A NEW SPECIES OF *DIAPHANA* FROM BATHYAL DEPTHS IN THE WEDDELL SEA, ANTARCTICA AND FIRST RECORD OF *DIAPHANA INFLATA* (STREBEL, 1908) IN THE HIGH ANTARCTIC (GASTROPODA: OPISTHOBRANCHIA)

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ABSTRACT

Diaphana haini n.sp. is described from Antarctica. With a depth range from about 400 to 2100 m, *D. haini* is the second Antarctic species of this genus to extend into the deep sea, the other being *D. inflata* (Strebel, 1908). Phylogenetic analysis has allowed *D. haini* to be incorporated within Schiøtte's (1998) cladogram for this genus and, thereby clarify its historical zoogeography. A record of *D. inflata* from the Weddell Sea extends its known distribution range. The recorded geographic distribution now ranges from South Georgia to the Antarctic continent, and the depth range is extended considerably, from 252–310 m to 1645 m.

INTRODUCTION

With 16 nominal species the Diaphanidae is the most species-rich shelled opisthobranch family in the Southern Ocean. It includes the genera *Diaphana* (five species), *Newnesia* (one species), and *Toledonia* (10 species). Schiøtte (1998) revised the genus *Diaphana*, and discussed its phylogeny and zoogeography. Before this revision eight nominal species of *Diaphana* were believed to occur, mostly allopatrically, in different regions of the Southern Ocean, except for South Georgia where four species were recorded by Strebel (1908): *D. paessleri* (Strebel, 1905), *D. anderssoni* (Strebel, 1908), *D. inflata* (Strebel, 1908), and *D. pfefferi* (Strebel, 1908). Schiøtte (1998, p. 90) synonymized the allopatric species *Diaphana extrema* Thiele, 1912 from the Gauss Station/Davis Sea, *D. kerguelensis* Thiele, 1912 from the Kerguelen Islands, *Retusa antarctica* Melvill & Standen, 1912 from South Orkney Islands, and *R. frigida* Hedley, 1916 from the Ross Sea, all with *Diaphana paessleri* Strebel, 1905, which was otherwise known from the Magellan region and Weddell Sea.

During the expeditions ANT VII/4 and ANT XV/3 with RV 'Polarstern' bathyal parts of the eastern Weddell Sea were sampled with an epibenthic sledge. Samples of *Diaphana* species were obtained from bathyal depths, and shell and soft parts studied. This material extended the known depth range and bathymetric distribution of *D. inflata*, and also included an undescribed species. Today five species of *Diaphana* are known from the Antarctic region, three of them are reported for the Weddell Sea.

MATERIAL AND METHODS

The present study is based on material obtained during cruises ANT VII/4 and ANT XV/3 of RV 'Polarstern' in the Eastern Weddell Sea (Figure1) in 1989 and 1998. The specimen in 1989 was collected by Agassiz trawl, while the specimens in 1998 were collected by the epinet of an epibenthic sledge (Brandt & Barthel 1995). The material from ANT VII/4 was processed as follows. A 50-l sediment subsample of the Agassiz trawl catch that passed through a 4-mm sieve was sieved on a 0.5-mm sieve. The remaining material was retained and fixed in 95% alcohol, and sorted under a stereomicroscope (Warén & Hain 1996, p. 278). The entire sediment sample from the epinet of the epibenthic sledge (0.5-mm net, 0.3-mm cod end) from ANT XV/3 was fixed in borax-buffered formalin for 48 h (turning jars upside down to facilitate formalin fixation), than transferred into 70% alcohol and sorted under a stereomicroscope.

To confirm the identification of *D. inflata*, syntype material from the Zoological Museum, Hamburg (ZMH) was examined.

The terminology used here is as explained by Schiøtte (1998). Drawings of animals were made with a stereomicroscope and drawing tube. Radula photographs were made on the scanning electron microscopes at Jeol JSM-840 (ZMUC, Copenhagen) and at LEO S360 (BAS, Cambridge). The addition of *Diaphana haini* to the cladogram, previously published by Schiøtte (1998), was performed by hand using Hennigian Argumentation (Lipscomb 1994). Six selected characters of *Diaphana* were used, with the following states and coding:

1. Shell shape: (0) *Toledonia*-like: slender, usually oval-cylindrical; (1) broad pentagonal, globose, or bottle-shaped.
2. Umbilicus: (0) without abapertural rim; (1) with abapertural rim (Figure 2 A-B).
3. Foot: (0) unforked; (1) forked.
4. Radula: (0) 5-seriate; (1) 3-seriate.
5. Median tooth: (0) triangular; (1) rectangular.
6. Prostate complex: (0) simple; (1) two long, separate tubes, a thick, and a thin.

