Portugal	AF312310[2]
Botryocarpa prolifera (Turner) Kützing	Coll. O. De Clerck, 24.Nov.1999, Yzerfontein, South Africa	AF254160[2]
Branchioglossum bipinnatifidum (Montage) M.J. Wynne	Culture collection, Mexico	AF254161[2]
Claudea batanensis Tanaka	Coll. S.-M. Lin, 22.Apr.1998, Dapdake, Bulusan, Luzon, Philippines	AF254171[2]
Cryptopleura ramosa (Hudson) Kylin ex Newton	Coll. M.H. & F. Hommersand, 22.Jul.1997, West Angle Bay, Pembrokeshire, Wales, UK	AF254175[2]
Delesseria decipiens J. Agardh	Coll. B. Wysor, 12.Jun.1998, South side of Sunset Bay, Cape Arago, Charleston, Oregon, USA	AF254181[2]
Delesseria sanguinea (Hudson) J.V. Lamouroux	Coll. C. Maggs, 15.Mar.1999, Newcastle, Co. Down, N. Ireland, UK	AF254182[2]
Hemineura frondosa (J.D. Hooker & Harvey) Harvey	Coll. M.H. & F. Hommersand, 28.Aug.1995, W. Port MacDonnell, Victoria, S. Australia	AF254189[2]
Hypoglossum hypoglossoides (Stackhouse) Collins & Hervey	Coll. M.H. & F. Hommersand, Wemeldinge, Zeeland, the Netherlands	AF257368[2]
Marionella prolifera (Kylin) Wagner	Coll. W. Nelson, Whahariki Beach, Northwest Nelson, South I., New Zealand	AF257373[2]
Membranoptera alata (Hudson) Stackhouse	Coll. E. Coppejans, 23.Aug.2005, St. Michel de Plouguerneau, France	JQ864359 (This study)
Membranoptera weeksiae Setchell & Gardner in Gardner	Coll. S. Fredericq, 11May1999, Boiler Pt., Oregon, USA	AF257384[2]
Paraglossum crassinervium (Montagne) S.-M. Lin, Fredericq & Hommersand, *comb. nov.*	Coll. W. Nelson, 6.Oct.1994, Ringaringa, South Island, New Zealand	AF257409[2]
Paraglossum epiglossum (J. Agardh) J. Agardh	Coll. S.-M. Lin & S. Fredericq, 4.Jan.1998, Rookery Bay, Stanley, E. Falkland I.	AF257410[2]
Paraglossum epiglossum (J. Agardh) J. Agardh	Coll. M.H. Hommersand, 31.Dec.1997, Rookery Bay, Stanley, E. Falkland I.	AF257411[2]
Paraglossum fuegiense (Skottsberg) S.-M. Lin, Fredericq & Hommersand, *comb. nov.*	Coll. S.-M. Lin & S. Fredericq, 8.Jan.1998, Sea Lion Island, E. Falkland I.	AF257412[2]
Paraglossum lancifolium (J. Agardh) J. Agardh	Coll. M.H. Hommersand, 28.Dec.1997, Rookery Bay, Stanley, E. Falkland I.	AF257413[2]
Paraglossum lancifolium (J. Agardh) J. Agardh	Coll. M.H. Hommersand, 1.Jan.1998, Rookery Bay, Stanley, E. Falkland I.	AF257414[2]
Paraglossum lancifolium (J. Agardh) J. Agardh	Coll. M.H. Hommersand, 5.Jan.1998, Rookery Bay, Stanley, E. Falkland I.	JQ864360 (This study)
Paraglossum lancifolium (J. Agardh) J. Agardh	Coll. M.L. Mendoza, Despar I., Tierra del Fuego, Argentina	AF257415[2]
Paraglossum lancifolium (J. Agardh) J. Agardh	Coll. S.-M. Lin & S. Fredericq, 1.Jan.1998, Rookery Bay, Stanley, E. Falkland I.	AF257416[2]
Paraglossum nereifolium (Harvey) S.-M. Lin, Fredericq & Hommersand, *comb. nov.*	Coll. W. Freshwater, 03.Nov.2004, Ulva Island, Patterson Inlet, Stewart Island, New Zealand (#NZ 04-295)	JQ864357 (This study)
Paraglossum papenfussii (M.J. Wynne) S.-M. Lin, Fredericq & Hommersand, *comb. nov.*	Coll. M.H. & F. Hommersand, 24.Nov.1999, Yzerfontein, South Africa	AF257417[2]
Paraglossum salicifolia (Reinsch) S.-M. Lin, Fredericq & Hommersand, *comb. nov.*	Coll. C. Amsler, 20.Apr.2003, Cormorant Island., S.W. Anvers I. area, Antarctica	JQ864361 (This study)
Paraglossum sp.	Coll. C. Amsler, 22.Apr.2003, Palmer Station, Antarctic Peninsula	JQ864362 (This study)
Paraglossum sp.	Coll. S. Fredericq & J. Rodrîguez, 9.Feb.1994, Punta Peñon, Bahia Fildes, King George I., S. Shetland Islands	AF257418[2]
Patulophycus eclipse A. Millar & M.J. Wynne	Coll. A. Millar & D. Hardin, 25.Oct.1995, the Docks, Jervis Bay, New South Wales, Australia	AF257419[2]
Phitymorphora linearis (Laing) Kylin	Coll. W. Nelson, 9.Oct.1998, Ringaringa, Stewart I., New Zealand	AF257421[2]
Phycodrys rubens (Linnaeus) Batters	Coll. M.H. & F. Hommersand, 22.Jul.1997, West Angle Bay, Pembrokeshire, Wales, UK	AF257429[2]
Pseudophycodrys phyllophora (J. Agardh) Skottsberg	Coll. S.-M. Lin & S. Fredericq, 5.Jan.1998, Rookery Bay, Stanley, E. Falkland I.	AF257441[2]
Zellera tawallina G. Martens	Coll. S.-M. Lin, 22.Apr.1998, Bulusan, Luzon, Philippines	AF257458[2]

[1]Lin (2000); [2]Lin *et al.* (2001).

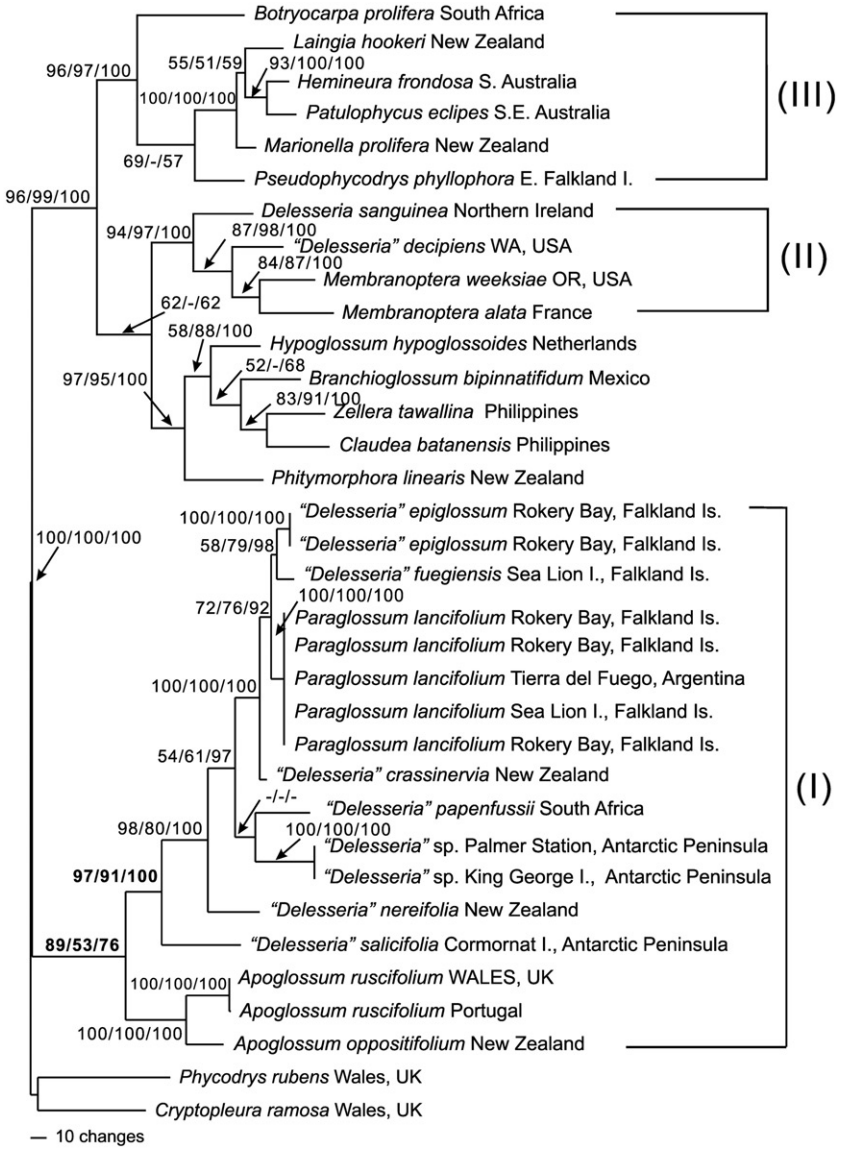


Fig. 1. *rbc*L phylogeny: single MP tree of the proposed tribe Apoglosseae and related tribes. Numbers above branches are MP bootstrap values, ML bootstrap values and Bayesian posterior probabilities in %, respectively. A dash indicates support values $< 50\%$. Roman numerals I, II and III represent the tribes Apoglosseae, Delesserieae and Botryocarpeae.

only distantly related to *Apoglossum* and the species of *Delesseria* from the southern ocean.

