NOTOFICULA THIELE, A NEOTENOUS GENUS OF ERATOID GASTROPOD FROM ANTARCTICA

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ABSTRACT. A new species of *Notoficula* is described from Signy Island, South Orkney Islands, Antarctica. This genus was originally placed within the Buccinacea but the anatomy and radula show a clear relationship to the Lamellariacea. *Notoficula* is compared with other Lamellariacean groups and is shown to be most closely related to the Eratoidae. It is postulated that *Notoficula* arose by a neotenous event from eratoid stock.

Six specimens of a bullate prosobranch were collected by Gordon Picken from Signy Island, South Orkney Islands, at 40–80 m depth. These specimens are similar to *Notoficula bouveti* Thiele 1912, but the radula is not rachiglossan, as one would expect from Thiele's decision to place *Notoficula* in the Buccinacea. Instead the radular structure is taenioglossan and consistent with that of the Lamellariacea. The shell, however, shows none of the characters typical of the Eratoidae or Lamellariidae. In view of Schilder's hypothesis (1936) that the early radiation of the Eratoidae occurred in sub-Antarctic waters, *Notoficula* may have some phylogenetic significance.

Notoficula signyensis n. sp.

Signyensis: L. Native of Signy, referring to type locality.

The shell (Fig. 1a, b) is wholly external, the foot and mantle capable of withdrawing within the apertural edge (Fig. 2a). The shell is thin, brittle, opaque, with a chalky white appearance; of 3–3½ whorls reaching maximum dimensions of 11 mm (length) by 9 mm (breadth). Body whorl large, aperture longer than wide but slightly auriculate, sharp edged and nowhere inturned, columellar lip visible anteriorly, slightly broadened and shining. Spire low but distinct. Outline, in total, somewhat bullate, resembling that of the juveniles of *Trivia* and *Erato*. Outer layer of shell eroded except on the body whorl where there are irregular longitudinal ridges crossed by a fine spiral sculpture of raised lines. The orientation of these lines varies between the longitudinal ridges giving an overall pattern not unlike that of architectural herring-bone work. A periostracum was not seen. The mantle edge is expanded and in retracted specimens projects beyond the sole of the foot (Fig. 2b). It might be expected that the mantle is capable of extending over the shell but this ability is usually associated with a smooth shell which *Notoficula* does not possess. The mantle appears to be smooth. A short siphon is present (Fig. 2b). The organs of the mantle cavity are typically lamellariacean (Bergh, 1886; Schilder, 1936; Fretter and Graham, 1962). The osphradium is concentric and bifid with 20–30 lamellae (Fig. 2c). The hypobranchial gland is extensive. The sexes are separate and the male has a large tapering penis. The snout and tentacles appear stubby. The jaws are simple and divided. The radula (Fig. 1c) is taenioglossate, formula 2–1–1–1–2, with 45–55 rows. The cusping and dentition are similar to other Lamellariaceans. The media is squarish with five to eight denticles on either side of the prominent central