SYSTEMATIC DESCRIPTIONS

Diaphanidae Odhner, 1914
Genus *Diaphana* Brown, 1827
***Diaphana haini* new species**
(Figures 3A, 4A,B, 5)

Doubtful *Diaphana paessleri*—Schiøtte 1998, pp. 91, 93, 136.

Type material. Holotype: specimen with soft parts, 2.2 mm from apex to base, with a broken outer lip, ZMH 2853, RV 'Polarstern' cruise ANT XV/3 Sta 48–272/EBS 13, Kapp Norvegia 71°28.78′S, 15°10.37′W–71°29.01′S, 15°10.28′W, 2077–1998 m, 26.02.1998, coarse sand with clay, and Foraminifera. Paratypes, all from the type locality, same lot as holotype two specimens,

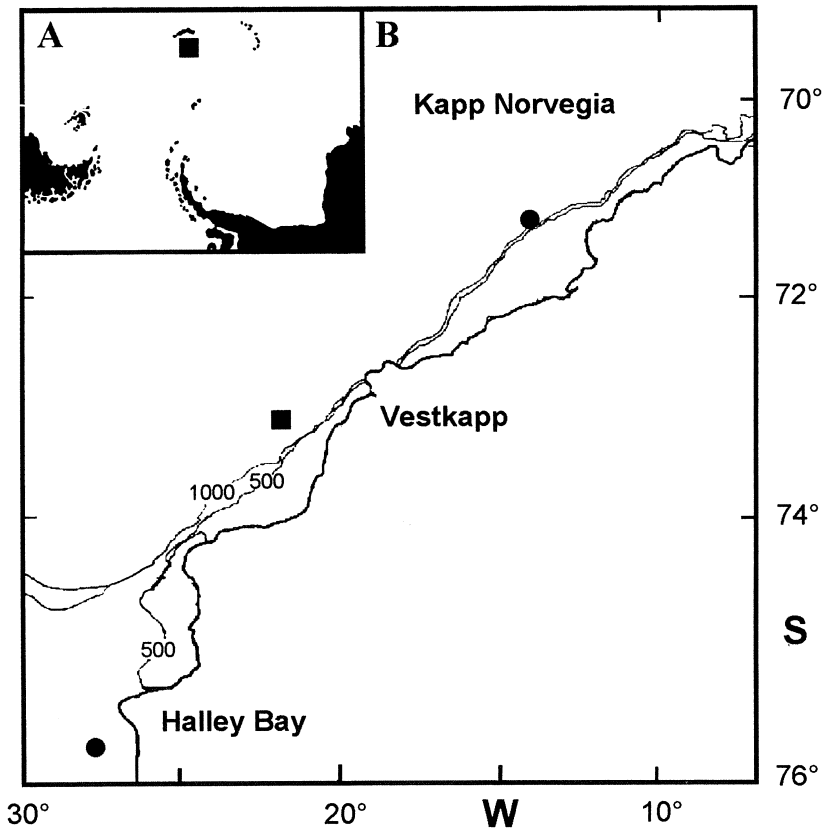

Figure 1. Location of collection sites (A) at South Georgia and (B) in the Weddell Sea. ●, *Diaphana haini* n. sp.; ■, *Diaphana inflata* (Strebel, 1908).

Figure 2. Morphology of umbilicus in *Diaphana*. Cross sections showing umbilicus (A) with a rim and (B) without a rim on the abapertural side.

one of them juvenile, ZMH 2854, 1 specimen, dissected + SEM-mounted radula, ZMH 2855, two specimens, juveniles, ZMUC GAS-425, one specimen, dissected + SEM-mounted radula, ZMUC GAS-426.

Type locality. Kapp Norvegia, Weddell Sea, 71°28.78′S, 15°10.37′W–71°29.01′S, 15°10.28′W, 2077–1998 m.