Morphological observations

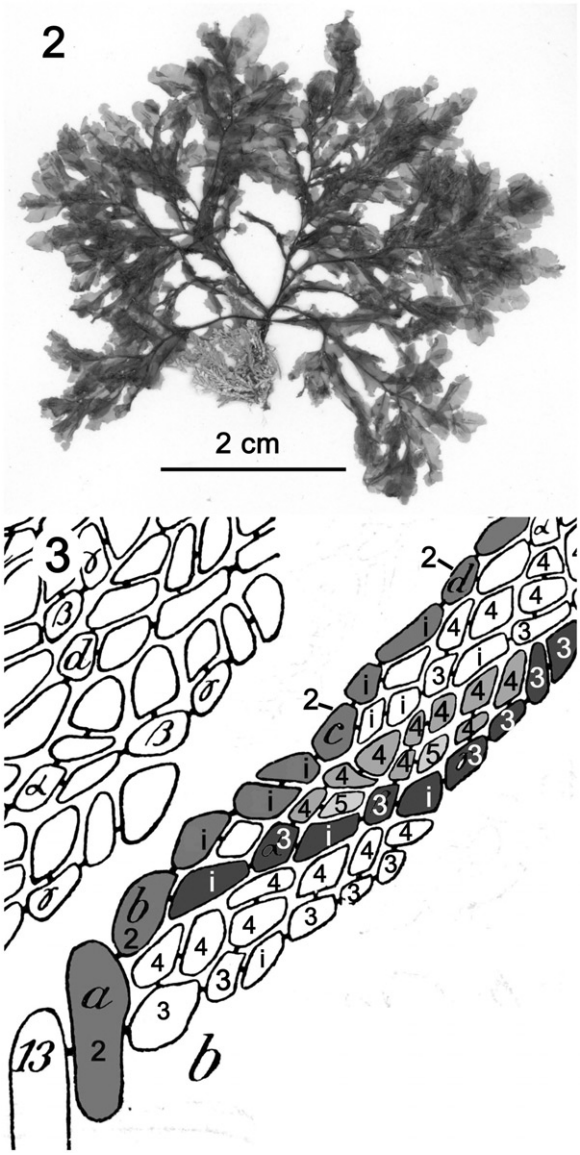
The molecular analyses showed that the species of *Apoglossum* and *Delesseria* from southern oceans formed a natural assemblage (Clade I, see Fig. 1) distinct from the Delesserieae (Clade III) from the northern hemisphere. Morphologically, Clade I was characterized by having (1) the auxiliary cell, supporting cell and sterile cells united into a more or less branched fusion cell and (2) pit-connections that broadened between the cells of the inner gonimoblast filaments; this clade is herein treated as the Apoglosseae *trib. nov.* In addition, (3) the elongated inner cortical cells seen in mature cystocarps in the Delesserieae were absent in the Apoglosseae. Therefore, it was important to document the developmental morphology of the lectotype species of *Apoglossum*, *A. ruscifolium*, the generitype of *Paraglossum*, *P. lancifolium* and *P. epiglossum*, genera and species combinations originally published by J. Agardh in 1898.

Apoglossum ruscifolium (Turner) J. Agardh 1898, p.194
(Figs 2–9)

Basionym: *Fucus ruscifolius* Turner 1802, p. 127, pl. 8, figs 1 and 2.

Holotype locality: Yarmouth, Norfolk, England.

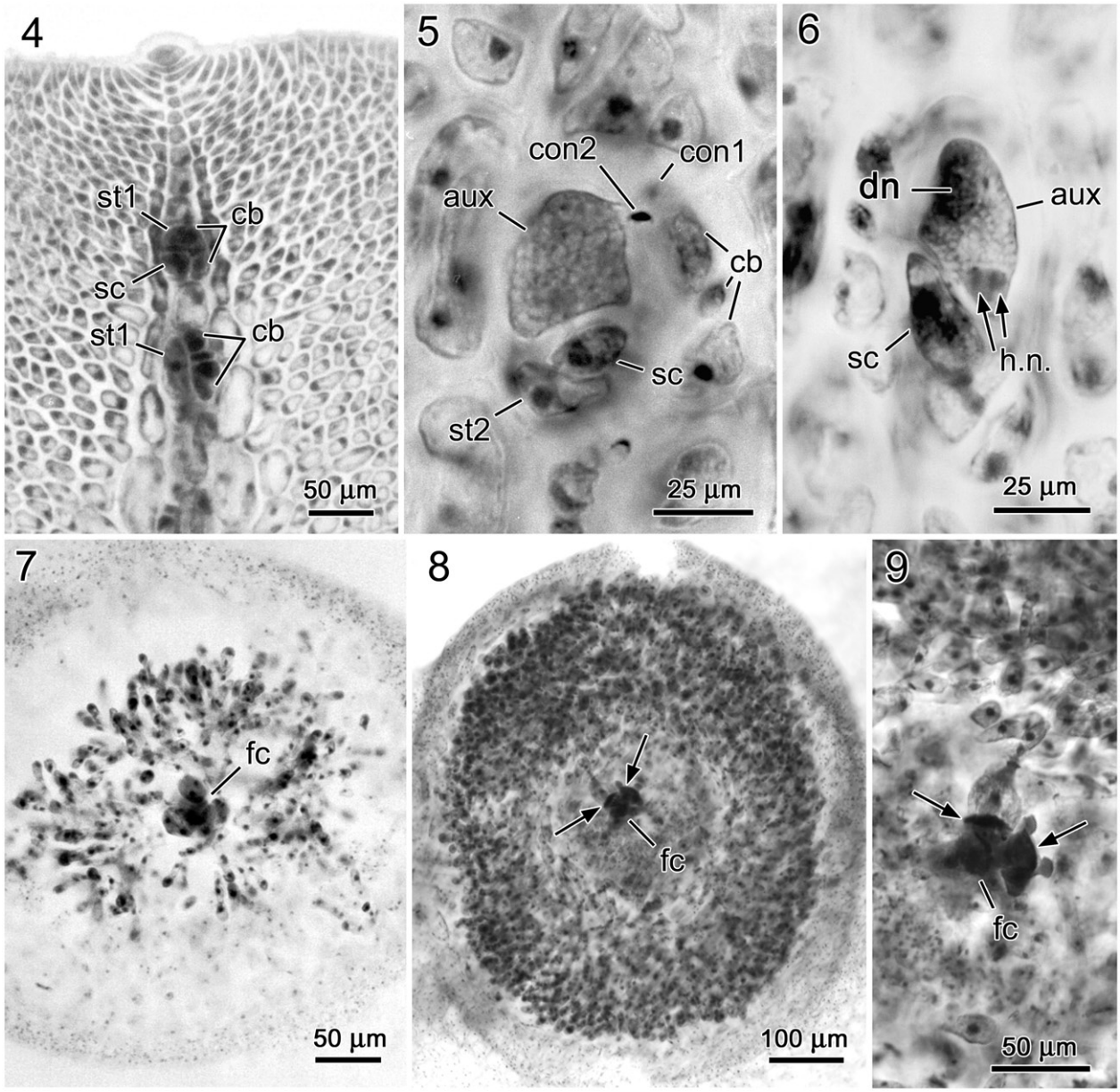
Specimens examined: **Morocco:** Punta Ceres, Strait of Gibraltar, coll. M.H. Hommersand, 13–14 June 1973; **France:** Santec, near Roscoff, coll. M.H. & E.A. Hommersand, 15 June 1991; **Spain:** Cabo Silleiro, west of Bayona, near Vigo, coll. M.H. Hommersand, 10 September 1968.



Figs 2–3 *Apoglossum ruscifolium*. **2.** Habit (seashore west of Bayona, Spain). **3.** Labelled higher-orders of cell rows, modified from Kylin's original fig. 54b (Kylin, 1923): 2, 3, 4, 5 represent second-order, third-order, fourth-order and fifth-order cell rows; i = intercalary cell; the other symbols are Kylin's original labels, which refer to the cells bearing higher-order of cell rows.

Vegetative morphology. The morphology of *Apoglossum ruscifolium* (Fig. 2) was investigated by Kylin (1923) along with that of *Delesseria sanguinea*. Our investigation largely agreed with that of Kylin. Growth is initiated in both species by a transversely dividing apical cell that produces a primary cell row or central axis in which intercalary cell divisions are absent. Intercalary cell divisions are absent in the periaxial cells produced from the central axis in *Apoglossum*, but are frequent to abundant in second- and higher-order cell rows in both genera, obscuring the original organization of the cell lineages. Second-order cell rows reach the thallus margins in both genera and bear descending third-order cell rows that do not all reach the margins (Kylin, 1923, figs 54, 61). Fourth-order cell rows are formed abaxially as descending files in *Delesseria sanguinea*, whereas in *Apoglossum ruscifolium* and all other investigated *Apoglossum* species they are produced adaxially in an ascending direction in young growing tips (Figs 3, 4; Kylin, 1923, fig. 54). Kylin stated that fifth-order cell rows are also produced on the inner sides of fourth-order cell rows (Kylin, 1923); however, an examination of Kylin's original drawing (*op. cit.*, fig. 54b) clearly shows that fifth-order cells rows are cut off to the outside, that is, abaxially (see our Fig. 3). The alternating pattern of third-order abaxial, fourth-order adaxial, and fifth-order abaxial cell rows gives *Apoglossum* its distinctive appearance and makes it easy to recognize compared with other members of the Delesserioideae. Branches originate from surface cells along the edges of the midrib in *Apoglossum* and never from the margins (Kylin, 1923, fig. 55b). Cells of the second and sometimes the third order may elongate later, forming microscopic veins (Kylin, 1923, fig. 55a). Kylin (1923, fig. 55c, d; 1956, fig. 319b and in the key, p. 428) emphasized the presence of small-celled external rhizoidal filaments surrounding the central axis as a distinguishing character of *Apoglossum ruscifolium*; however, this feature appears to be absent in most other correctly named species of *Apoglossum*.

