

Morphological Review of *Pelvetia* and *Silvetia* (Fucaceae, Phaeophyta) with an Emphasis on Phylogenetic Relationships

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We compared the morphology of all four members of *Pelvetia* and *Silvetia* (Fucaceae, Phaeophyta), with an emphasis on phylogenetic relationships. *Silvetia* is segregated from *Pelvetia* because it has two, longitudinally divided eggs in the oogonium. In contrast, the eggs of the genus *Pelvetia* are transversally divided. A cladistic analysis, based on 17 morphological features, shows that *Pelvetia* is closely related to *Hesperophycus* and *Pelvetiopsis*, as are three species of *Silvetia*. We can infer from the cladistic tree and biogeographic information that some silvetian ancestor populations from the northern Pacific region likely evolved to *S. babingtonii* in northern Japan and then moved to Korea and California (USA), where *S. siliquosa* and *S. compressa*, respectively, diverged. Our morphological study corroborates the DNA-based phylogeny and the ensuing taxonomy for the two genera. These results demonstrate the necessity for systematically revising the family Fucaceae to emphasize egg development, rather than egg number, in the oogonium, as a diagnostic character.

Keywords: Brown algae, cladistics, Fucales, phylogeography, taxonomy

The genus *Pelvetia* Decaisne et Thuret was segregated from the genus *Fucus* Linnaeus because only two eggs develop in the oogonium of the former, compared with eight in the latter (Decaisne and Thuret, 1845). Since then, three other members, each with two eggs in their oogonia, have been described: *P. babingtonii* (Harvey) De Toni, *P. compressa* (J. Agardh) De Toni, and *P. siliquosa* Tseng et Chang. Egg division in *P. canaliculata* is transversal (Decaisne and Thuret, 1845; Oltmanns, 1889). In contrast, Yendo (1907) observed longitudinal division in *P. babingtonii* [as *P. wrightii* (Harvey) Yendo], but did not consider the divisional pattern to be important enough to warrant a new generic position. Likewise, the same developmental pattern was observed in *P. compressa* (Gardner, 1910) and *P. siliquosa* (Tseng and Chang, 1953; Song et al., 1996). Regardless, the heterogeneity of egg production in *Pelvetia* remains controversial (Song et al., 1996).

The taxonomic potential of egg development in *Pelvetia* is realized based on nrDNA 18S sequence data (Lee et al., 1998). In an extensive study of ITS sequences, Serrão et al. (1999) established a new genus *Silvetia* Serrão, Cho, Boo, and Brawley, of which the diagnostic character is longitudinal egg division. The new

genus includes *S. babingtonii* (Harvey) Serrão, Cho, Boo, and Brawley; *S. compressa* (J. Agardh) Serrão, Cho, Boo, and Brawley; and *S. siliquosa* (Tseng et Chang) Serrão, Cho, Boo, and Brawley, all of which had previously belonged to *Pelvetia*. This ITS-based taxonomy is strongly supported by plastid-encoded DNA sequence data (Lee et al., 1999).

Despite its importance to taxonomy, the comparative developmental morphology of *Pelvetia* or *Silvetia* has not been examined. Therefore, our goals were to 1) review the comparative morphology of both genera, and 2) understand the morphology-based phylogeny. Based on our collections and those specimens on loan from established herbaria, we have studied in detail the structure and reproduction of each member, and have constructed a cladogram using the morphological data. This is the first paper that deals with the comparative morphology of all members of both genera.

MATERIALS AND METHOD

All specimens of *Pelvetia* and *Silvetia* were initially observed for morphology while alive, and were then preserved in 5% formaldehyde-seawater for further anatomical observations. The liquid-preserved specimens were dehydrated with 25% ethyl alcohol solu-

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Table 1. Characters and their states used in cladistic analysis.

Character	Code	Description
Vegetative characters		
1. Habit	0, 1	bushy, typical
2. Frond	0, 1	straight, curved
3. Grooved stem	0, 1	absent, present
4. Stem shape	0, 1	flat, (sub) cylindrical
5. Maximum width of stem	0, 1	>1 cm, <1 cm
6. Arrangement of cortical cells	0, 1	compact, loose
Reproductive characters		
7. Form receptacle	0, 1, 2, 3, 4	bead, club, rod, swollen, fusiform
8. Maximum length of receptacle	0, 1, 2	<1.5 cm, 1.5 - 3.0 cm, >5.0 cm
9. Surface form of receptacle	0, 1, 2	flat, submerged, protuberance
10. Oogonium size	0, 1, 2	<55 μm , 100 - 145 μm , >170 μm
11. Longitudinally divided oogonium	0, 1	present, absent
12. Transversally divided oogonium	0, 1	present, absent
13. Number of eggs per oogonium	0, 1, 2	four, two, one
14. Mesochite	0, 1	absent, present
15. Formation time of disintegrated nuclei	0, 1	after the second cytokinesis, the first cytokinesis
16. Position of disintegrated nuclei	0, 1, 2	subsidiary, basal, surface
17. Monoecy or dioecy	0, 1	dioecy, monoecy

tion, hand-dissected by fine razor under the dissecting microscope, and then stained with 1% aniline blue in water. The developmental sequences of vegetative and reproductive cells and tissues were followed by serially sectioning the material. For quantitative characters, 25 measurements were taken whenever possible to obtain mean values. Drawings were made with a camera lucida attached to an Olympus microscope. Herbarium specimens from AST, TNS, and UC (Holmgren et al., 1990) were compared with our collections. Specimens from our collections are now deposited on sheets or in liquid in the herbarium of the Department of Biology, Chungnam National University ('CNUK'), Daejeon, Korea.

The characters used for the cladistic analysis were descriptive features of each species. Seventeen such characteristics (Table 1) were selected for the analysis after a morphological review of the numerous specimens collected on coasts worldwide. A data matrix (Table 2) was compiled by translating qualitative characters into multi-state or additive binary codes. These quantitative characters were incorporated only when gaps in the measurements were unambiguous. Our cladogram was produced from the unweighted data, using the exhaustive search algorithm of PAUP v.4.03 (Swofford, 1999). Character changes in the resulting cladogram were evaluated through MacClade v. 3.0.4 (Maddison and Maddison, 1992).

Pelvetiopsis Gardner and *Hesperophycus* Setchell et Gardner have only one egg per oogonium, whereas *Ascophyllum* Stackhouse has four. These species were included in the cladistic analysis because a gradual

progression of either fewer or more eggs is implied in the Fucaceae (Clayton, 1984). *Pelvetiopsis limitata* (Setchell) Gardner, *H. californicus* P. C. Silva, and *A. nodosum* (L.) Le Jolis all were candidates for the outgroup. The final tree was then constructed based on only the latter species as the outgroup.