Material examined. RV 'Polarstern' cruise ANT VII/4 Sta 235/AGT 7, 75°08.9′S, 27°33.2′W–75°08.1′S, 27°49.5′W, 404–399 m, 31.01.1989, small stones (one specimen, ZMH); RV 'Polarstern' cruise ANT XV/3 Sta 48–272/EBS 13, Kapp Norvegia 71°28.78′S, 15°10.37′W–71 °29.01′S, 15°10.28′W, 2077–1998 m, 26.02.1998, coarse sand with clay, and Foraminifera (seven specimens, ZMH, ZMUC).

Diagnosis. Diaphana with a protoconch of less than one whorl and a strongly asymmetrical radula.

Description. Shell, general: cylindrical-pentagonal, widest about 2/5 of its height from the base, smooth except for fine growth lines. Transparent to white. Height to at least 2.2 mm. Height/width about 1.6 (inferred from damaged shells). About 1.6 teleoconch whorl on a 2-mm high specimen.

Spire: acuminate with protoconch projecting. Shoulders slightly angled, separated from preceding whorl by an unrimmed groove.

Aperture: 80–85 % of shell height. Widest around half of height from base. Outer lip hyperbolically rounded around lower 1/3 of shell, apparently almost straight above that until it reaches top of aperture, where it forms a small arch (inferred from damaged specimens). Inner lip running in shallow, even curve from top of aperture to about halfway to base, where it joins columella at an angle of 155–160°, continuing in almost straight line to base.

Umbilicus: open, 9–11% of shell width, with no abapertural rim.

Protoconch: rounded lecithotrophic type, smooth, about 0.5 mm wide with 0.7–0.8 whorls.

Angle between teleoconch and protoconch axis about 140°.

External anatomy: foot forked posteriorly. Eyes not visible.

Radula: formula 1.1.1, asymmetrical with left laterals only about 60% size of right ones (Figure 4A,B).

Pharynx: strongly displaced to the left in the body with the oesophagus leaving from the upper left side (Figure 5).

Prostate gland: A single tube situated to the right of the pharynx, the distal part bending toward the left side of the animal.

Distribution. Known only from the Weddell Sea from about 400 to about 2100 m.

Comparison with other species. Most similar to *Diaphana paessleri* from which it is, however, easily separated by its forked foot and the lack of an abapertural rim on the umbilicus.