Reproductive morphology. Procarps are formed along both sides of the central axis in *Apoglossum* in essentially the same manner as in most Delesserioideae (Fig. 4; Kylin, 1923, figs 53b, 56a, b). The sterile cells are unicellular and uninucleate before fertilization, and the second sterile cell lies directly beneath the first or only a little offset from a straight line. Kylin did not see the stages immediately following fertilization. The supporting cell divides transversely to cut off a large terminal auxiliary cell, leaving behind the remnant of the smaller supporting cell. Each fertilized carpogonium produces two connecting cells. The first is cut off terminally from the carpogonium in the direction of the withered trichogyne, while the second is cut off below the first and moves laterally towards the anterior end of the auxiliary cell (Fig. 5). It consists of a highly condensed nucleus, which is surrounded by a hyaline region bounded by an outer membrane or thin cell wall. This cell fuses with the auxiliary cell and transfers the diploid nucleus, which expands and divides inside the auxiliary cell (Fig. 6). The original haploid nucleus moves to the outer side of the basal part of the auxiliary cell and divides into two small nuclei without cutting off a foot cell. The two sterile cells appear to remain undivided after fertilization, whereas their nuclei may divide (Fig. 5). This result



Figs 4–9. *Apoglossum ruscifolium*. Developmental stages in the female reproductive system (Figs 4–7: Santec, near Roscoff, France; Figs 8, 9: Punta Ceres, Morocco). **4.** Tip with two procarps along central axis showing positions of the supporting cell (sc), sterile cell 1 (st1) and carpogonial branch (cb). **5.** Early post-fertilization stage showing sterile cell 2 (st2), a supporting cell (sc) that has cut off an auxiliary cell (aux), and the lateral carpogonial branch (cb). The carpogonium has cut off two connecting cells from its terminal end, the first (con 1) with a degenerating nucleus and the second (con 2) adjacent to the auxiliary cell and with a functional nucleus surrounded by a hyaline area and surface membrane. Note that sterile group 1 is not in focus and is above the auxiliary cell. **6.** Stage in which the diploid nucleus (dn), located inside the auxiliary cell (aux) is undergoing division and the basal haploid nucleus (hn) has divided into two nuclei. **7.** Optical section of cystocarp with small lobed fusion cell (fc) and radiating gonimoblast filaments. **8.** Surface view of a mature cystocarp showing the lobed fusion cell (fc) with enlarged pit connections (arrows) bearing gonimoblast filaments and carposporangia. **9.** Close-up of rotated view of Fig. 6 showing the lobed fusion cell (fc) and enlarged pit connections (arrows).

appears to be contrary to Kylin's observation (1923, fig. 57a, b), which shows the sterile cells dividing to form three-celled filaments in developing cystocarps. This discrepancy remains unresolved. A later stage shows an unusually small fusion cell bearing the gonimoblasts (Fig. 7). The fusion cell appears to consist of the central cell and supporting cell, along with the auxiliary cell and the two sterile cells that remain distinct. The gonimoblast cells branch profusely and bear branched chains of carposporangia (Fig. 8). A close examination of the central cell shows that it does not enlarge significantly and that the two sterile cells remain on the fusion cell as extensions linked by broadened pit plugs (Figs 8, 9). Pit connections between inner gonimoblast cells enlarge and broaden (Fig. 9). The cystocarp forms a prominent pericarp with a central ostiole (Kylin, 1923,

fig. 58a, b). Spermatangial and tetrasporangial development are typical for the Delesserioideae (Kylin, 1923, figs 59a, b, 60a, b): tetrasporangia are cut off from inner cortical cells on both sides of the thallus and are covered by a single outer layer of surface cells.

Paraglossum lancifolium (J. Agardh) J. Agardh 1898, p. 217
(Figs 10–40)

Basionym: *Delesseria lancifolia* J. Agardh 1872, p. 59.

Holotype: LD, Agardh Herbarium 31749, *ex* Gray Herbarium at BM.

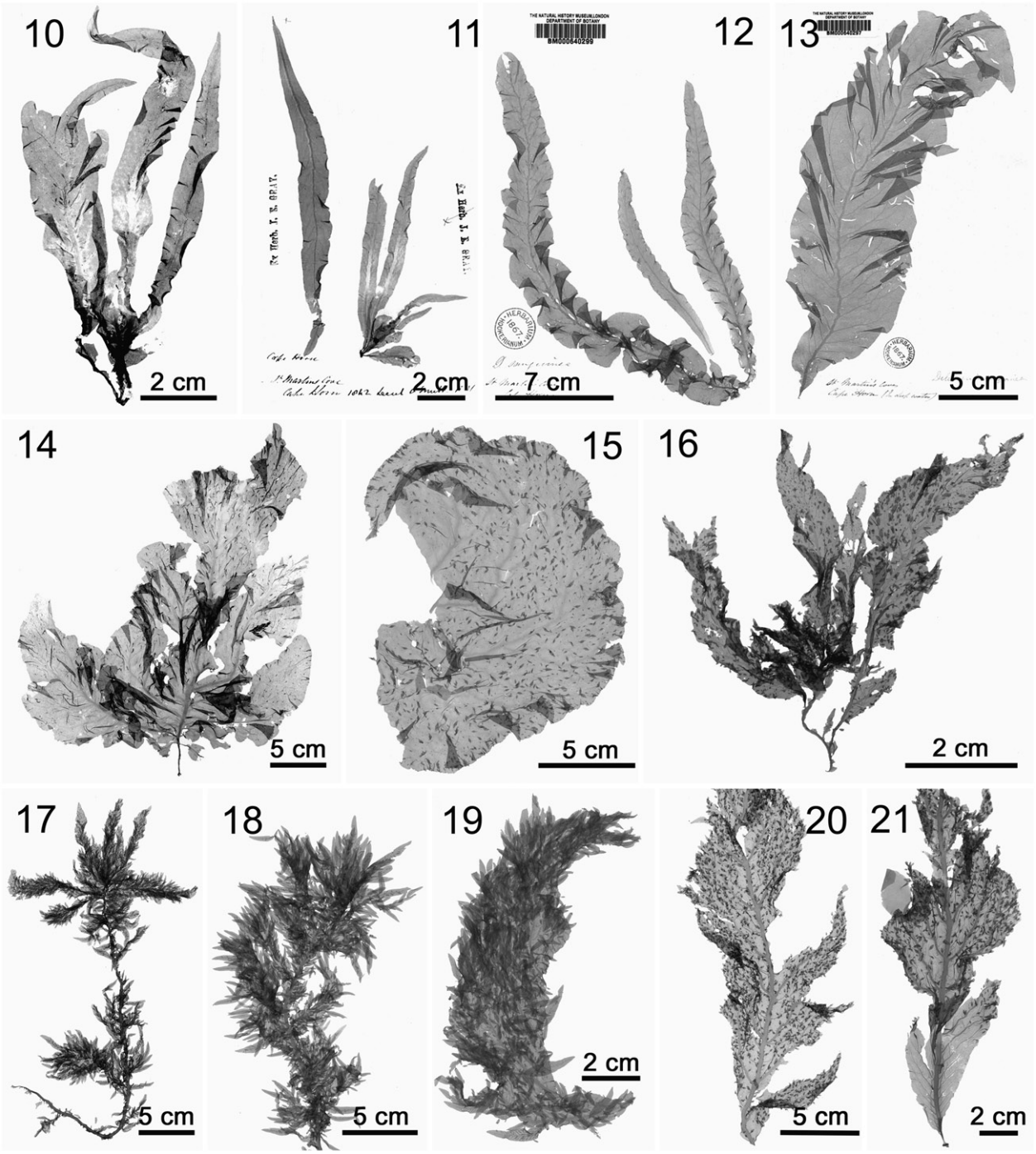
Type locality: St Martin's Cove, Hermite Island 1842 (Cape Horn), coll. O. Smith R.M.

Synonymy & distribution: *Delesseria sanguinea* var. *lancifolia*: Hooker 1847, p. 470 (on rocks and dredged to 5–6 fathoms, Hermite Island, Cape Horn). *Delesseria crassinervia* ß *costa angustiore*: Hooker 1847, p. 471 (Cape Horn, Falkland Islands). *Delesseria lancifolia*: Agardh 1876, p. 496 (Cape Horn); Hariot 1889, p. 93, pl. 9, fig. 3 [Note: pl. 9, fig. 3 illustrates the left branch of Agardh Herbarium 31754]; Kylin & Skottsberg 1919, p. 41 (Feuerland, in deep water); Skottsberg 1923, pp. 25–26, figs 6d, 7c (Drift, Slogget Bay, Fuegia); Taylor 1939, p. 155 (dredged 26–28 metres, north side, Port William, Falkland Islands); Papenfuss 1964, p. 52 (Fuegia, Falkland Islands, Macquarie Island?). *Paraglossum lancifolium*: Cotton 1915, pp. 183–184 (West Point Island, West Falkland Islands).

Specimens examined: **Chile**: St. Martin's Cove, Hermite Island (Cape Horn): holotype in Herb. Agardh, 31749 (as *Delesseria lancifolia* J. Agardh), coll. Lieut. Smith; ex Herb. J.E. Gray, BM000640294 (as *Delesseria sanguinea* var. ß *lancifolia*); near the shore, St. Martin's Cove, Cape Horn, ex Herb Kew, BM000640299 & BM000640297 (as *Delesseria sanguinea* var. ß *lancifolia*); Strait of Magellan near Punta Arenas, drift, coll. M.H. Hommersand, 9 January 1979 (NCU591385). **Argentina**: Despar Island, Tierra del Fuego, coll. M.L. Mendoza (as *Pseudolaingia larsenii*). **Falkland Islands**: Sea Lion Island, S.-M Lin & S. Fredericq, 8 January 1998 (LAF-8-1-08-1-1, LAF-8-1-98-1-2, LAF-8-1-98-1-3, females & tetrasporophytes); Rookery Bay, near Stanley, drift, M.H. Hommersand, 28 December 1997 (NCU591408, NCU591397), 29 xii 1997 (NCU591390), 2 January 1998 (NCU531387).