RESULTS AND DISCUSSION

Morphological Observations and Taxonomy

Pelvetia Decaisne et Thuret (1845)

Pelvetia is traditionally a well-recognized genus, being circumscribed with the production of two eggs in the oogonium of the female conceptacle (Decaisne and Thuret, 1845). As mentioned above, because three members now belong to the new genus *Silvetia* (Serrão et al., 1999), the concept for the genus *Pelvetia* has been revised as having the character of two, transversely divided eggs. Other characteristics of the genus remain as reported by Decaisne and Thuret (1845). The type and only species is *P. canaliculata*, from the European coast.

Pelvetia canaliculata (L.) Decaisne et Thuret (1845); Figures. 1-14.

Basionym: *Fucus canaliculatus* Linnaeus (1767).

Representative specimens examined: France; St. Malo, 21 August 1992, S.M. Boo, CNUK C005878 to

Table 2. Character state matrix for the OTUs used in this study.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Pelvetia canaliculata</i>	1	1	1	0	1	1	1	0	2	2	1	0	1	1	0	2	1
<i>Silvetia babingtonii</i>	1	0	0	0	1	0	2	2	1	1	0	1	1	0	0	0	1
<i>S. compressa</i>	0	0	0	1	1	0	1	0	0	1	0	1	1	0	0	0	1
<i>S. siliquosa</i>	1	0	0	1	1	0	4	1	0	1	0	1	1	0	0	0	1
<i>Ascophyllum nodosum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0
<i>Hesperophycus californicus</i>	1	0	0	0	0	?	3	1	2	?	1	0	2	0	1	1	1
<i>Pelvetiopsis limitata</i>	1	0	0	1	1	0	1	0	0	0	1	0	2	0	1	1	1

C005880, C005885, C005902 to 3, C005905; Cap Blanc Nez, August 1997, J.H. Kim, CNUK number not given; England; Isle of Man, February 1997, A. Star, CNUK number not given.

Description: Plants are perennial, 4 to 7 cm long, and 0.2 cm in diameter. They consist of one to several yellowish-brown, crooked fronds as well as discoid-conical holdfasts. The fronds are simple, smooth, and regularly dichotomous. They are grooved on one side and rounded on the other, and are composed of medulla and cortex (Fig. 3). The medullary cells are filamentous and aligned in longitudinal rows, and are perpendicularly produced from inner cortical cells. The cortices are compact in the grooved portion (Fig. 5) and loose in the rounded part (Fig. 4), and are composed of three to four cell layers. The cortical cells are ovoid to rectangular, with numerous phaeoplasts. They are $22 \pm 3 \mu\text{m}$ long and $10 \pm 2 \mu\text{m}$ ($n = 11$) in diameter.

The reproductive plants are monoecious (Fig. 6). Receptacles are club-form (Fig. 1), with some 1.5 cm long. They are simple or becoming branched, and are produced on the upper branches, bearing conceptacles on the protuberant surface (Fig. 2). The conceptacles are spherical, $968 \pm 66 \mu\text{m}$ long, and $908 \pm 56 \mu\text{m}$ in diameter ($n = 10$). They are composed of paraphyses, antheridia, and oogonia (Fig. 6). Paraphyses are filamentous and occur between the oogonia and antheridia. The antheridia arise on stalk cells or paraphyses, and are elongate-ovoid, bearing numerous spermatozooids. The oogonia stand on the wall of the conceptacle (Fig. 6) and include plentiful oil drops. They are ovoid, $185 \pm 11 \mu\text{m}$ long, and $122 \pm 10 \mu\text{m}$ in diameter ($n = 10$). Eight nuclei are produced after three successive nuclear divisions (Figs. 7-10). Two egg cells, each having one functional nucleus, are produced by transversal division of the cytoplasm, and are surrounded with a thick and gelatinous cell wall (Figs. 11-14). Six supernumerary nuclei are extruded on the oogonium surface (Fig. 13).

Remark: *Pelvetia canaliculata* is characterized by a grooved frond and two, transversally divided eggs in

the oogonium. The type material is housed in the Museum of the Linnean Society, London. Morphology is so variable that some taxonomic varieties and forms have been reported, i.e., var. *acutilobata* Lami, f. *interposita* Lami; var. *libera* Baker, *coralloides* Baker; and *radicans* Foslie. However, these forms are not recognized in the ensuing manuals and floristics (Ardré, 1970). Plastid-encoded Rubisco spacer sequences are identical among plants collected from Isle of Man, England, and Cap Blanc Nez, France (Lee et al., 1999). *P. canaliculata* is distributed on the European coast from Portugal (Ardré, 1970) to England, northern Norway, and Iceland (Newton, 1931).

Silvetia Serrão, Cho, Boo, and Brawley in Serrão et al. (1999)

Silvetia is characterized by two, longitudinally to obliquely divided eggs in the oogonium, and is similar in its other morphology to *Pelvetia* (Serrão et al., 1999). The genus is typified as *S. compressa* and includes *S. babingtonii* and *S. siliquosa* (Serrão et al., 1999).