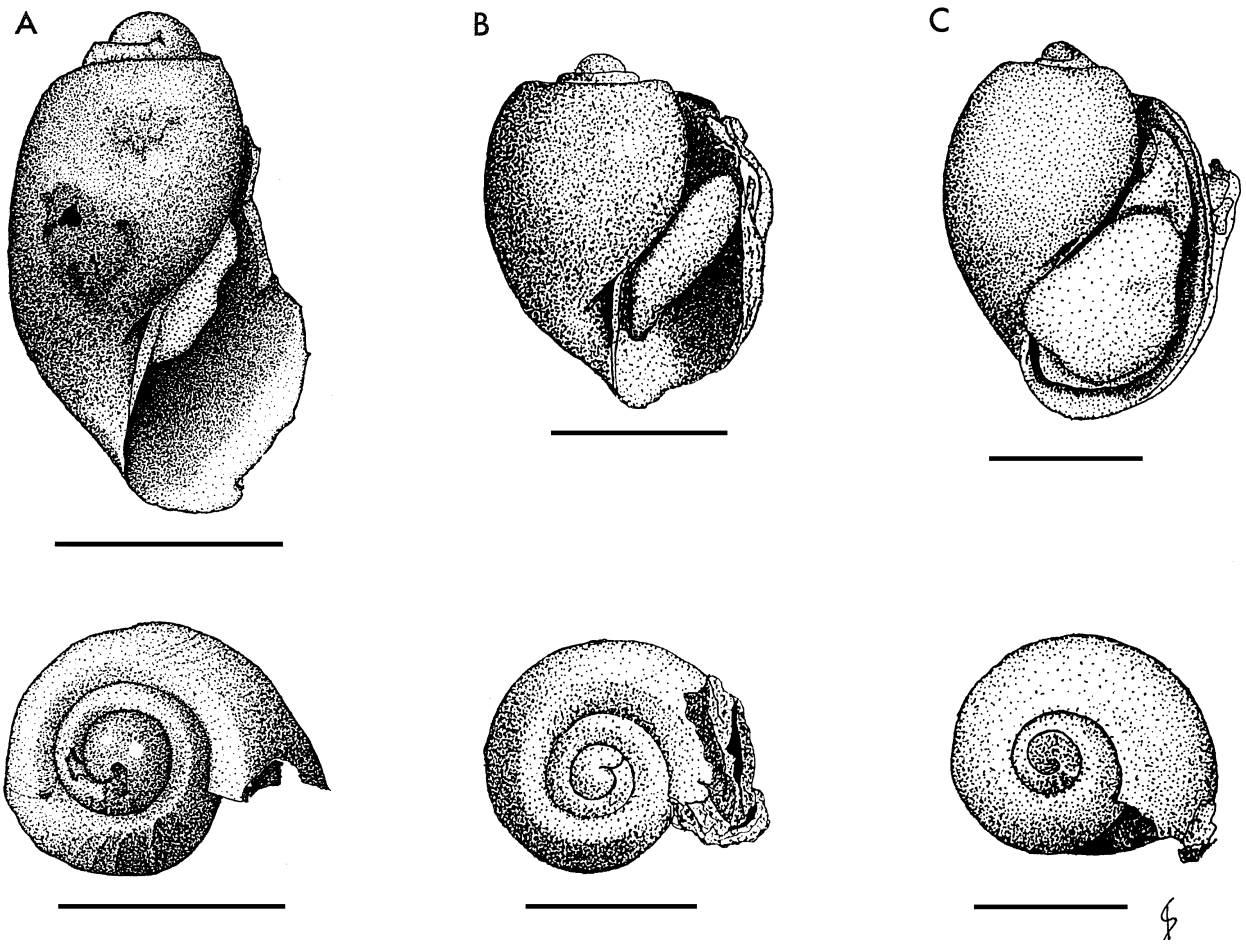

Figure 3. Ventral and apical views of (A) holotype of *Diaphana haini* n. sp., RV 'Polarstern' cruise ANT XV/3, Sta 48–272/EBS 13, Weddell Sea, 2077–1998 m (ZMH 2853). (B) *Diaphana inflata* (Strebel), RV 'Polarstern' cruise ANT XV/3, Sta 48–089/EBS 1, Weddell Sea, 1645–1639 m (ZMH). (C) Syntype of *Diaphana inflata* (Strebel), Cumberland Bay, South Georgia, 252–310 m (ZMH 18.5/383.2). All scale bars = 1.0 mm.

Remarks. The general shell shape in *D. haini* is much like that of *D. paessleri*, the most common *Diaphana* species in the Antarctic area. This *Toledonia*-like shell was regarded as plesiomorphic by Schiøtte (1998). The forked foot and the asymmetric radula, however, would be apomorphic character states.

Etymology. Diaphana haini is named after Stefan Hain who in 1989 collected the very first specimen of that species known to us.

***Diaphana inflata* (Strebel, 1908)**
(Figure 3B,C)

Retusa inflata Strebel, 1908: 10, pl. 2: 18a–d.

Diaphana inflata: Thiele, 1912, p. 266; Powell, 1951, p. 60; Castellanos, Landoni & Dadon, 1993, pp. 10–11; Schiøtte, 1998, pp. 93–95, 134–135, figure 11L–N.

Type material. Two syntypes, specimen, 2.5 mm high, and broken shell, Swedish South Polar Expedition 1901–1903 st. 34, 54°11′S, 36°18′W, Cumberland Bay, South Georgia, 252–310 m, 5 Jun 1902, ZMH 18.5/383.2 & SMNH Type coll. 1011, respectively.

Material examined. One syntype, Swedish South Polar expedition 1901–1903 st. 34, 54°11′S, 36°18′W, Cumberland Bay, South Georgia, 252–310 m, 05.06.1902, ZMH 18.5/383.2; one specimen, 2.5 mm high, RV 'Polarstern' cruise ANT XV/3 Sta 48–089/EBS 1, southwest of Vestkapp 73°27.26′S, 22°45.67′W–73°27.27′S, 22° 46.52′W, 1645–1639 m, 04.02.1998 (ZMH).

Type locality. Cumberland Bay, South Georgia, 54°11′S, 36°18′W, 252–310 m.

Diagnosis. Slightly amended from Schiøtte 1998, p. 93. Shell ovate-globose with a height/width relationship of 1.2–1.5, foot unforked, symmetrical radula with formula 1.1.1.

Redescription. As given by Schiøtte (1998) with the following emendations:

(1) shell height/width relationship 1.2 to 1.5;
(2) shoulders rounded to moderately angled;
(3) umbilicus open, 1–12% of shell width, without an abapertural rim.