Habit. Establishing the structure and range of forms of *P. lancifolium* is complicated by the fact that all of the materials cited in the original description of *Delesseria sanguinea* var. ß *lancifolia* (Hooker, 1847, p. 470) were young sterile plants. Those that were collected near the shore (Figs 11, 12) were narrowly lanceolate with a faint midrib and barely recognizable lateral veins, and those that were dredged in six to eight fathoms (*c*. 10–15 m) of water (Fig. 13) were taller and broadly lanceolate, again with a faint midrib and inconspicuous lateral veins. The holotype (LD, Agardh Herbarium 31749, Fig. 10), bore tetrasporangial sori on minute transverse bladelets between the midrib and margin of the blade (Agardh, 1876, p. 496; Ricker, 1987, fig. 110c). Figure 14 illustrates a large, broad plant from Tierra del Fuego collected by Mendoza, whose *rbc*L sequence was identical to that obtained in our collections from the Falkland Islands. The fragment collected near Punta Arenas in the Strait of Magellan (Fig. 15) was not sequenced but bore tetrasporangial leaflets over the surface of monostromatic portions of the thallus. The only sterile specimen we collected from the East Falkland Islands that bore a resemblance to the Agardh holotype is illustrated in Fig. 16. The remaining collections were all fertile and either cystocarpic or tetrasporangial with procarps, cystocarps or tetrasporangia usually borne in bladelets either from the margins of the midrib and major veins or, more often, from monostromatic portions of the thallus surface (Figs 17–21).

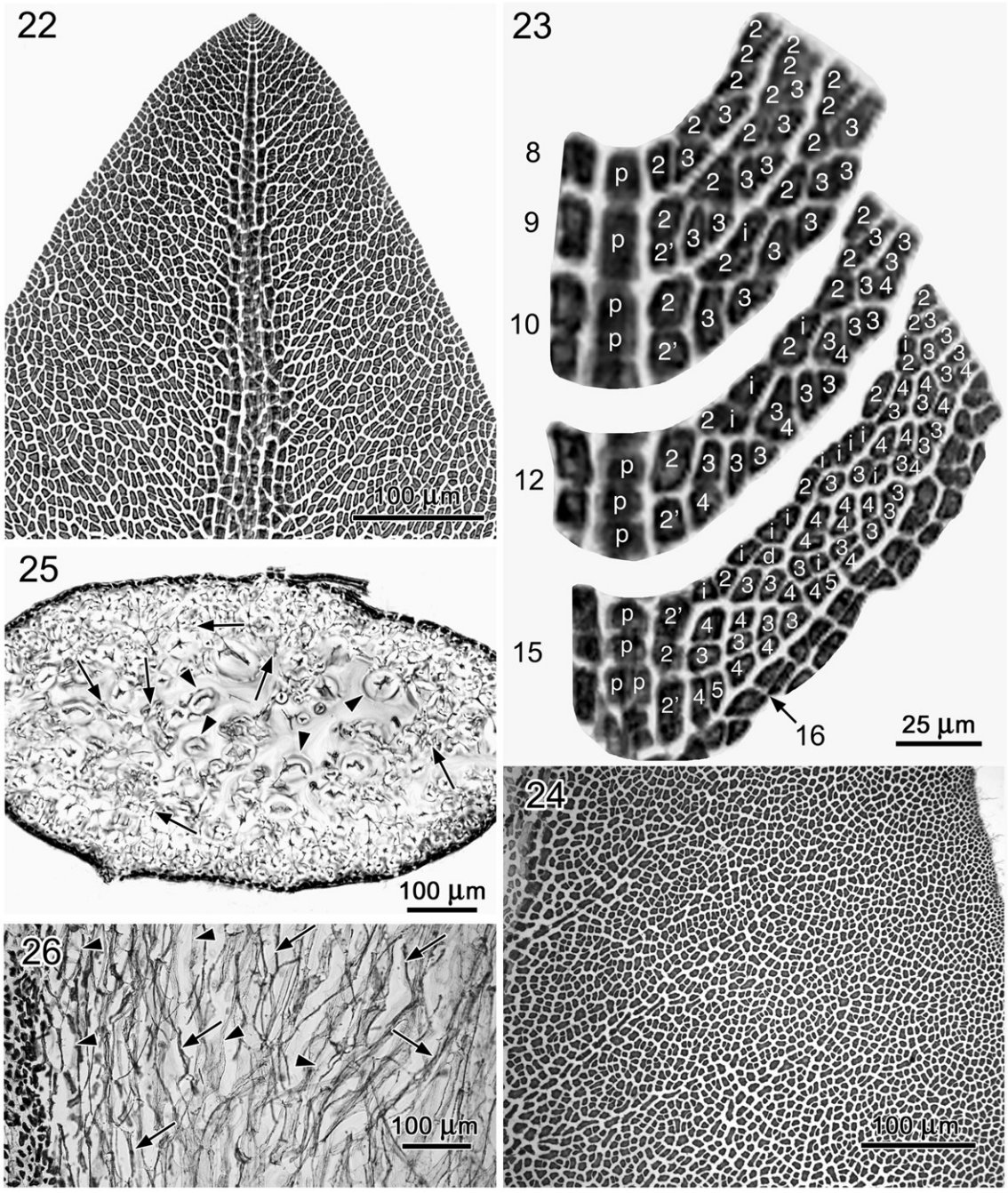
Vegetative morphology. An actively growing tip is illustrated in Fig. 22. Growth takes place by means of a transversely dividing apical cell to produce the primary cell row and midrib. All second-order cell rows reach the margin. Some, but not all, third-order rows reach the margin. Fourth-order cell rows may be cut off abaxially or adaxially but tend to lie in vertical rows (Figs 22, 23). The result is a distinctive growth pattern in which triangle-shaped units are formed behind the leading axis of third-order cell rows that are characteristic of the species. In this tip, intercalary transverse cell divisions are first seen in second-order cell rows beginning with segment 10 and extend to third-order cell rows by segment 15 (Fig. 23). Intercalary longitudinal cell divisions of second-order cell rows commence with row 16 to initiate a microscopic vein, as labelled in Figure 23. Intercalary divisions extend rapidly to cells of all cell rows, except the central axis, as the thallus margin expands. The original growth pattern is lost at this point, except that microscopic veins may still be visible (Fig. 24). Macroscopic veins and lateral ribs develop by continued growth and thickening of the originally microscopic veins in still older plants, especially towards the base of the thallus (Figs 20, 21). Cells in the centre of the midrib elongate towards the base of the thallus and



Figs 10–21. *Paraglossum lancifolium*, Habit. **10.** Holotype (Herb. Agardh, 31749), **11.** *Delesseria sanguinea* var. ß *lancifolia* (BM000640294). **12.** *Delesseria sanguinea* var. ß *lancifolia* (BM000640299). **13.** *Delesseria sanguinea* var. ß *lancifolia* (BM000640297). **14.** A collection from Despar Island, Tierra del Fuego sent by Mendoza as *Pseudolaingia larsenii*. **15.** Large fragment bearing female leaflets, Strait of Magellan near Punta Arenas (NCU591385). **16.** Young sterile plant, Sea Lion Island, Falkland Islands (LAF-8-1-08-1-1). **17.** Mature tetrasporangial plant, Sea Lion Island, Falkland Islands (LAF-8-1-08-1-2). **18.** Tip of large tetrasporangial plant, Rookery Bay, near Stanley, Falkland Islands (NCU591408). **19.** Broad tip of a young plant bearing tetrasporangial bladelets, Sea Lion Island, Falkland Islands (LAF-8-1-08-1-3). **20.** Segment of thallus bearing mature cystocarpic bladelets, Rookery Bay, near Stanley, Falkland Islands (NCU591390). **21.** Base of tetrasporangial plant Rookery Bay, near Stanley, Falkland Island (NCU591397).

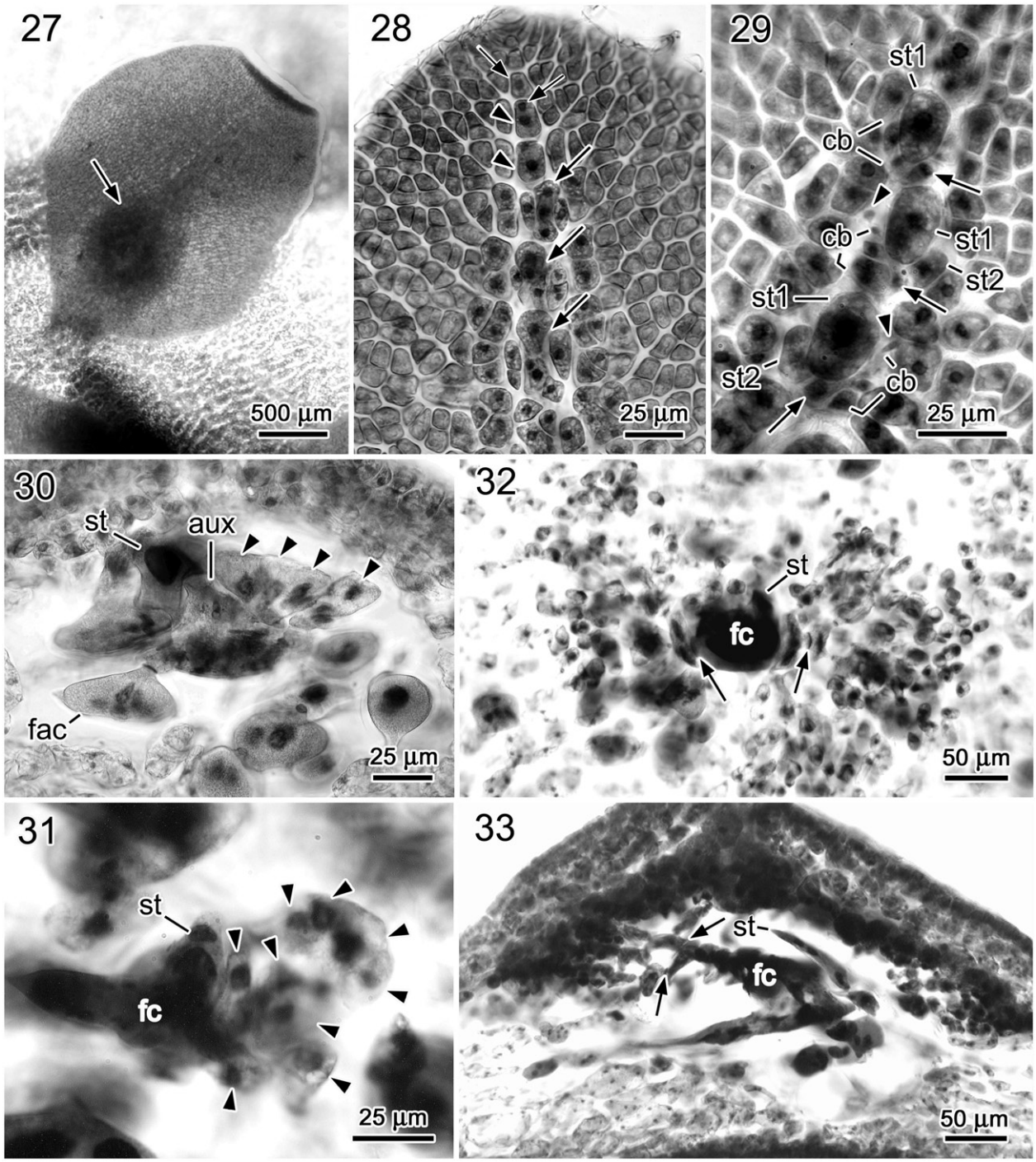
each cell is surrounded by rhizoidal filaments, as seen in both cross and longitudinal sections (Figs 25, 26, arrows).