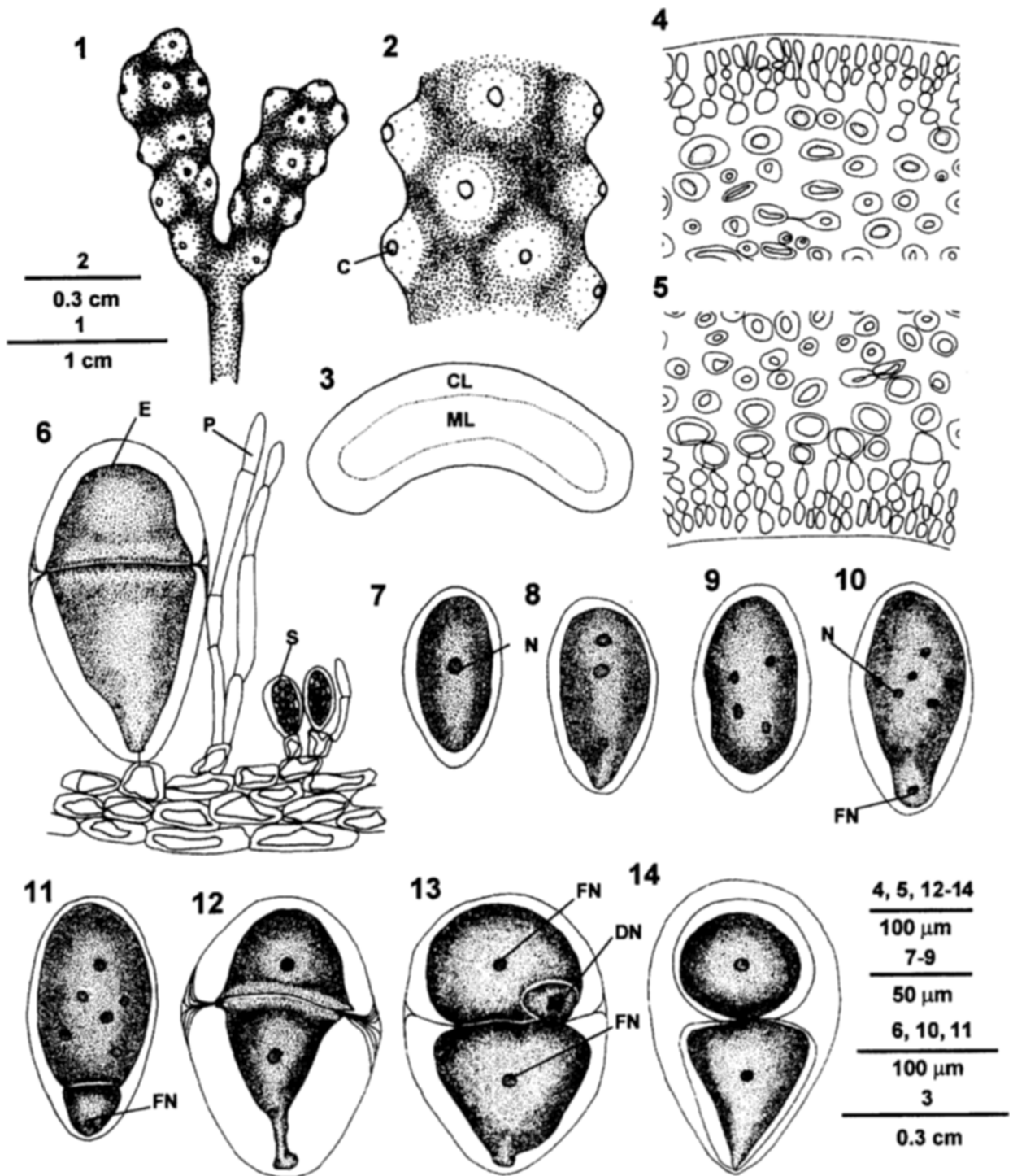
Silvetia babingtonii (Harvey) Serrão, Cho, Boo, and Brawley in Serrão et al. (1999); Figures. 15-25.

Basionym: *Fucus (Fucodium) wrightii* Harvey (1859).

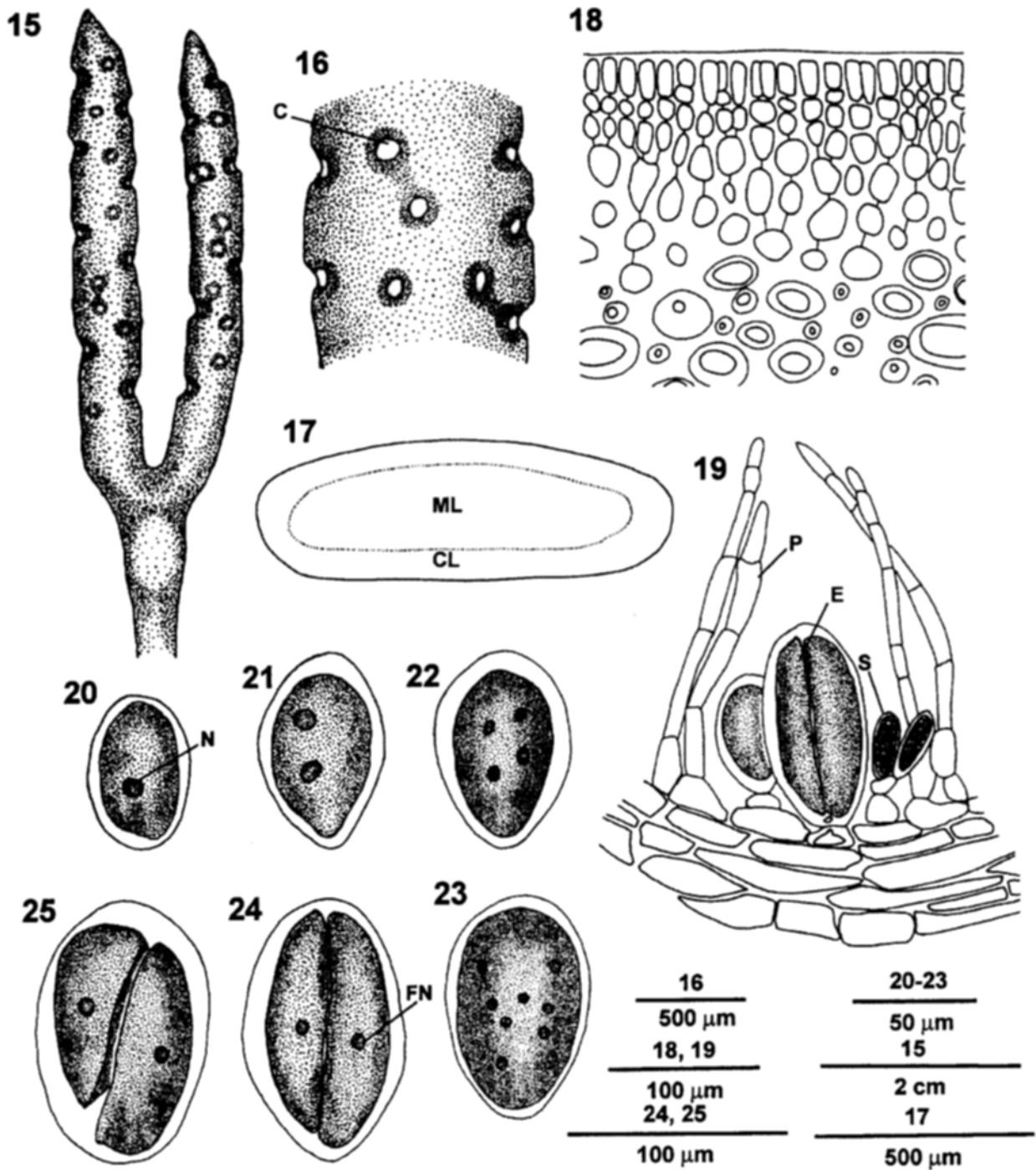
Homotypic synonym: *P. babingtonii* (Harvey) De Toni (1895).