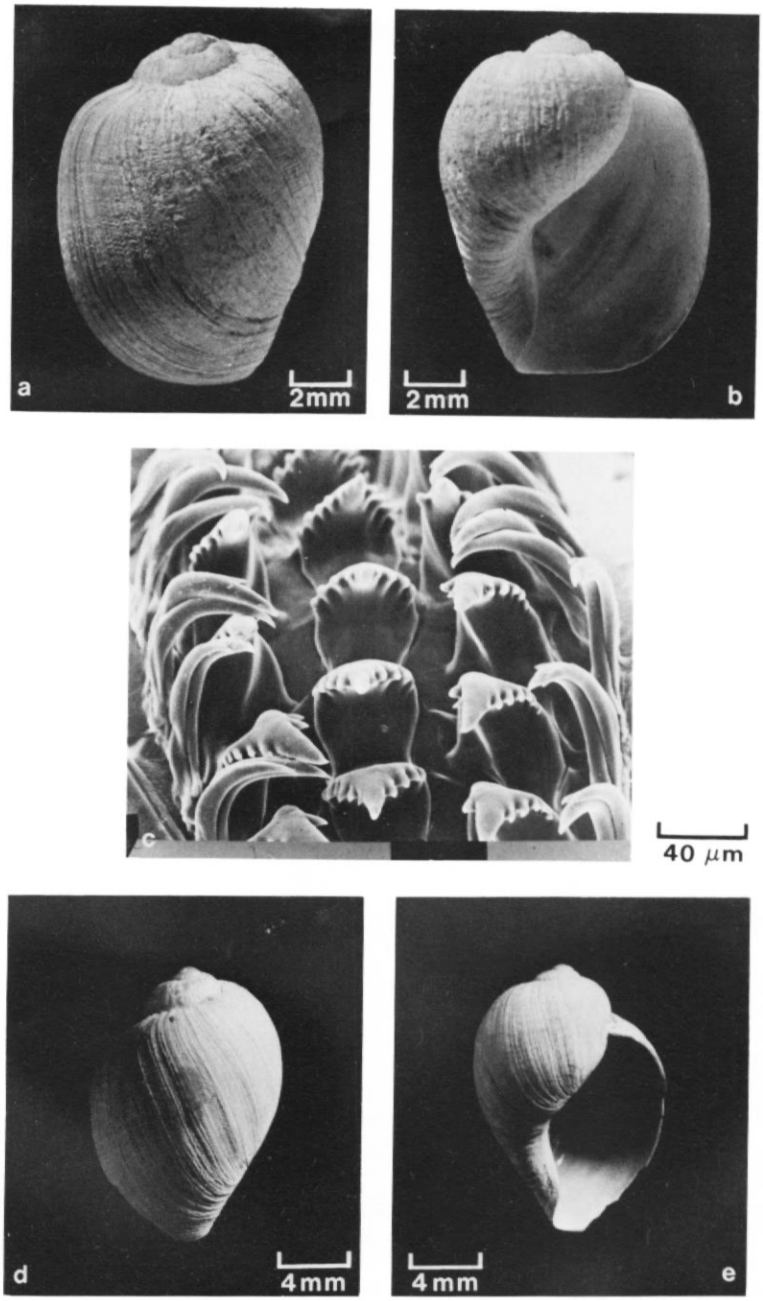

Fig. 1a, b. *Notoficula signyensis* n. sp. Holotype NMWZ.1979.002.3. Abapertural and apertural views.
c. *Notoficula signyensis* n. sp. Radula.
d, e. *Notoficula bouveti* Thiele, 1912. Holotype Humboldt Museum for Naturkunde, Berlin.