Reproductive morphology. Male material was absent in our collections of *P. lancifolium* but occurred in soral patches between the veins and margins of mature blades in *P. epiglossum* (see below). In *P. lancifolium*, cystocarps were initially produced along the main axis of erect bladelets (Fig. 27). Typically only one cystocarp matured per leaflet; however, some leaflets had two



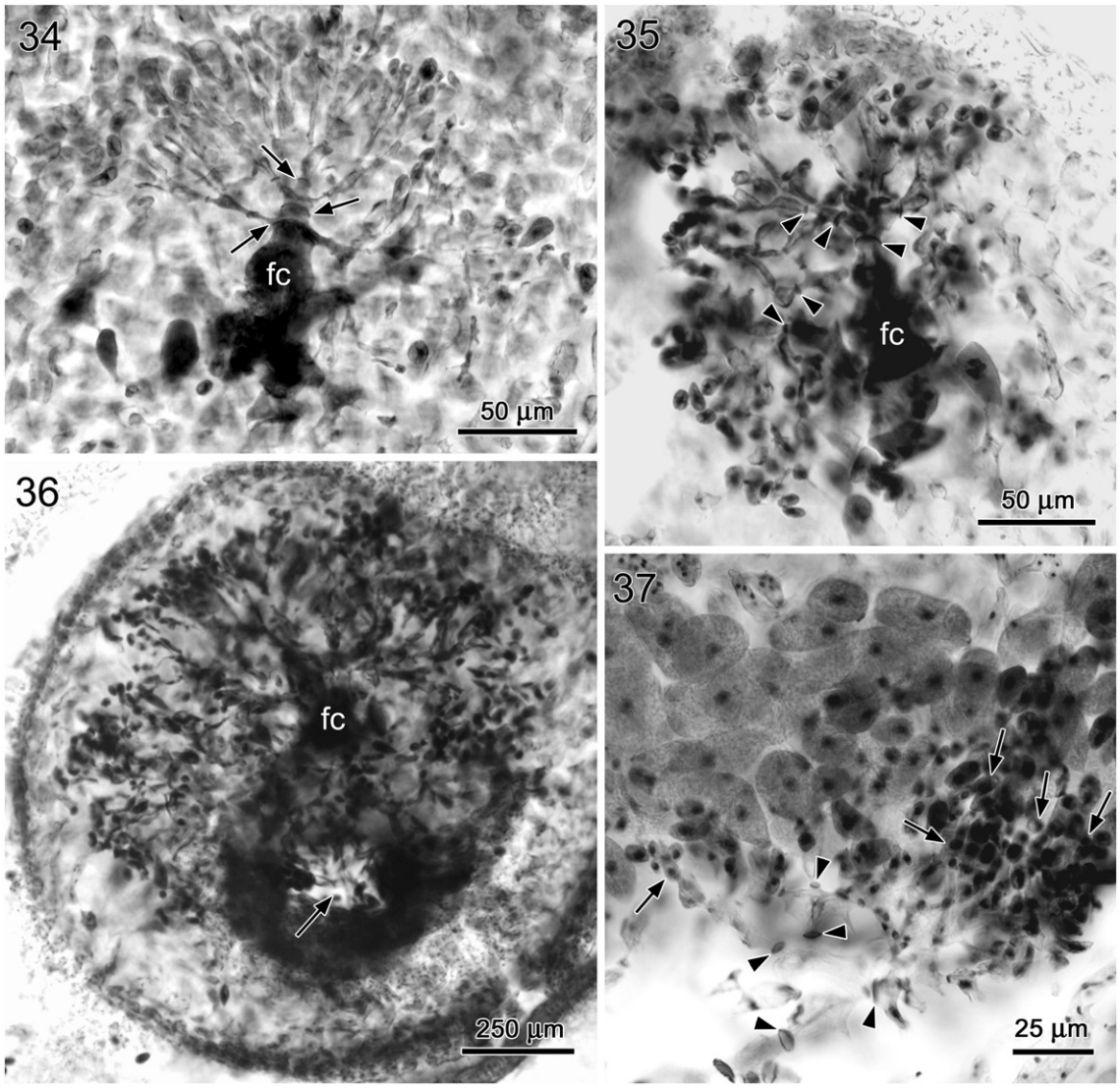
Figs 22–26. *Paraglossum lancifolium*, vegetative anatomy. **22.** Actively growing tip (Sea Lion Island. Falkland Islands). **23.** Analysis of pattern of cell divisions in tip shown in Fig. 22. The numerical position (8–10, 12, 15, 16) is given on the left for each segment below the apical cell. Notations are as follow: p = periaxial cell; i = intercalary cell; 2, 3, 4 represent second-order, third-order and fourth-order cell rows. **24.** Region below the apex at a point at which cells of higher-order cell rows have undergone intercalary cell divisions randomly; microscopic veins are barely visible (Rookery Bay, Falkland Islands). **25.** Cross-section of basal midrib showing vegetative cells (arrowheads) surrounded by rhizoidal filaments (arrows) (Sea Lion Island, Falkland Islands). **26.** Longitudinal section of basal midrib showing vegetative cells (arrowheads) surrounded by rhizoidal filaments (arrows) (Rookery Bay, Falkland Islands).

cystocarps. The pattern of procarp and cystocarp development described here was characteristic of other species of *Paraglossum* examined. Procarps were restricted to the apex of the bladelets and are formed on both sides of first-order cell rows (Fig. 28). The fertile axial cell initially cuts off a periaxial cell transversely on each side of the bladelet that becomes the supporting cell. Each supporting cell in turn produces a one-celled sterile group-1 at the distal end, a straight four-celled carpogonial branch laterally, and a one-celled sterile group-2 at the posterior end (Figs 28, 29). Sterile group-2 lies directly below sterile group-1, or only slightly to one side (Fig. 28). Early



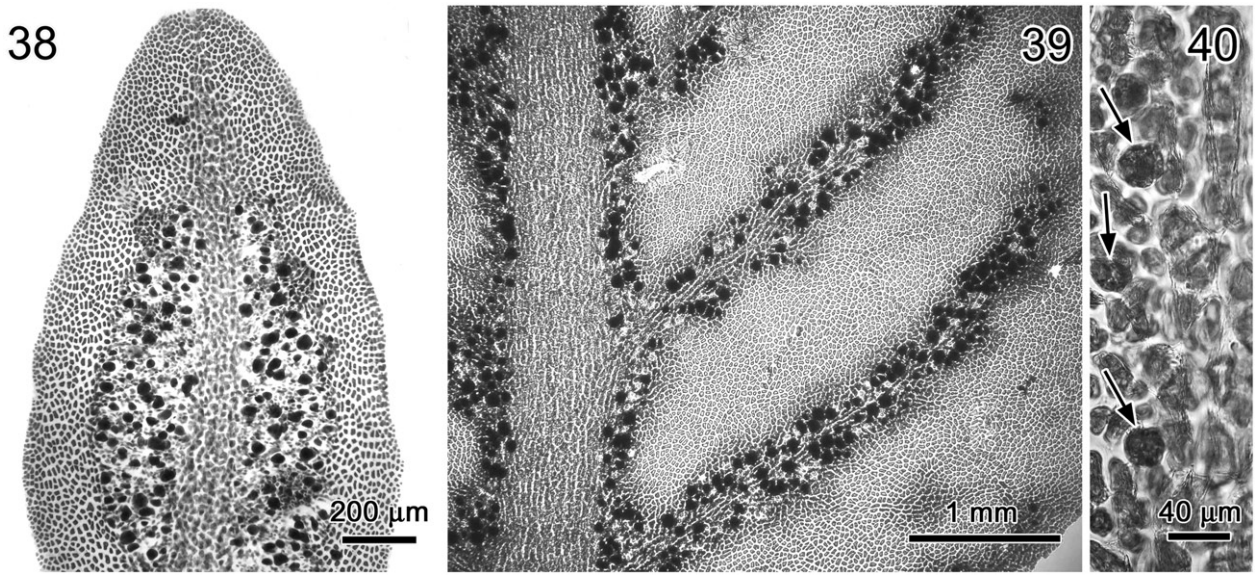
Figs 27–33. *Paraglossum lancifolium*, procarp and cystocarp development (Sea Lion Island, Falkland Islands). **27.** Fertile bladelet bearing a cystocarp (arrow). **28.** Tip bearing fertile axial cells (arrowheads), and supporting cells with carpogonial branches (arrows). **29.** Close up of procarps, consisting of two 1-celled sterile groups (st1 & st2) and one 3- or 4-celled carpogonial branch (cb) with trichogyne (arrowheads) borne on a supporting cell (arrows). **30.** Early post-fertilization stage showing auxiliary cell (aux), primary gonimoblast initials (arrowheads), and the remaining sterile group (st). Note that the fertile axial cell (fac) is distinct at this stage. **31.** Newly formed fusion cell (fc) bearing the primary gonimoblast cells (arrowheads) and the remaining sterile group (st). **32.** Surface view of immature cystocarp showing the remaining sterile cell (st), the fusion cell (fc) bearing gonimoblasts on both sides, and the enlarged pit connections (arrows) between the innermost cells of the gonimoblast filaments and the fusion cell. **33.** Cross-section through an immature cystocarp showing the fusion cell (fc) and elongated multinucleate sterile group, and enlarged pit connections (arrows) between cells of the gonimoblast filaments.