Heterotypic synonyms: *F. (Fucodium) wrightii* Harvey (1859), p. 329. *P. wrightii* Okamura (1902), p. 138 (according to Yoshida and Silva, 1992).

Representative specimens examined: Japan: Akkeshi, Hokkaido, 25 August 1997, S.M. Boo, CNUK C005881, C005906; 10 May 1999, CNUK, C005897, C005900; Hakodate, Hokkaido, August 1990, T. Motomura, CNUK C005898; Muroran, Hokkaido, May 1996, T. Motomura, CNUK C005882 to 84, C005889 to 91; TNS number not given, July, 1956, T. Kitayama, September 1956, June 1967, February 1991, August 1996; Shiriya, Aomori prefecture, T. Kitayama, TNS number not given, January, March, May, June, July,



Figures. 1-14. *Pelvetia canaliculata*. **1.** Receptacles bearing conceptacles. **2.** Conceptacles (C) on the protuberant surface of receptacles. **3.** Transversal section showing cortical layer (CL) and medullary layer (ML) of grooved frond. **4.** Transversal section showing loose arrangement of cortical cells on the rounded side. **5.** Transversal section showing compact arrangement of cortical cells on the grooved side. **6.** Conceptacle bearing oogonium with eggs (E), antheridia with spermatozoids (S), and paraphyses (P). **7-14.** Development of egg showing functional nuclei (FN) and disintegrated nuclei (DN) from oogonium with eight nuclei (N).



Figures. 15-25. *Silvetia babingtonii*. **15.** Receptacles bearing conceptacles. **16.** Conceptacles (C) on the subsided surface of receptacles. **17.** Transversal section showing cortical layer (CL) and medullary layer (ML). **18.** Transversal section showing compact arrangement of cortical cells. **19.** Conceptacle bearing oogonium with eggs (E), antheridia with spermatozoids (S), and paraphyses (P). **20-25.** Development of egg showing functional nuclei (FN) from oogonium with eight nuclei (N).

August, October 1987, T. Kitayama.
 Description: Plants are 15 to 28 cm long and 0.5

cm in diameter. They consist of one to several axes and holdfasts. Holdfasts are discoid-conical. The fronds

are regularly dichotomous and occasionally with vesicles in the branching point. They are compressed throughout and composed of medulla and cortex (Fig. 17). The medullary cells are filamentous and aligned in longitudinal rows, and are perpendicular from the inner cortical cells. The cortices are compact and composed of five to six cell layers (Fig. 18). Cortical cells are spherical or ovoid, with numerous phaeoplasts, and are $24 \pm 2 \mu\text{m}$ long and $13 \pm 1 \mu\text{m}$ in diameter ($n = 15$).

The reproductive plants are monoecious (Fig. 19). Receptacles are rod-shaped (Fig. 15), and 5 to 7 cm long. They are simple or becoming branched, produced on the upper branches, and bearing conceptacles on the subsided surface (Fig. 16). The conceptacles are spherical, and $82 \pm 116 \mu\text{m}$ long and $610 \pm 63 \mu\text{m}$ in diameter. They are composed of paraphyses, antheridia, and oogonia (Fig. 19). Paraphyses are filamentous and branched, surrounding the oogonia and antheridia. The antheridia arise on stalk cells or branched paraphyses, and bear numerous spermatozooids (Fig. 22). They are elongate-ovoid, $43 \pm 9 \mu\text{m}$ long, and $13 \pm 2 \mu\text{m}$ in diameter ($n = 10$). The oogonia are ovoid with or without stalk cells, $110 \pm 10 \mu\text{m}$ long, and $70 \pm 9 \mu\text{m}$ in diameter ($n = 10$). Eight nuclei are produced after three successive nuclear divisions (Figs. 20-23). Two egg cells, each having one functional nucleus, are produced by longitudinal to oblique divisions of the cytoplasm (Figs. 24 and 25). Six supernumerary nuclei are extruded between the egg cells.

Remark: *S. babingtonii* is characterized by its vesicles on the frond and a long receptacle. The type material is housed at the Harvey herbarium of the TCD herbarium in Ireland. The type sheet is annotated as "Japan, Dr. Babington", but without detailed location (Yoshida and Silva, 1992). Yendo (1907) classified this species [as *P. wrightii* (Harvey) Yendo] into three intraspecific taxa: f. *wrightii*, *babingtonii*, and *japonica*, but that classification is not adopted in the ensuing manuals or floristics (Yoshida, 1998). Yoshida and Silva (1992) studied the type, nomenclature, and morphology of *S. babingtonii* (as *P. babingtonii*) and reported that thallus size, vesicle characteristics, and receptacle morphology all varied in response to habit and season of growth. The Rubisco spacer sequences are identical among plants from quite different locations, i.e., one at Muroran on the east side of Hokkaido, the other at Akkeshi on the west side (Lee et al., 1999). Although the species is reported to occur in Korea (Yoshida, 1998), we have not found it there despite conducting many collections along all the

coasts. The Rubisco spacer sequences are also quite different between *S. babingtonii* from Japan and *S. siliquosa* from Korea (Lee et al., 1999). The report of *S. babingtonii* in Korea (Yoshida, 1998, p. 367) is concluded to be a result of misidentification. *S. babingtonii* is distributed in northern Honshu and Hokkaido, Japan, and at Vladivostok in the far east of Russia (Adrianov and Kussakin, 1998).

Silvetia compressa (J. Agardh) Serrão, Cho, Boo, and Brawley in Serrão et al. (1999); Figures. 26-35.

Basionym: *Fucus compressa* J. Agardh (1824).