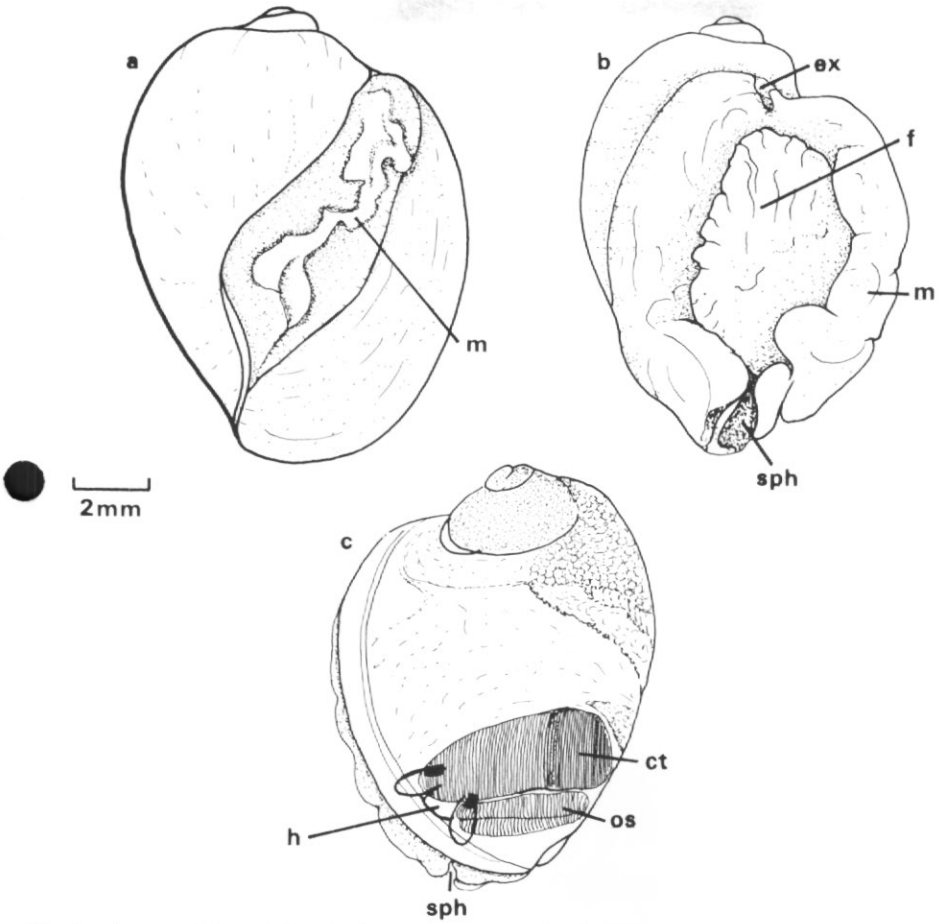

Fig. 2a. Apertural view of *Notoficula signyensis* n. sp. showing mantle, only partly retracted into shell.
b. Apertural view of *Notoficula signyensis* n. sp. with shell removed showing position of ventilation apertures and the expanded mantle.
c. Dorsal view of *Notoficula signyensis* n. sp. with shell removed showing the position of the ctenidium and osphradium relative to the siphonal aperture. The position of the head and tentacles is shown in outline only.

Abbreviations:

ct.	ctenidium
ex.	exhalant aperture
f.	foot
h.	head
m.	mantle
os.	osphradium
sph.	siphon

denticle, the admedian is slightly larger and bears two denticles on the inner edge. The first marginal bears a single denticle and the second marginal only occasionally bears a similar denticle.

Type locality: Borge Bay, Signy Island, South Orkney Islands. 60° 41′ S, 45° 36′ W, 40–80 m depth.

Specimens were collected by Agassiz trawl in an area of Borge Bay approximately 2 km north-east of the British Antarctic Survey station. The bottom here is gently sloping and consists of patchily distributed small stones and cobbles set in muddy sand. Principal members of the epifauna in this area are sponges *Rossella* sp., anemones, alcyonarians *Primnoella* sp., bryozoans, holothurians *Cucumariae* sp., the isopod *Glyptonotus antarcticus*, the pycnogonid *Dodecalopoda* sp. and large starfish *Labidiaster* sp.

Type material: National Museum of Wales, Cardiff. Holotype: NMWZ:1979.002.3. Paratypes: NMW.1979.002.4/5/6/7.

Specific affinities: The shells of *N. bouveti* (Fig. 1d, e) and *N. signyensis* are very similar especially in sculptural details. *N. bouveti* is slightly larger, reaching 15 mm, has a narrower aperture and the spire is relatively more extended. Unfortunately *N. bouveti* is known only from the holotype and the significance of the above differences is subjective. Faunistic similarities between Bouvetøya and the South Orkney Islands are inconclusive on the present data, although there are a number of species common to both regions (Powell, 1951). In both buccinids and muricids, Oliver (pers. obs.) has noted species pairs occurring on the South Orkney Islands and South Georgia. These pairs probably represent recent divergences caused by geographical isolation and the subsequent lack of genetic mixing. Because most Antarctic prosobranchs reproduce without a pelagic larval stage (Picken, 1979), dispersal and exchange will be further restricted and the process of divergence enhanced. Warén (pers. comm.) has observed similar population divergences in Arctic prosobranchs. The resulting small morphological differences can be interpreted as population differences or specific differences, but without genetic or interbreeding experiments any decision remains subjective. However, because of the geographical separation of Signy Island and Bouvetøya, and general lack of long-lived dispersive stages in Antarctic prosobranchs, it is felt that small morphological differences may well represent specific differences.

Systematic position of Notoficula

Notoficula was originally allied with *Cominella* (Thiele, 1912) and later with *Chlanidota* (Thiele, 1929), both genera belonging to the Buccinacea. The radula and anatomy of *N. signyensis* are in all respects lamellariacean and the shells clearly link that species with the genotype *N. bouveti*. Powell (1951) described another species of *Notoficula, N. problematica*, from between the Falkland Islands and Argentina. Since Powell (1951) stated that this species has a radula similar to that of the buccinid genera *Pareuthria* and *Tromina*, it cannot remain in *Notoficula*.

Systematic relationships of Notoficula within the Lamellariacea

The relationship of *Notoficula* within the Lamellariacea are not clear because the form of what is presumed to be an echinospira larval stage is not known. Without this information relationships must be inferred from the anatomy and morphology of the adult alone.