post-fertilization stages were not observed in *P. lancifolium*. After presumed fertilization, the nucleus of each sterile group enlarges and primary gonimoblast cells issue from gonimoblast initials cut off from the distal end of the auxiliary cell (Fig. 30) and branch radially (Fig. 31). Lateral branching proceeds rapidly from each of the primary gonimoblast cells (Fig. 32). At the same time,



Figs 34–37. *Paraglossum lancifolium*, cystocarp development (Sea Lion Island, Falkland Islands). **34.** Optical section showing a massive fusion cell (fc) and immature gonimoblasts united into branched files with broadened pit connections (arrows). **35.** Optical section of immature cystocarp showing a massive fusion cell (fc) bearing gonimoblast filaments in which the cells are separated by enlarged pit connections (arrowheads). **36.** Optical section of mature cystocarp with ostiole (arrow) showing the fusion cell (fc) bearing highly branched gonimoblasts. **37.** Cross-section through mature cystocarp showing enlarged pit connections (arrowheads) between inner gonimoblast cells, mature carposporangia, and clusters of secondary carposporangia (arrows).

the fertile axial cell, supporting cell, auxiliary cell and some inner primary gonimoblast cells unite to form a large fusion cell (Figs 31, 32). The remaining sterile cell elongates, and its nucleus may divide once or twice (Fig. 33). Fusion of the inner gonimoblast cells continues as the gonimoblast filaments grow (Figs 32–34) and the pit connections between the outer files of gonimoblast cells broaden (Fig. 35). As a result, the fusion cell becomes highly branched and flanked by an elongated sterile cell. Elongated inner cortical cells are absent in mature cystocarps. Young carposporangia differentiate terminally in short chains, as seen in optical section, and an ostiole forms to the outside (Fig. 36, arrow). The carposporangia mature into chains of subspherical cells as the pit connections between the inner gonimoblast cells continue to enlarge (Fig. 37). Clusters of secondary carposporangia are formed at the same time that the primary carposporangia mature (Fig. 37). Tetrasporangia occur both on the bladelets and on the main thallus in our material. The ones on bladelets were situated in the monostromatic portion between the midrib and the sterile margin and were cut off laterally from cells in the monostromatic central layer (Fig. 38). Additional tetrasporangia were formed in older plants along the margins of the midrib and in central portions of the broadened microscopic veins (Fig. 39): they were cut off laterally from surface cells adjacent



Figs 38–40. *Paraglossum lancifolium*, tetrasporangia formation (Rookery Bay, East Falkland Islands, NCU531387). **38.** Position of tetrasporangia between the midrib and blade margin in a leaflet. **39.** Tetrasporangia borne along the midrib and lateral veins at base of mature thallus. **40.** Tetrasporangial initials cut off laterally from monostromatic region adjacent to midrib (arrows).

to the midrib or from central cells in the membranous portions of the modified microscopic veins (Fig. 40).

Paraglossum epiglossum (J. Agardh) J. Agardh 1898, p. 217
(Figs 41–51)

Basionym: *Delesseria epiglossum* J. Agardh 1872, p. 59.

Lectotype: LD: Agardh Herbarium 31754, *ex* Gray Herbarium at BM, selected by Skottsberg 1923, p. 24.

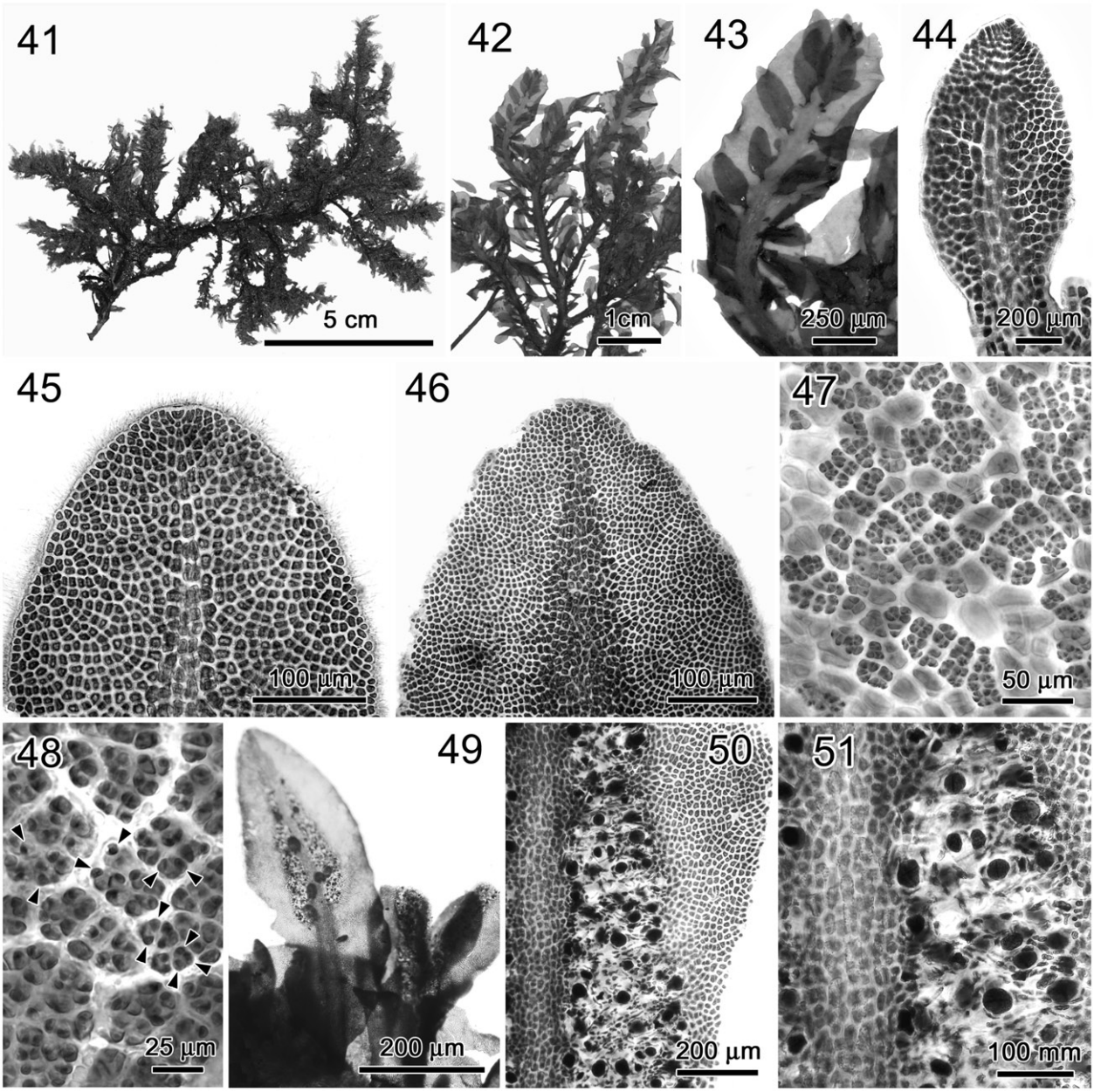
Type locality: Falkland Islands, coll. Captain Abbott, 1859.

Synonymy & distribution: *Delesseria crassinervia*: Hooker 1847, *pro parte* (Port William, Falkland Islands) [cited in Skottsberg 1923, p. 25]. *Delesseria epiglossum*: Agardh 1876, p. 496; Skottsberg 1923, pp. 24–25, fig. 7a, b [tide pools, Westpoint Island (male, female), Cape Pembroke (tetrasporangial), Falkland Islands]; Taylor 1939, p. 155 (Port Stanley, Falkland Islands, Schmitt 96, 307) [These are large drift specimens and fragments that are not representative of *D. epiglossum*]; Papenfuss 1964, p. 52 and included references (Fuegia?, Falkland Islands, Kerguelen?); Ricker 1987, pp. 264–268 (Macquarie Island?). *Paraglossum epiglossum*: Cotton 1915, p. 184 (East Falklands, Hooker) [Note: this identification requires confirmation.]

Specimens examined: **Falkland Islands**: Rookery Bay, near Stanley, coll. M.H. Hommersand, intertidal plant, 31 December 1997; males and tetrasporophytes, 1 January 1998 (NCU591342).

Vegetative morphology. *Paraglossum epiglossum* was a common intertidal species at Rookery Bay, East Falkland Island. Plants varied in size up to 8 (exceptionally 11) cm tall but, in general, were smaller than *P. lancifolium* and bushy, being densely branched from all sides with lateral branches usually no more than 2 cm long (Fig. 41). Branches bear ovate to ovate-lanceolate branchlets in opposite pairs along the edges of the midrib on both sides of the blade (Figs 42, 43; Skottsberg, 1923, p. 25, fig. 7A), with most branchlets remaining limited in growth and only a few developing into branches of the next higher order. Branchlets develop initially in the same manner as described above for *P. lancifolium*, with second-order cell rows reaching the margins and third-order cell rows producing both descending and ascending fourth-order cell rows (Figs 44, 45). Undulate monostromatic bladelets with broad, thick midribs mature rapidly into branches of limited growth but do not bear microscopic veins, and the growth pattern of the lamina is obscured by intercalary cell divisions (Fig. 46).