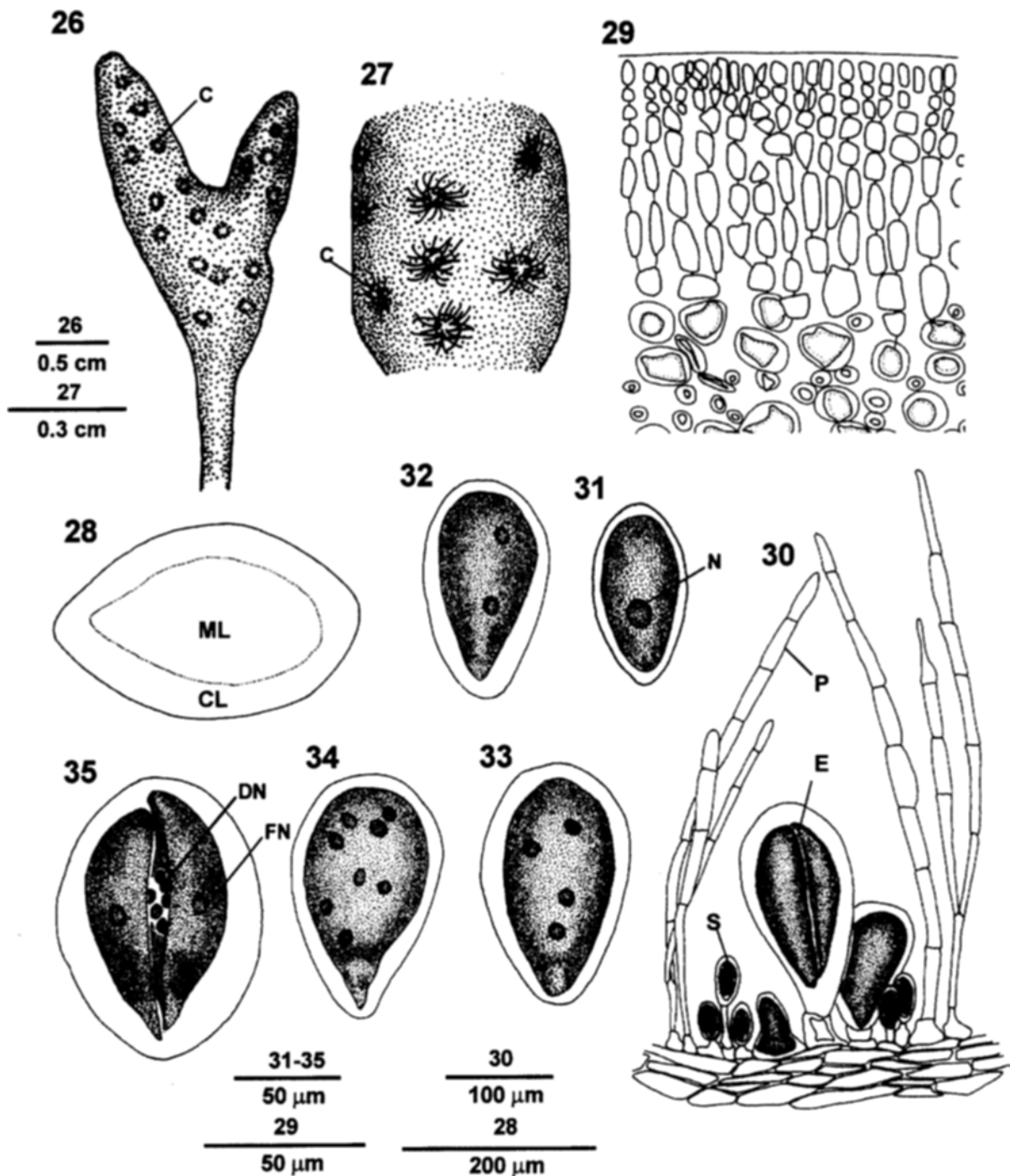
Homotypic synonym: *P. compressa* (J. Agardh) De Toni (1895).

Heterotypic synonyms: *Fucus fastigiatus* J. Agardh (1841); *Pelvetia fastigiata* (J. Agardh) De Toni (1895) (according to Silva, 1996).

Representative specimens examined: USA: Carmel Bay, California, August 1998, T.O. Cho, CNUK number not given; Pacific Grove, California, May 1997, J. Watanabe, CNUK C005851, C005888, C005892 to 3; Lands End, San Francisco, DS 304724, UC 207094; Pebble Beach, California, 1917, Gardner 2997, N.L. Gardner.

Description: Plants are 35 to 70 cm long, and consist of several greenish- to dark-brown axes and holdfasts. Holdfasts are discoid-conical. The fronds are regularly dichotomous throughout, cylindrical near the base, and subcylindrical in the middle and upper portions (Fig. 28). They are composed of medulla and cortex (Fig. 28). Medullary cells are filamentous and aligned in longitudinal rows. The cortices are compact (Fig. 29) and composed of seven to eight cell layers. The cortical cells are ovoid, $18 \pm 2 \mu\text{m}$ long and $10 \pm 1 \mu\text{m}$ in diameter ($n = 16$).

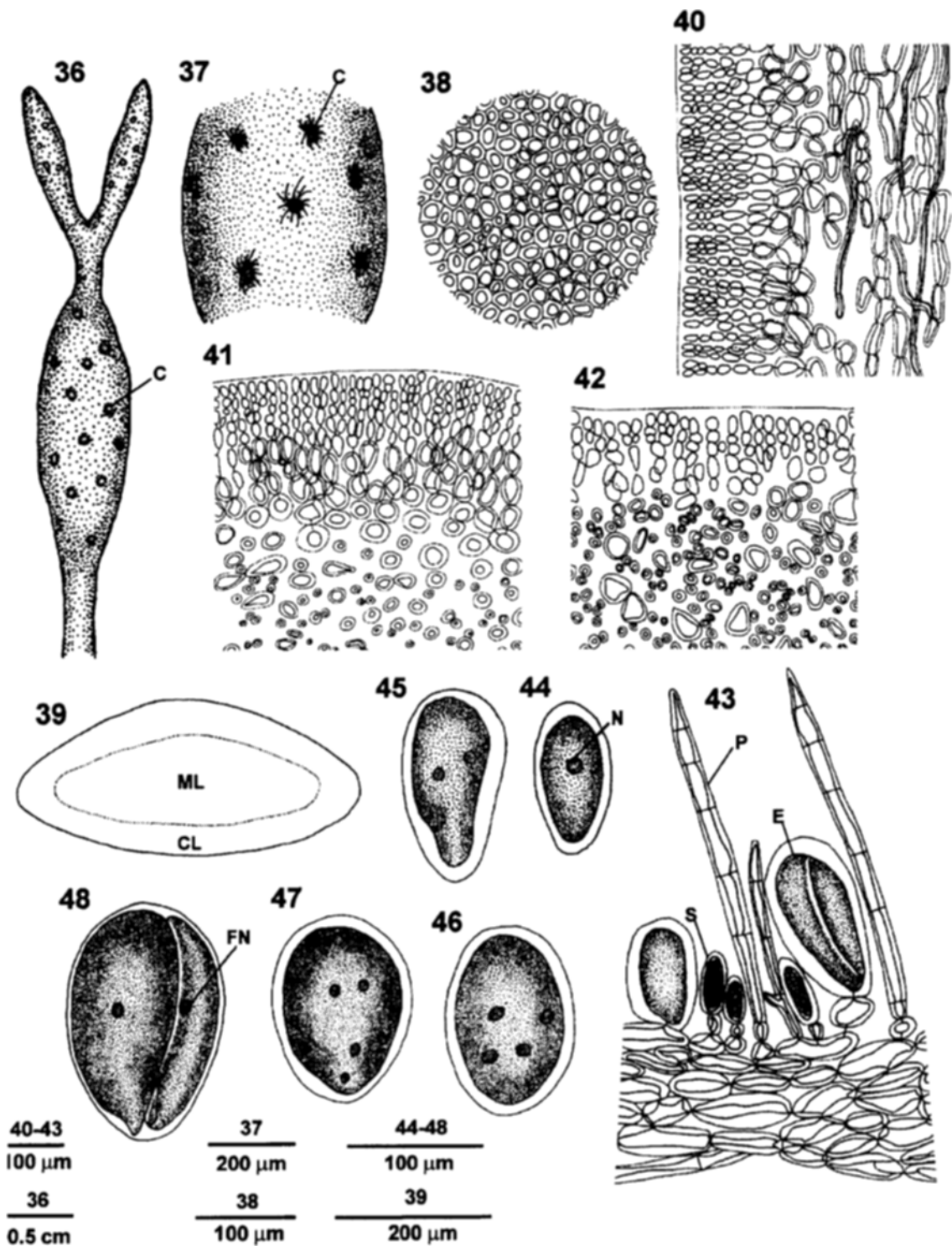
Reproductive plants are monoecious (Fig. 30). The receptacles are club-form (Fig. 26) and 1.0 to 1.5 cm long. They are simple or becoming branched, produced in the upper branches, and bearing conceptacles on the flat surface (Fig. 27). The conceptacles are spherical, $749 \pm 85 \mu\text{m}$ long and $769 \pm 42 \mu\text{m}$ in diameter ($n = 11$). They are composed of paraphyses, antheridia, and oogonia (Fig. 30). Paraphyses are filamentous, branched, and surrounding the oogonia and antheridia. The antheridia arise on stalk cells or branched paraphyses, and are elongate-ovoid, bearing numerous spermatozooids (Fig. 30). Oogonia are ovoid, with or without stalk cells, $131 \pm 11 \mu\text{m}$ long and $99 \pm 9 \mu\text{m}$ in diameter ($n = 10$). Eight nuclei are produced after three successive nuclear divisions (Figs. 31-34). Two egg cells, each having one func-