Distribution. Known from South Georgia (type locality) and Weddell Sea (this study). Known depth range 252–1645 m (Strebel 1908; Schiøtte 1998; this study).

Remarks. The new specimen of *Diaphana inflata* differs from the type material and other material seen by Schiøtte (1998) in a minor degree on three points:

(1) it is more globose;
(2) the shoulders are moderately angular;
(3) the umbilicus is wider, which makes it easier to see its shape in the stereomicroscope.

With respect to the latter point a re-examination of the ZMH syntype has confirmed that it also lacks the abapertural rim as the new specimen certainly does.

The differences, in our opinion, are not large enough to warrant description of the new specimen as a separate species. Such variation is expected, considering the lecithotrophic development mode associated with the species on basis of the protoconch. We have refrained from a comparison of the internal anatomy because the material at hand is so extremely limited.

The depth range for the species has with the newest find been extended considerably. Schiøtte (1998) believed the upper limit of the depth range at South Georgia to be quite shallow. This was partly based on the fact that two of the specimens recently found deposited in the Swedish Museum of

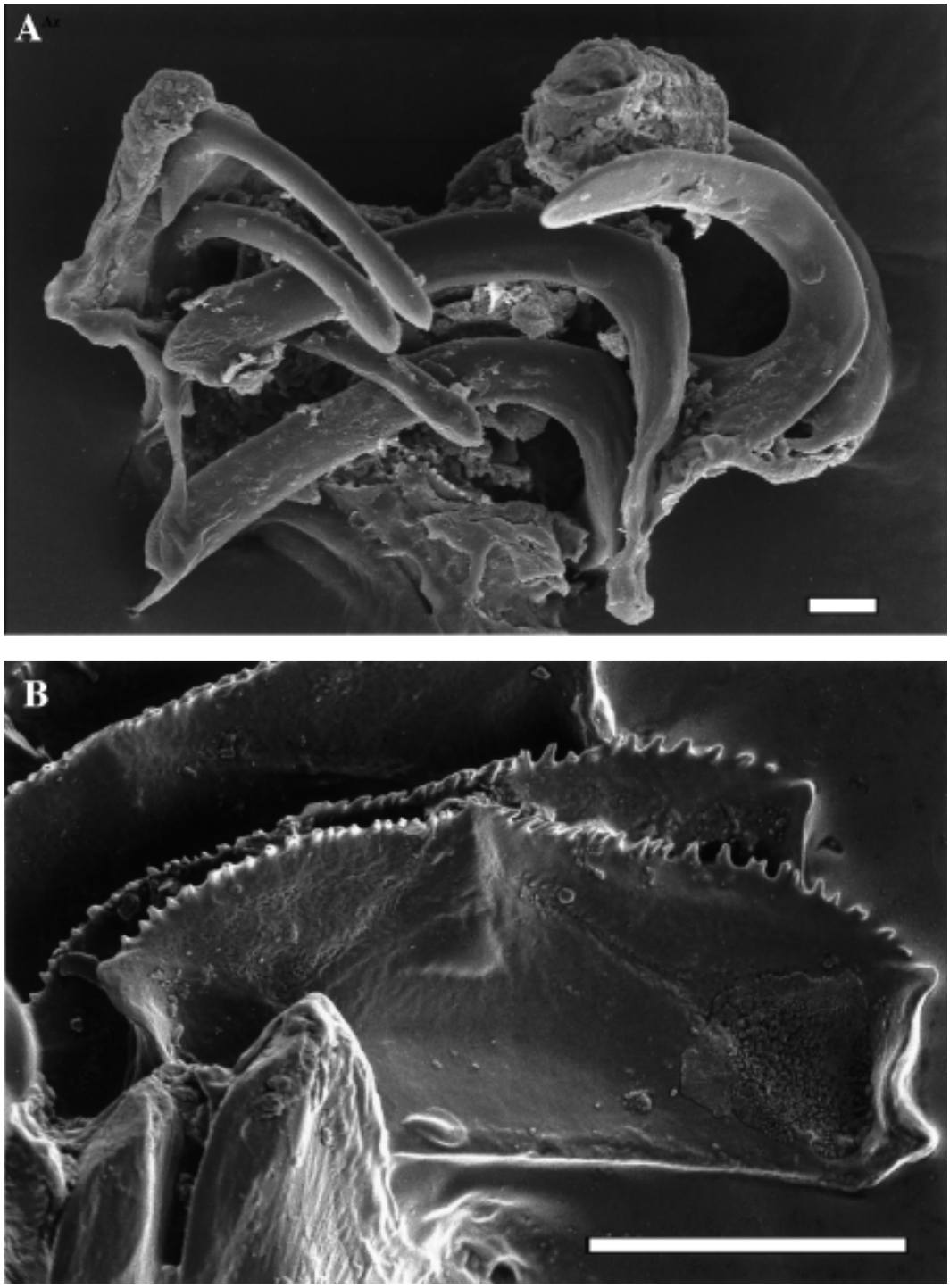

Figure 4. Scanning electron micrographs of the radulae of (A) paratype of *Diaphana haini* n.sp., with some rows of the radula showing the asymmetry (ZMUC GAS-426); scale bar = 10 μm. (B) Paratype of *Diaphana haini* n. sp., rachidian teeth showing asymmetry (ZMH 2854); scale bar = 20 μm.

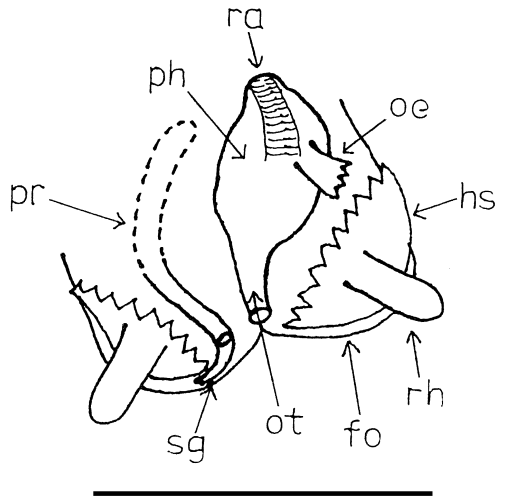

Figure 5. *Diaphana haini* n.sp., anterior part of body opened with penis-prostate complex and pharynx visible. Based on paratype ZMUC GAS-426, originally 2–2.5 mm shell length. Abbreviations: fo, foot; hs, head shield; oe, oesophagus; ot, oral tube; ph, pharynx; pr, prostate; ra, radula; rh, rhinophore; sg, seminal groove; scale bar = 1.0 mm.

Natural History had been taken from hapteria of *Macrocystis* algae. The only collecting depth hitherto known with certainty, however, has been 252–310 m. It is likely that the species, also in subantarctic areas, lives generally deeper than *Diaphana paessleri*. For both species, however, the water masses they inhabit in the High Antarctic have characteristics