Reproductive morphology. Spermatangia, tetrasporangia and cystocarps are borne on ordinary blades of any order and not on special sporophylls (Skottsberg, 1923, p. 24). We saw only male and tetrasporangial plants and female plants with undeveloped or aborted procarps. Spermatangia develop in sori from the surface of the bladelets, each sorus being derived from a single cell in the



Figs 41–51. *Paraglossum epiglossum*, habit and vegetative and reproductive development (Rookery Bay, Falkland Islands)**. 41.** Habit (NCU591342). **42.** Tip of large plant. **43.** Tip from Fig. 42 showing paired arrangement of branchlets emerging from margins of midrib. **44.** Developing leaflet borne on margin of midrib. **45.** Actively growing tip showing the primary midrib and banding pattern of second and higher-order cell rows. **46.** Mature apex with broad midrib and monostromatic blade showing irregular pattern of intercalary cell divisions. **47.** Fertile male area in thallus blade showing arrangement of spermatangial clusters and scattered sterile cells. **48.** Surface view of spermatangial clusters showing spermatangia (arrowheads). **49.** Tip containing tetrasporangial leaflets. **50.** Part of a tetrasporangial leaflet showing tetrasporangia between midrib and leaflet margin. **51.** Enlarged view of Fig. 50 showing tetrasporangia cut off laterally from cells in inner margin of leaflet.

lamina of a blade (Fig. 47). Spermatangial parent cells are one cell layer thick with each parent cell producing one or at most two spermatangia more or less laterally, 2–3 µm wide by 4–5 µm long, each with a terminal nucleus and basal vesicle (Fig. 48). The cystocarps were described by Skottsberg (1923, p. 24) as developing along the midribs of blades of variable size. Tetrasporangia are formed in the lamina outside the midrib and inside the sterile margin of blades of any order (Figs 49, 50). The tetrasporangial initials are cut off laterally from cells in the monostromatic layer and divide tetrahedrally to form four tetraspores (Fig. 51). Mature tetrasporangia are 42–45 µm wide by 45–48 (−51) µm long.

Taxonomic conclusions

The Delesseriaceae was divided into two subfamilies by De Toni (1900): the Nitophylloideae

(as subfamily Nitophylleae) and the Delesserioideae (as subfamily Delesserieae). The Nitophylloideae were reinterpreted by Lin *et al.* (2001) with the recognition of a third subfamily, the Phycodryoideae. Kylin (1924, 1956) identified eight groups in the Delesserieae and Wynne (2001) recognized 14 tribes in the subfamily Delesserioideae and 23 tribes for the entire family, based primarily on the architecture of the developing apex, especially on (1) whether growth takes place from the midrib or the thallus margin, (2) whether or not cell rows higher than the second-order reach the thallus margin, and (3) the extent of intercalary cell divisions in second- and higher-order cell rows. *Apoglossum* was placed by Kylin in the *Delesseria* group, in which branching takes place primarily from the midrib, only second-order and initials of third-order cell rows reach the margin, and intercalary divisions are abundant in second- and higher-order cell rows. At the same time Kylin placed a large group of species from the southern hemisphere in *Delesseria*. Our molecular analyses (Fig. 1; also see Lin *et al.*, 2001) demonstrate that genera having a *Delesseria*-type apex *sensu* Kylin are polyphyletic and cluster into three natural assemblages (Clades I–III, see Fig. 1). Clade I includes the generitype of *Apoglossum* and the species from the southern hemisphere presently placed in *Delesseria*. In the following treatment we establish the tribe Apoglosseae to include the genera *Apoglossum* and *Paraglossum*. Guiry & Guiry (2012) list 12 names under *Apoglossum*, eight of which are flagged as currently recognized species: five from the southern hemisphere and three from the northern hemisphere. They treat *Paraglossum* as 'taxonomic status uncertain'. We recognize the genus *Paraglossum* to include most of the species from the southern hemisphere originally placed under *Delesseria* and establish new combinations under *Paraglossum* for those species we have sequenced and for the plant presently known as *Pseudolaingia larsenii* (Skottsberg) Levring.

New and remodelled taxa

Apoglosseae S.-M. Lin, Fredericq & Hommersand *trib. nov.*

Type genus: *Apoglossum* J. Agardh 1898, p. 190, selected here by S.-M. Lin, Fredericq & Hommersand.

Description: Thalli erect, developing from a transversely dividing apical cell, the primary cell row not undergoing intercalary cell divisions, but with cell rows of higher orders undergoing intercalary cell divisions; only second-order and initials of third-order cell rows reaching the thallus margin; fourth-order cell rows produced abaxially and adaxially (*Paraglossum*) or only adaxially (*Apoglossum*). Fifth-order cell rows mostly abaxial or their orientation unknown. Life cycle triphasic with isomorphic gametophytes and tetrasporophytes; spermatangia borne in sori between the midrib and the thallus margin; cystocarps ostiolate, either borne on ultimate orders of branches or on erect bladelets of limited growth; procarps consisting of a single sterile cell-1, a straight, 4-celled carpogonial branch, and a single sterile cell-2 that is formed on the same side as sterile cell-1 and more or less directly below it; each fertilized carpogonium cuts off two connecting cells in tandem from its terminal end, the first usually being non-functional and the second uniting with the anterior part of the auxiliary cell; auxiliary cell initiating one or more gonimoblast initials from its anterior end and retaining the haploid nucleus towards its base, which normally divides into two nuclei without cutting off a foot cell; sterile cells usually not dividing after fertilization but uniting with the fusion cell and becoming multinucleate; gonimoblasts radiating from the gonimoblast initials in all directions, linked by broadening pit connections, and bearing carposporangia in branched terminal chains; fusion cell small with limited cell fusions (*Apoglossum*) or large and incorporating the supporting cell, cells in the floor of the cystocarp, and the branched inner gonimoblast cells (*Paraglossum*); elongated cortical filaments absent in the floor of the cystocarp; tetrasporangia either formed in sori in the thallus surface or on erect bladelets of limited growth, the tetrasporangia cut off from the bearing cell towards the outside (*Apoglossum*) or laterally in the plane of the blade (*Paraglossum*).

Paraglossum J. Agardh 1898

Lectotype species: *Paraglossum lancifolium* (J. Agardh) J. Agardh, selected here.

Emended description. *Paraglossum* resembles *Apoglossum* in that cells of the primary cell row or main axis remain undivided. Cell rows of the fourth order are usually cut off on the adaxial (inner) sides and also on the abaxial (outer) sides of third-order cell rows and typically form both ascending and descending filaments. Intercalary cell divisions are usually present in second- and higher-order cell rows and may become abundant in some species. The periaxial cells undergo intercalary cell divisions into two or more cells adjacent to the axial cell, a feature that is not found in *Apoglossum*. *Paraglossum* species range in size; however, most are larger than typical species of *Apoglossum,* and some are especially tall (up to 50 cm long). Lateral microscopic veins or

macroscopic nerves may be present and conspicuous, inconspicuous, or absent. Ordinary branching takes place as in *Apoglossum*, mainly by means of branchlets formed along the margins of the midrib. In a few species the branches may arise from the surface of the blades or the margins may be irregular and form branches. Spermatangia resemble those in *Apoglossum* and are borne on the thallus surface of main axes or bladelets; however, the spermatangial parent cells form a layer cut off in sori from a cortical cell, and the spermatangia are formed more or less laterally from the spermatangial parent cells and the two tend to lie in a single layer. Cystocarps are found almost exclusively on leaflets formed along the margins of the midribs, or the leaflets are scattered over the thallus surface either on prominent veins or, in some cases, from monostromatic portions of the thallus. The fertile bladelets of some species are either produced in a regular sequence on opposite sides, or large numbers of secondary bladelets may be produced adventitiously from the margins of the midrib. Procarps are initiated from transverse periaxial cells on both sides of main axes and are frequently formed in successive segments. As in *Apoglossum*, carpogonial branches are relatively straight, and the two sterile groups are unicellular and uninucleate before fertilization with the second sterile group lying directly below the first or only slightly offset. The sterile groups remain undivided, but may become multinucleate after fertilization. A fertilized carpogonium cuts off two connecting cells from its anterior end as in *Apoglossum*. Diploidization of the auxiliary cell is usually effected by the second connecting cell, which lies adjacent to the middle or anterior portion of the auxiliary cell. A diploidized auxiliary cell produces several gonimoblast initials that are highly branched and grow in all directions. The fusion cell is larger than in *Apoglossum* and incorporates a significant portion of the branched inner gonimoblast cells and cells in the floor of the cystocarp in addition to the supporting cell and auxiliary cell. Carposporangia are numerous and are borne in branched chains much as in *Apoglossum*. One or sometimes two cystocarps may become quite large on the bearing leaflet, each with an ostiole. Tetrasporangia are formed either in sori in the thallus surface or along the margins of the midribs or scattered over the monostromatic portion of the blade. Alternatively, they are formed in sori in monostromatic portions of the blade, depending on the species. They are also produced along the edges of macroscopic veins of the main thallus in some species. Tetrasporangial initials tend to be cut off laterally from monostromatic cells in the centre of a bladelet or, in some cases, from surface cells in polystromatic portions of the blade.

***Paraglossum larsenii* (Skottsberg) S.-M. Lin, Fredericq & Hommersand, *comb. nov*.**

Basionym: *Delesseria* (*Paraglossum*) *larsenii* Skottsberg in H. Kylin & C. Skottsberg (1919). In *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903* (Nordenskjöld, O., editor), vol. 4, fasc. 15, p. 41, figs 20, 21a.

Holotype: Tetrasporangial plant from South Georgia sent by Skottsberg to S.

Type locality: Drift, tetrasporangial in May, South Georgia.

Synonymy & distribution: *Delesseria larsenii*: Skottsberg 1923, pp. 26–27, figs 7d, e; 8. (South Georgia). *Pseudolaingia larsenii* (Skottsberg) Levring: Levring 1944, pp. 19–20, figs 12a–c, 13 (Kerguelen); Mendoza 1973, pp. 211–217, pl. 1, figs 1–6; pl. 2, figs 7–12; pl. 3, figs 13–15 (Beagle Channel, Tierra del Fuego & Isla de los Estados, Argentina); Wynne 1989, pp. 39–45, figs 1–6 (Punta Arenas in southern Chile, Tierra del Fuego, Falkland Islands, Kerguelen Island).

Description: As Skottsberg noted (1923, p. 26, as *Delesseria larsenii*), *P. larsenii* comes close to *P. lancifolium*. He described it as differing in its colour, being dark brownish red in the thicker portions of the fronds, and in having more richly developed anastomosing tertiary nerves. Mendoza (1973) illustrated the formation of microscopic veins at the apex by longitudinal division of second-order cell rows in exactly the same manner that we described in *P. lancifolium* from the Falkland Islands. The distributions of the two species largely overlap, occurring on Tierra del Fuego, Falkland Islands, Kerguelen Island and perhaps Macquarie Island. *Paraglossum larsenii* differs from *P. lancifolium* by the formation of both microscopic and macroscopic veins from third and fourth order cell rows and by the formation of tetrasporangia in sori in the surface of main blades rather than in bladelets (Skottsberg 1923, Mendoza 1973, Wynne 1989). For Wynne, the main distinguishing character of *P*(*araglossum*) *larsenii* is the production of cystocarpic proliferations randomly from the surface of the blade and not just from the midrib and major veins. However, this character holds for our material of *P. lancifolium* as well.