Figures 26-35. *Silvetia compressa*. **26.** Receptacles bearing conceptacles (C). **27.** Conceptacles on the flat surface of receptacles. **28.** Transversal section showing cortical layer (CL) and medullary layer (ML). **29.** Transversal section showing compact arrangement of cortical cells. **30.** Conceptacle bearing oogonium with eggs (E), antheridia with spermatozoids (S), and paraphyses (P). **31-35.** Development of egg showing functional nuclei (FN) and disintegrated nuclei (DN) from oogonium with eight nuclei (N).

tional nucleus, are produced by longitudinal to oblique division of the cytoplasm (Fig. 35). However,

four functional eggs rarely are produced. Six supernumerary nuclei are extruded between the egg cells



Figures. 36-48. *Silvetia siliquosa*. **36.** Receptacles bearing conceptacles (C). **37.** Conceptacles on the flat surface of receptacles. **38.** Frond surface showing the terminal cells. **39.** Transversal section showing cortical layer (CL) and medullary layer (ML). **40.** Longitudinal section showing filamentous medullary cells. **41.** Transversal section showing compact arrangement of cortical cells. **42.** Transversal section showing loose arrangement of cortical cells. **43.** Conceptacle bearing oogonium with eggs (E), antheridia with spermatozooids (S), and paraphyses (P). **44-48.** Development of egg showing functional nuclei (FN) and disintegrated nuclei from oogonium with eight nuclei (N).

(Fig. 35).

Remark: *S. compressa* is characterized by bushy, tall fronds, and small receptacles. The type material is Gardner 2997 in the Agardh herbarium at Lund, Sweden; the type locality is Pebble Beach, Carmel Bay, California, USA. Development of the egg in the oogonium is well illustrated by Gardner (1910). This species is subdivided into f. *compressa* with a typical form, and f. *gracilis* Setchell et Gardner in Gardner (1917), with very slender fronds. Although it was listed as part of the marine flora at Coos Bay, Oregon (Setchell and Gardner, 1925), recent floristic studies by Silva (1996) have reported that *S. compressa* is distributed from California, U.S.A, to Baja California, Mexico.

Silvetia siliquosa (Tseng et C.F. Chang) Serrão, Cho, Boo, and Brawley in Serrão et al. (1999); Figures. 36-48.

Basionym: *P. siliquosa* Tseng et Chang (1953).

Heterotypic synonym: *Pelvetia minor* Noda (1966).

Representative specimens examined: Korea: Boryung, West Coast, March 1992, S.M. Boo & T.O. Cho, CNUK C004154; 13 June 1992, S.M. Boo & K.S. Seo, CNUK C004310, C004581; 15 July 1992, S.M. Boo & K.S. Seo, CNUK C004690; 26 September 1992, S.M. Boo & T.O. Cho, CNUK C004372; Padori, West Coast, January - December 1992, January - May 1993, liquid materials; Geojedo, South Coast, April 1993, H.S. Song & H.S. Yoon, CNUK C005838; Jindo, South Coast, April 1993, H.S. Song & H.S. Yoon, CNUK number not given; Oeyondo, West Coast, 19 January 1992, T.O. Cho & H.S. Yoon, CNUK C002216 to 20, C002227 to 8, C002281 to 2; 21 March 1992, T.O. Cho, W.G. Shin & H.S. Yoon, CNUK C002176 to 8, C002180; 16 May 1992, T.O. Cho, H.S. Yoon & H.S. Song, CNUK C002190 to 6; 21 July 1992, T.O. Cho & W.G. Shin, CNUK C002197; 23 September 1992, T.O. Cho, H.S. Yoon & A.L. Cho, CNUK C002198 to 210; 23 December 1992, T.O. Cho & H.S. Yoon, CNUK C000696, C000751; 26 January 1993, S.M. Boo & T.O. Cho, CNUK C002008, C002010, C002014 to 7; 26 March 1993, T.O. Cho & H.S. Yoon, CNUK C002004 to 7, C002009, C002018; 6 May 1993, T.O. Cho & H.S. Yoon, CNUK C002020; 14 June 1993, T.O. Cho & H.S. Yoon, CNUK C002022; 19 September 1993, T.O. Cho & H.S. Yoon, CNUK C002028, C002021; 29 January 1999, T.O. Cho, CNUK C000407; Seochun, West Coast (13 June 1992, S.M. Boo & T.O. Cho, CNUK C004106; Sabsido, West Coast, 6 July 1998, T.O. Cho, CNUK C002878 to 9, C002881.