quite different from those of the Subantarctic or South American waters, as shown by Schiøtte (1998, p. 93) for *Diaphana paessleri*. Like *D. paessleri*, *D. inflata* probably forms separate populations, but in a deep-sea species, as *D. inflata* must now be considered, the populations are probably separated more by differences in water masses (temperature, salinity) than by geographical features.

The lack of an abapertural rim on the umbilicus moves *D. inflata* out of Schiøtte's (1998, p. 135) monophyletic species group 2 (Figure 6A), but this change has no implications for historical zoogeography.

DISCUSSION

Anatomy

Schiøtte (1998, p. 124), when redescribing *Diaphana lactea* (Jeffreys, 1877), noted a displacement of the pharynx to the left as in *D. haini*. The examinations of radulae made by the second author in preparation for his revision (Schiøtte, 1998) included many specimens of every species wherever sufficient material was at hand. This was the case with for examples *Diaphana minuta* Brown, 1827, and *D. lactea*, two species that showed very different degrees of asymmetry in the radula. The examinations proved that the degree of asymmetry is very constant within a given species. It appears that the asymmetric radula found in some *Diaphana* species, such as *D. lactea*, has developed in response to an enlargement of the prostate, which has displaced the pharynx to the left side of the animal. It is probable that this development in the radula can be reversed or that it has happened several times, two possible explanations why many species in the *Diaphana minuta* species group, otherwise showing many apomorphic character states, have more or less symmetrical radulae. In these species, an alternative position for the large prostate has been found on top of the pharynx.

Differences in shell morphology over geographic distance

Investigating several *Diaphana* species with a wide geographical distribution combined with intra-capsular development, Schiøtte (1998) noted that such species tended to form local populations that were within themselves rather uniform in shell characters, such as the width of the umbilicus. Differences between geographically distant populations could be considerably larger. In the opinion of the authors such differences do not in themselves warrant description of different species.