***Paraglossum papenfussii* (M.J. Wynne) S.-M. Lin, Fredericq & Hommersand, *comb. nov*.**

Basionym: *Delesseria papenfussii* M.J. Wynne (1984). *South African Journal of Botany* 3: 138–141, pl. 2, 1–8 and pl. 3, 9–15.

Holotype: Male, 7359 in MICH.

TYPE LOCALITY: Attached, lower littoral to sublittoral, Kommetje, Western Cape Peninsula, Cape Province, South Africa.

SYNONYMY & DISTRIBUTION: *Delesseria papenfussii*: Stegenga, Bolton & Anderson 1997, p. 471, pl. 188, figs 1–4 (Port Nolloth to Brandfontein, South Africa); Rull Lluch 2002 (Namibia).

DESCRIPTION: Thalli up to 10 cm tall with the midrib 1–2 mm wide, becoming denuded at the base; branching alternate or opposite from the midrib up to 5 orders, the blades 3–5 mm wide with microscopic veins formed by longitudinal divisions of second-order filaments, up to three cells wide near the midrib and anastomosing elsewhere by means of interconnecting cells; initial branching of second and higher cell orders as in *P. lancifolium*, with numerous intercalary cell divisions; spermatangia in sori separated by sterile cells; cystocarps 1–3 formed alongside the midribs; tetrasporangia in linear sori on both sides of fertile blades.

Paraglossum crassinervium* (Montagne) S.-M. Lin, Fredericq & Hommersand, *comb. nov.

BASIONYM: *Delessseria crassinervia* Montagne (1842). In *Prodromus generum specierumque phycearum novarum, in itinere ad polum antarcticum*, p. 3.

TYPE: At PC, collected by d'Urville and illustrated by Montagne, 1845, pl. 8, fig. 1.

TYPE LOCALITY: Auckland Islands, New Zealand.

SYNONYMY & DISTRIBUTION: *Delesseria crassinervia*: Montagne 1845, p. 164, pl. 8, fig. 1 (Auckland Islands); Harvey & Hooker 1845, p. 184 (Lord Aucklands group and Campbell's Island); Laing 1902, pp. 346–347 (St. Claire, Wycliffe Bay, trawling outside Otago Heads); Kylin 1929, p. 7, pl. 2, fig. 6 (St. Claire-Dunedin, collected by Laing); Adams 1994, p. 279, pl. 98 (South Island from Otago Peninsula to Foveaux Strait, Stewart I., Chatham Is.; Snares, Bounty, Antipodes, Auckland and Campbell Is.); Womersley 2003, p. 146. [Womersley stated that records from Tasmania, Australia, remain in doubt.]

DESCRIPTION: Thalli up to 50 cm tall from a discoid holdfast with a thick midrib up to 6 mm wide and monostromatic blades up to 1.5 cm broad, with minutely toothed margins; microscopic and macroscopic lateral veins absent; indeterminate branches and determinate branchlets opposite or alternate from surface cells adjacent to the primary midrib; midribs often densely covered with adventitious bladelets in older plants. Spermatangia, procarps, cystocarps and tetrasporangia borne mainly on determinate bladelets but also on main axes. Spermatangia and tetrasporangia in discontinuous longitudinal sori on both sides between the midrib and the margins. Procarps are often produced either in successive segments with the second sterile group directly below the first or only slightly offset; the carpogonium cutting off two connecting cells in tandem with the subterminal connecting cell fusing with the auxiliary cell, as described above for *Apoglossum*. [Note: this description is based on plants from the South Island, New Zealand.]

Paraglossum fuegiense* (Skottsberg) S.-M. Lin, Fredericq & Hommersand, *comb. nov.

BASIONYM: *Delesseria fuegiensis* Skottsberg (1923). *Kungliga Svenska Vetenskapsakademiens Handlingar* 63(8), pp. 22–23, figs 5a–c, 6a–c.

TYPE: Not known, possibly at GB.

TYPE LOCALITY: Drift, Slogget Bay, Fuegia, cystocarpic and tetrasporangial plants.

SYNONYMY & DISTRIBUTION: *Delesseria fuegiensis*: Mendoza 1974, pp. 484–486, pl. 1, figs 1–4, pl. 2, figs 5–9; pl. 4, figs 10–13 (attached, Tierra del Fuego, Argentina); Lin 2000, pls 13A, B, 15E, F (Sea Lion Island, Falkland Islands).

DESCRIPTION: Thalli up to 35 cm tall, growing from a disc and short stipe with midribs up to 4 mm broad and 1.75 mm thick, bearing conspicuous simple, opposite macroscopic nerves; microscopic veins absent; bladelets opposite, linear-lanceolate, up to 15 cm long and 1–2 cm broad, from the margins of the midribs above the lateral nerves. Cystocarps and tetrasporangia found mostly on the bladelets, with the cystocarps central, and the tetrasporangia formed in linear sori alongside the midrib.

Paraglossum nereifolium* (Harvey) S.-M. Lin, Fredericq & Hommersand, *comb. nov.

BASIONYM: *Delesseria nereifolia* Harvey (1855). In *The Botany of the Antarctic Voyage of H.M. Discovery Ships 'Erebus' and 'Terror' in the years 1839–1843. Vol. 2. Flora Novae-Zelandiae, Pt. 2. Flowerless Plants* (Hooker, J.D., editor), p. 238.

SYNTYPES: BM, drift, Preservation Harbour, West Coast Middle Island (=South Island) and east side of Stewart Island, New Zealand, coll. David Lyall.

TYPE LOCALITY: As above.

SYNONYMY & DISTRIBUTION: *Delesseria nereifolia*: Adams 1994, p. 279, pl. 98 (North Island at Cooks Strait, South Island, Stewart Island, Snares Islands, Auckland Islands, Campbell Island). *Schizoneura laurifolia* J. Agardh: Agardh

1898, pp. 168–169. *Delesseria laurifolia* (J. Agardh) Kylin: Kylin 1924, p. 26; Kylin 1929, p. 8, pl. 3, fig. 7.

Description. Thalli, variable, up to 15 cm tall, with a thick stipe and midrib, and bearing numerous lanceolate blades from the midrib each up to 10 cm long and either narrow or broad, up to 3 cm wide, with blunt apices and conspicuous opposite macroscopic nerves and reticulate anastomosing microscopic veins. Larger plants have been referred to *D. laurifolia*; however, both size ranges have the same reported distribution according to Adams (1994).

Paraglossum salicifolium* (Reinsch) S.-M. Lin, Fredericq & Hommersand, *comb. nov.

Basionym: *Delesseria salicifolia* Reinsch (1888). *Berichte der Deutschen Botanischen Gesellschaft*, **6**: 149–150, pl. 20.

Lectotype: A sterile plant at M (67.83/49) collected in the drift by Wille on February 1883, selected and illustrated by Ricker 1987, pp. 264–265, fig. 109c.

Type locality: South Georgia, epiphytic on Ptiloteae.

Synonymy & distribution: *Delesseria salicifolia*: Reinsch 1890, pp. 388–389, pl. 4, figs 1–5 (South Georgia); Kylin & Skottsberg 1919, p. 45, pl. 1, fig. 3 (South Georgia, tetrasporangia in June); Skottsberg 1923, pp. 21–22, fig. 4a, b (sublittoral 5 m, Cumberland Bay, Boiler Harbour, South Georgia); Wynne 1982, pp. 326–367, figs 1–9, including the synonymy (South Sandwich Islands); Ricker 1987, pp. 254–265, fig 109c, a photograph of the lectotype; Wiencke & Clayton 2002, pp. 79–80, pl. 20 and references included there (Antarctic Peninsula, South Shetland Is., South Orkney Islands, South Sandwich Islands, South Georgia). '*Delesseria*' *salicifolia* Reinsch in Hommersand *et al*. 2009, pp. 518–519 and citations included there (Antarctic Peninsula). *Hydrolapathum stephanocarpum* A. Gepp & E.S. Gepp 1905, p. 195, pl. 472, figs 5–7 (Scotia Bay, South Orkney Islands); A. Gepp & E.S. Gepp 1912, pp. 79–80, pl. 2, figs 12–14. *Delesseria stephanocarpa* (A. Gepp & E.S. Gepp) Skottsberg in Skottsberg 1941, pp. 78, 81 (West Antarctica); Moe & De Laca 1976, p. 22 (Antarctic Peninsula).

Description. Thalli up to 25 cm tall, once or twice oppositely branched from the midrib, the blades arising from the margins of midribs, 4–18 mm wide, and with entire margins and acute apices; blades with simple, conspicuous lateral macroscopic veins that extend almost to the margins; cystocarps subterminal on special small leaflets along the midrib up to 1 mm long and 0.5 mm wide with prominent appendages or spines; tetrasporangia on special small leaflets up to 1.2 mm long and 0.7 mm wide, with serrated margins that are borne along the margins of the midribs. [Note: the plants sequenced were from the Antarctic Peninsula.]

Acknowledgements

This project was partly supported by a grant from National Science Council (Taiwan) (NSC 100-2321-B-019-009 -MY2) and a research grant from NTOU's Center of Excellence for Marine Bioenvironment and Biotechnology to S.-M. Lin. Fredericq and Hommersand were supported by NSF grant DEB0937978 to J.M. Lopez Bautista, M.H. Hommersand and S. Fredericq. We thank Fran Hommersand for help curating the algae collections at NCU, Sonja Stiefel, formerly at UNC, for help in preparing figures of *Apoglossum*, Charles and Margaret Amsler for providing material from the Antarctic Peninsula, Per Lassen for photographs of type material from the Agardh herbarium at LD, Jo Wilbraham for photographs of type material at BM, Susan Whitfield at NCU for her help in preparing the illustrations, and Michael Wynne for his careful review of the manuscript which added significantly to this study.

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