Schilder (1936) was the first to present a comprehensive analysis of the phylogeny of the Cypreacea, in which he included the Lamellariacea. Despite the considerable amount of relevant data Schilder's conclusions are devalued by his use of *Zittelia*, a Jurassic form, as the model ancestor, a view now considered unwarranted because it has little foundation (Dr Noel Morris, pers. comm.). Fretter and Graham (1962) briefly considered the echinospira group as a whole, i.e. the Calyptracea and

Lamellariacea. Within the Lamellariacea they indicated that there are two major groups, the Lamellariidae and Eratoidae, the former tending towards internalization of the shell (although in *Marsenina* the shell remains partially exposed (Bergh, 1886)) and the latter towards a cowrie form. The separating characters cited were the larval form, shell aperture size and presence or absence of the periostracum. Cernohorsky (1971) gave some more characters of the Lamellariidae, including a sharp labial lip, smooth columella, united jaws and no distinct siphon. In *Onchidiopsis* however the jaws are divided (Bergh, 1853) but in all other respects this genus is lamellariid with a reduced wholly internal shell. Cernohorsky (1971), like Schilder (1936), prefers to ally the Eratoidae with the Cypreacea, presumably on the grounds of shell characters alone. *Notoficula* has a combination of the characters of both the Eratoidae and Lamellariidae. Of the former, it possesses the external shell, siphon and divided jaws and of the latter, the unenamelled shell, sharp labial lip and smooth columella. On the data presented it would seem that there is no clear affinity with the Lamellariidae rather than with the Eratoidae. However, if one has regard to the characters of the juvenile shell in the Eratoidae, i.e. the bullate shape, sharp labial lip and smooth columella (personal observation on *Trivia monacha* and *Erato voluta*), the situation is considerably altered. The only remaining characters not shared by the Lamellariidae and Eratoidae are the shell shape, siphonal condition and jaw condition. *Notoficula* shares all three of these with the Eratoidae. The radiation of the Eratoidae is apparently dominated by the changing of the shell form, from the open apertured, spired type, represented by *Archierato* through the type with a narrow aperture (*Erato*) to the cowrie-like Triviinae. The narrowing of the aperture has led to a change in the relationship of the mantle cavity to the shell aperture and along with it, the direction of the ventilation current (Fretter, pers. comm.). The position of the pallial siphon in *Notoficula* (Fig. 2c) conforms with that of *Trivia* and *Erato* and further enhances the conclusion that *Notoficula* is close to the Eratoidae. The radula is of a generalized form similar to those of both the Eratoidae (*Erato*; pers. obs.) and Lamellariidae (*Marseniopsis*; Bergh, 1886). Of all the characters considered, the orientation of the ventilation current is perhaps the most significant. *Notoficula* shares no acquired characteristics with the Lamellariidae but the direction of the ventilation current is an acquired characteristic of Eratoidae. Disregarding the paedomorphic external appearance of *Notoficula* this character alone clearly places *Notoficula* in the Eratoidae.

Notoficula: A neotenous eratoid?

In most regions of the world both Eratoidae and Lamellariidae are represented and this is true for most circumantarctic regions such as New Zealand and South Australia. Eratoids are apparently absent from the Magellan Province (Strebel, 1906) and until now absent from the Antarctic proper. By contrast, the Lamellariidae are represented in the present Antarctic fauna by three genera and ten species. Only *Notoficula* represents the Eratoidae in Antarctica. This situation could have arisen either geographically by separated centres of radiation of the Lamellariidae and Eratoidae or by some ecological restriction acting on the Eratoidae.

In all but the cold water regions of the world both the Lamellariidae and Eratoidae co-exist. If geographical separation were the cause of the discontinuous distribution one may expect to find at least a few species of Eratoidae invading the Antarctic. This is not observed except for the appearance of the paedomorphic genus *Notoficula*. *Notoficula* cannot be regarded as an independent line arising from an ancestral lamellariacean stock as it possesses the acquired anatomical characters of

the eratoids. The paedomorphic appearance of *Notoficula* can be explained as a retardation of adult shell form, i.e. a neotenous event (Gould, 1977). All eratoids have a tendency to develop heavy enamelled shells with narrow apertures. Vermeij (1978) reviews the effect of low temperature on shell form and restates the observation that thick, tall-spired or narrow-apertured shells are almost unknown from cold water environments and that this is a result of the increased energy required to metabolize calcium in cold water environments. This phenomenon can explain the dominance of the thin internally shelled Lamellariidae in the Antarctic. However, a neotenous event in the Eratoid line giving rise to a thin-shelled form would have considerable adaptive advantage. It is probable that both the Lamellariidae and Eratoidae had a continuous distribution throughout Gondwanaland. After the separation and subsequent cooling of the Antarctic province the Eratoidae were gradually excluded allowing the Lamellariidae to radiate and subsequently dominate in their niche of carnivores feeding predominantly on tunicates. The eratoid line is now represented only by the single neotenous event which gave rise to the thin-shelled, open-apertured genus *Notoficula*.

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