Geographic distribution and phylogeny

As a result of this study, the genus *Diaphana* in the Southern Hemisphere now includes seven species: *D. tasmanica* of a very ancient type, *D. inflata*, *D. paessleri*, and *D. pfefferi* belonging to later developed groups, *D. haini*, which is a true deep-sea species with even more apomorphic traits, and thus can be said to form a linkage with the deep Central and North Atlantic *D. lactea*, *D. brazieri* belonging to the most derived group, and *D. anderssoni* which can not be assigned to any group (Table 1, Figure 6). In *D. anderssoni* the soft parts are unknown so that the assignment of the species is not possible. Schiøtte (1998, p. 125) noted that it probably belongs to the *Diaphana paessleri* species group.

The discovery of the Antarctic deep-sea species *D. haini* enabled us to rerun Schiøtte's (1998) phylogenetic analysis. In the character matrix *Diaphana haini* scores 0,0,1,1,1,0 (Table 2). This is the same score as *Diaphana lactea* and the new species therefore belongs in Schiøtte's paraphyletic species group 3. This fits well into the zoogeographic history of the genus as suggested by Schiøtte (1998, p. 136) according to which the majority of the species, those that had lost their marginal teeth, originated in the Antarctic and spread north through the Atlantic ocean after it opened.

Diaphana tasmanica has been found only in southern Australia and the southern Stewart Island. The oldest type of *Diaphana* is thus today absent from the High Antarctic and Southern Ocean. *D. brazieri* is recorded from Southern Australia and New Zealand. The absence of the most derived group in the Southern Ocean might be caused by the circumpolar current that developed 23.5–17 Ma (Barker & Burrell

Table 1. Distribution of *Diaphana* species in the Southern Hemisphere.

Species	Distribution	Depth range (m)
Diaphana anderssoni (Strebel, 1908)	South Georgia	22
Diaphana brazieri Angas, 1877	Stewart Island, South, and North Island; Victoria, Tasman Sea, and New South Wales; Japan	2–610
Diaphana haini n. sp.	Weddell Sea	399–2077
Diaphana inflata (Strebel, 1908)	South Georgia and Weddell Sea	252–1645
Diaphana paessleri (Strebel, 1905)	Tierra del Fuego and Falkland Islands; South Georgia, South Orkney Islands, Adelie Land, Kaiser Wilhelm II Land, Ross Sea and Weddell Sea	8–580
Diaphana pfefferi (Strebel, 1908)	South Georgia	12–15
Diaphana tasmanica (Beddome, 1883)	Stewart Island; Victoria and Tasmania	1–13

1977), and seems to have acted as a migration barrier for shallow-water and shelf species since then.

Within the Southern Ocean, *D. paessleri* seems by far to be the most distributionally successful species, having spread apparently all around the High Antarctic, to several Subantarctic islands, and even to southern South America. *D. pfefferi*, known only from South Georgia, could have separated from *D. paessleri* during periods of isolation. The same periods of isolation might have separated *D. anderssoni*, which is also endemic to South Georgia, and resembles *D. pfefferi* in shell characteristics.