China: Rushan, Qingdao, Shantung Province, May 1996, S. Lu, CNUK number not given; Prope Mashan, Shantung Peninsula, July 1951, C.K. Tseng, AST no 51-942.

Description: Plants are 8 to 10 cm long and 0.3 cm in diameter, and are composed of one to several yellowish-brown axes and discoid-conical holdfasts. The fronds are subcylindrical in shape, regularly dichotomous throughout, and composed of medulla and cortex (Fig. 39). The medullary cells are filamentous and aligned in longitudinal rows (Fig. 40). Cortices are compact (Figs. 38 and 40) and composed of seven to nine cell layers (Figs. 41 and 42). The cortical cells are spherical to ovoid with numerous phaeoplasts, $26 \pm 4 \mu\text{m}$ long and $11 \pm 3 \mu\text{m}$ in diameter ($n = 16$).

Reproductive plants are monoecious (Fig. 43). The receptacles are club-form to fusiform (Fig. 36), 1.8 to 3.0 cm long, and 0.5 cm in diameter. They are branched, produced in the upper part, and bear conceptacles on the flat surface (Fig. 37). The conceptacles are spherical, and are composed of paraphyses, antheridia, and oogonia (Fig. 43). Paraphyses are filamentous, surrounding the oogonia and antheridia (Fig. 43). The antheridia arise on stalk cells or branched paraphyses and are elongate-ovoid, bearing numerous spermatozooids (Fig. 43). They are $43 \pm 9 \mu\text{m}$ long and $13 \pm 2 \mu\text{m}$ in diameter ($n = 10$). Oogonia are ovoid, with or without stalk cells, $112 \pm 10 \mu\text{m}$ long, and $85 \pm 7 \mu\text{m}$ in diameter ($n = 10$). Eight nuclei are produced after three successive nuclear divisions (Figs. 44-47). Two egg cells, each having one functional nucleus, are produced by longitudinal to oblique division of the cytoplasm (Fig. 48). However, four functional eggs rarely are produced. Six supernumerary nuclei are extruded between the egg cells.

Remark: *S. siliquosa* is characterized by small fronds and a fusiform receptacle. The largest plant is reported to be 18.4 cm (Song et al., 1996), which is much smaller than the 10- to 90-cm *S. babingtonii* (Yoshida, 1998) or the 15- to 40-cm *S. compressa* (Smith, 1944). Although rare on the southern coast of Korea, the fusiform receptacles of *S. siliquosa* occur consistently throughout the year (Song et al., 1996). The type material is No 51-942 in AST, Qingdao; the type locality is Prope Mashan, Shantung Peninsula, China. Because of its luxuriant growth, Tseng (1983/1984) speculated that *S. siliquosa* speciated on the southern coast of Korea and was then further distributed to the Liaodong and Shantung districts of China. This species is found from the south and west coasts of Korea to the Shantung peninsula of China (Song et al., 1996).

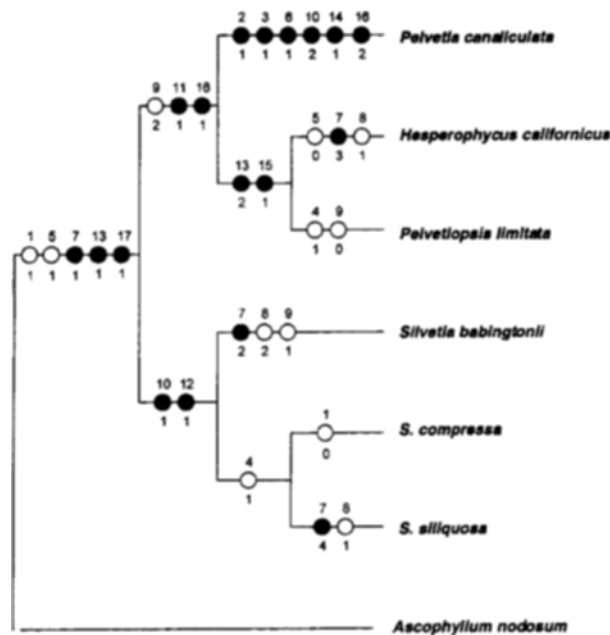


Figure 49. Maximum parsimonious tree constructed by cladistic analysis. Character code numbers are given as numbers above circles and character state changes are given as numbers below circles. Dark circle indicates single character change and white circle indicates parallelism or reversal.

Key to the Members of *Pelvetia* and *Silvetia*

- 1. Two eggs produced by transversal division of oogonium *P. canaliculata*
 - 1. Two eggs produced by longitudinal division of oogonium 2
 - 2. Axes compressed; receptacle subsided, rod-shaped..... *S. babingtonii*
 - 2. Axes subcylindrical; receptacle flat, club-form 3
 - 3. Thalli simply branched, small (<20 cm); receptacle <3 cm *S. siliquosa*
 - 3. Thalli bushy, tall (to 40 cm); receptacle <1.5 cm *S. compressa*

Cladogram and Phylogenetic Relationships

Cladistic analysis of the data matrix resulted in one of the most parsimonious trees, 30 steps long (Fig. 49), with a consistency index (CI) of 0.833, and a retention index (RI) of 0.643.

The taxa in the cladogram were divided into two clades: 1) the *Pelvetia*, consisting of *Pelvetia*, *Pelvetiopsis*, and *Hesperophycus*; and 2) the *Silvetia*, including its own species. The results from analysis of the morphological data corroborate the previous DNA-

based segregation of *Silvetia* from *Pelvetia* (Serrão et al., 1999). The divergence of the ITS (13.3%; Serrão et al., 1999) and the Rubisco spacer (6.1%; Lee et al., 1999) sequences between these two genera also is of a very large order of magnitude compared with those of other brown genera. Therefore, we can conclude that the developmental pattern of an egg, rather than its number, provides more information about the phylogeny of the fucacean algae that have one to two eggs. This is diagramed in Figure 50. We agree with the view of Serrão et al. (1999) that the number of eggs per oogonium has not followed a gradual reduction during the evolution of the Fucaceae. Therefore, the traditional taxonomy of the family Fucaceae, founded primarily on the number of eggs in the oogonium (Oltmanns, 1889; Yendo, 1907; Gardner, 1910; Powell, 1963; Yoshida, 1998), should be revised to be based instead on the egg developmental pattern.