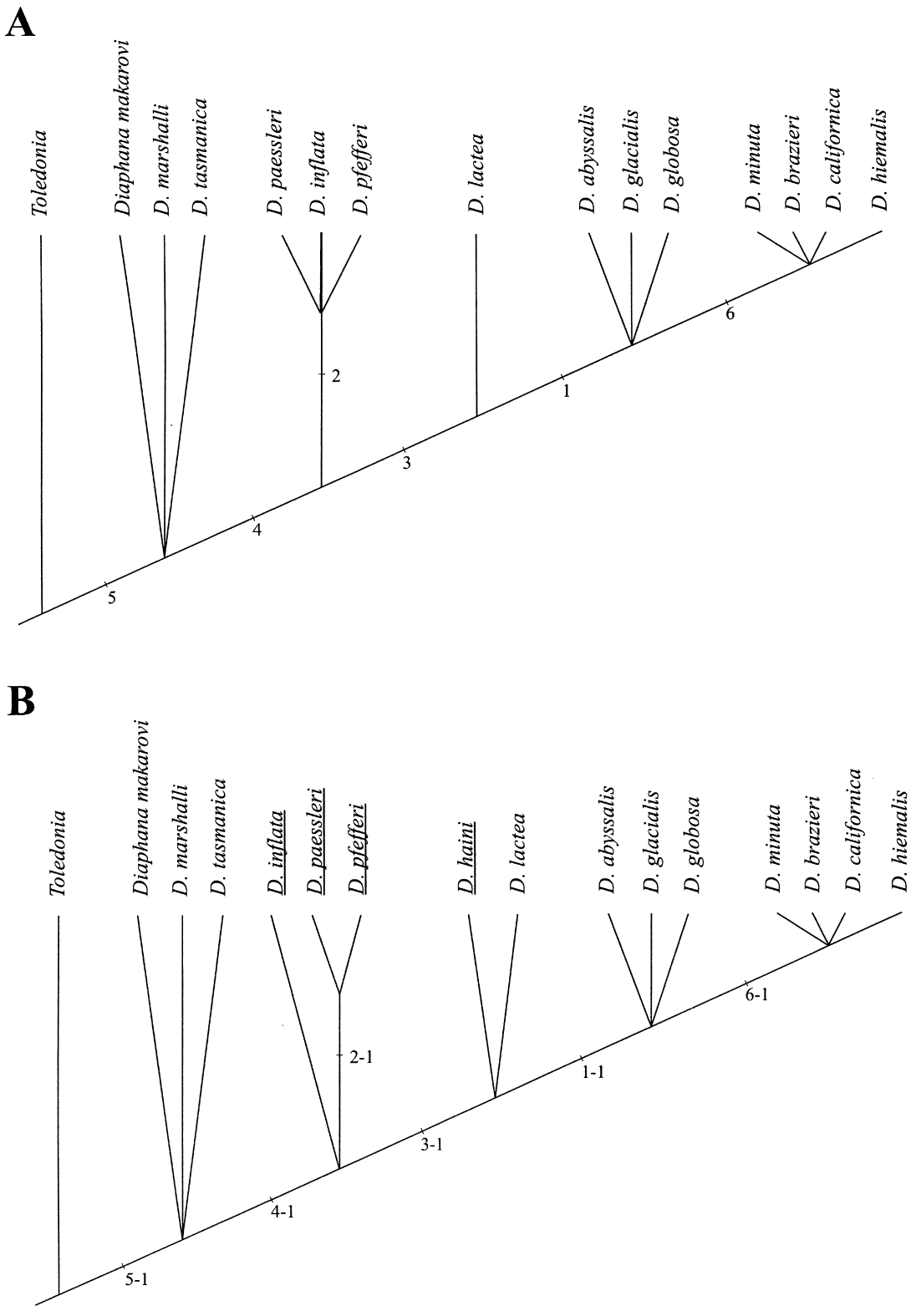

Figure 6. Cladogram for selected species of *Diaphana*. (A) Schiøtte 1998. (B) This study. Antarctic species are underlined. Character numbers are represented on the left of the bar, character states on the right.

Table 2. Character matrix for cladistic analysis of *Diaphana*.

Character number	1	2	3	4	5	6
Toledonia	0	0	0	*	0	0
Diaphana markarovi	0	0	0	0	1	0
Diaphana marshalli	0	0	0	0	1	?0
Diaphana tasmanica	0	0	0	0	1	?0
Diaphana paessleri	0	1	0	1	1	0
Diaphana pfefferi	0	1	0	1	1	?0
Diaphana inflata	0	0	0	1	1	?0
Diaphana minuta	1	0	1	1	1	1
Diaphana californica	1	0	1	1	1	1
Diaphana abyssalis	1	0	1	1	1	?0
Diaphana glacialis	1	0	1	1	1	0
Diaphana hiemalis	1	0	1	1	1	1
Diaphana lactea	0	0	1	1	1	0
***Diaphana haini* n. sp.**	**0**	**0**	**1**	**1**	**1**	**0**
Diaphana globosa	1	0	1	1	1	0
Diaphana brazieri	1	0	1	?1	?1	?1

*Both configurations found within the genus. ?Character states that have been indicated, but cannot be stated with certainty.

D. inflata, which can now be considered primarily bathyal, and known from South Georgia and the Weddell Sea could ultimately prove to be more widespread than formerly thought. Future collecting activities will be needed to verify or refute that interpretation. This is true also for *D. haini*, found so far only in the Weddell Sea.

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