The *Pelvetia* clade is supported by two synapomorphies: the absence of a longitudinally divided oogonium (character 11:1) and the basal position of the disintegrated nuclei (character 16:1). *Pelvetia* is considered monotypic because of its six autapomorphic characters: curved frond (character 2:1), grooved stem (character 3:1), loose arrangement of cortical cells (character 6:1), oogonium >170 μm (character 10:2), the presence of mesochite (character 14:1), and the surface position of the disintegrated nuclei (16:2). The hypothesis that *Pelvetia* shares a common ancestor with *Pelvetiopsis* and *Hesperophycus* is strongly supported by the published data of the ITS (Serrão et al., 1999) and the Rubisco spacer (Lee et al., 1999) sequences.

The monophyly of *Pelvetiopsis* and *Hesperophycus* is supported by two synapomorphies: one egg per oogonium (character 13:2) and the production of disintegrated nuclei after the first cytokinesis (character 15:1). We observed that both genera are very similar in their other morphology (figures not shown), as was reported by Gardner (1910, 1913, 1917). Because the monophyly is also strongly supported by the ITS sequence data (Serrão et al., 1999), the classification of *Pelvetiopsis* and *Hesperophycus* should be revised into a single genus. The Rubisco spacer sequences of the latter genus are being analyzed for this probable revision, and will be reported later.

The *Silvetia* clade, including *S. babingtonii*, *S. compressa*, and *S. siliquosa*, is supported by two synapomorphies: the absence of a transversally divided oogonium (character 12:1), and the mid-size (100 to 145 μm) of the oogonium (character 10:1). *S. babingtonii*

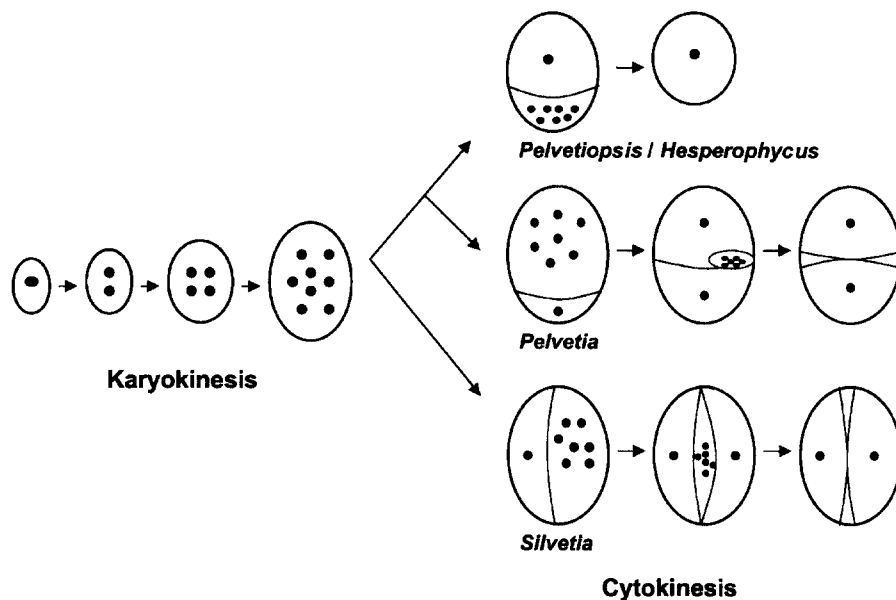


Figure 50. A diagram of egg development in oogonium of *Hesperophycus*, *Pelvetia*, *Pelvetiopsis*, and *Silvetia*.

tonii is characterized by a rod-shaped receptacle (character 7:2). However, the autapomorphy of *S. compressa* is its bushy habit; that of *S. siliquosa*, its fusiform receptacle (character 7:4). These species are very similar in their DNA sequences, exhibiting a divergence of 0.8 to 2% (Serrão et al., 1999) in the ITS and 0.9% in the Rubisco spacer region (Lee et al., 1999). Both divergences are of a very low order of magnitude compared with those of other brown taxa (see Lee et al., 1999).

Notably, these phyletic differences between *Pelvetia* and *Silvetia* are also reflected in their distribution patterns: the former occurring in the North Atlantic (Newton, 1931; Ardré, 1970), the latter in the North Pacific (Silva, 1996; Song et al., 1996; Yoshida, 1998). The occurrence of *Pelvetia* is difficult to explain herein because of its discontinuity from the related genera, i.e., *Pelvetiopsis* is found from British Columbia, Canada, to Oregon, USA (Scagel et al., 1986), while *Hesperophycus* occurs on the California coast in the Pacific (Silva, 1996).

It is biogeographically interesting that all three members of *Silvetia* are distributed in the North Pacific: *S. babingtonii* in northern Honshu via Hokkaido of Japan (Yoshida, 1998) to Vladivostok, Russia (Adrianov and Kussakin, 1998); *S. siliquosa* on the south and east coasts of Korea (Song et al., 1996) to Shantung Province of China (Tseng and Chang, 1953); and *S. compressa*, from California, USA to Baja California, Mexico (Silva, 1996). This particular distribution

of each species may have resulted from both ecological processes and/or historical events. Their habitats are the same, i.e., the upper intertidal zone (Yoshida and Silva, 1992; Silva, 1996; Song et al., 1996). All these species probably grow well in coastal regions during the seasons when cold currents meet warm, as has been discussed by Tseng and Chang (1953).

Sharing the same phyletic lineage and ecology, plus having low divergence of nucleotide sequences in all the *Silvetia* species suggests that they likely diverged in the recent history of evolution. Based on the occurrence of two species in the western Pacific versus only one in the eastern Pacific, we speculate that some brown silvetian ancestor populations from the North Pacific likely evolved to *S. babingtonii* in northern Japan, then moved to Korea and North America, where *S. compressa* and *S. siliquosa* diverged, respectively. Because the west coast of Korea is generally estimated to have risen above sea level >15,000 years ago (Chung, 1970), we hypothesize that this might be the period for phylogenetic divergence and speciation between *S. siliquosa* and *S. babingtonii*. This agrees with Shchapova (1946), who supposed that migration from the northern coast of Japan to the Pacific coast of North America must be post-glacial, i.e., during the Quaternary. Because few fossils remain that could be considered as ancestors of the present-day fucacean algae (Clayton, 1984), further study on additional samples is necessary to test these phylogenetic hypotheses.

ACKNOWLEDGEMENTS

The authors thank Prof. Paul C. Silva of the University of California, Berkeley, for loaning UC herbarium specimens; as well as Dr. T. Kitayama of TNS, Tsukuba, and Dr. K. Wu of AST, Qingdao, for their hospitality in accessing herbarium specimens. Dr. K. J. Ahn of Chungnam National University helped with our cladistic analysis. This work was facilitated by support from the Basic Science Program of KOSEF to SMB (No. 2000-1-20200-003-3).

Received February 6, 2001; accepted March 8, 2001.

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