

DYOLIA N. GEN. FROM THE EUROPEAN MIOCENE- PLEISTOCENE (PROTOBRANCHIA: NUCULANIDAE)

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Abstract The nuculanids *Leda mendax* Meneghini in Appellius, 1871, from the Plio-Pleistocene of Italy and *Leda reussi* Hörnes, 1865, from the Middle Miocene of Austria, are almost equilateral in shape, not rostrate, with a very shallow pallial sinus and a posterior radial swelling terminating in a rounded postero-ventral projection. Such a combination of shell characters is known only in these two species. For them, *Dyolia* n. gen. is proposed, with *Leda mendax* as type species. Relations with other nuculanids and the origin of *Dyolia* n. gen. are unclear. Taphonomic and morphofunctional observations on *Dyolia mendax* and *D. reussi* point to a specialization for muddy, soupy bottoms of the inner shelf, as shallow burrowers.

Key words *Protobranchia*, *Nuculanidae*, new genus, Neogene, Pleistocene, deposit feeding.

INTRODUCTION

Leda mendax Meneghini in Appellius, 1871, from the Mediterranean Plio-Pleistocene (Italy) and *Leda reussi* Hörnes, 1865, from the Middle Miocene of Central Paratethys (Lower Austria), are two unusual protobranch bivalves. The specific attribute *mendax*, i.e. false, lying, was most probably suggested by the odd shape of this species, notably different from that of a typical *Leda* (a genus name widely used in the early literature). The present paper focuses on the shell characters of these two species and their systematic position in a new genus. The relations of the new genus with other protobranchs are discussed and some palaeoecological considerations are made.

MATERIAL AND METHODS

No type material of *Leda mendax* is known. This species was studied from 14 valves from the Early Pleistocene (Emilian) section of Montefiore dell'Aso, central-eastern Italy (Ragaini *et al.*, 2006). *Leda reussi* was examined from high resolution digital photographs of the type material (two syntypes) kindly provided by O. Schultz (Naturhistorischen Museum in Wien), and of a valve from the type locality, kindly sent by M. Zuschin (Universität Wien).

ABBREVIATIONS

MGGC Museo Geologico "Giovanni Capellini",
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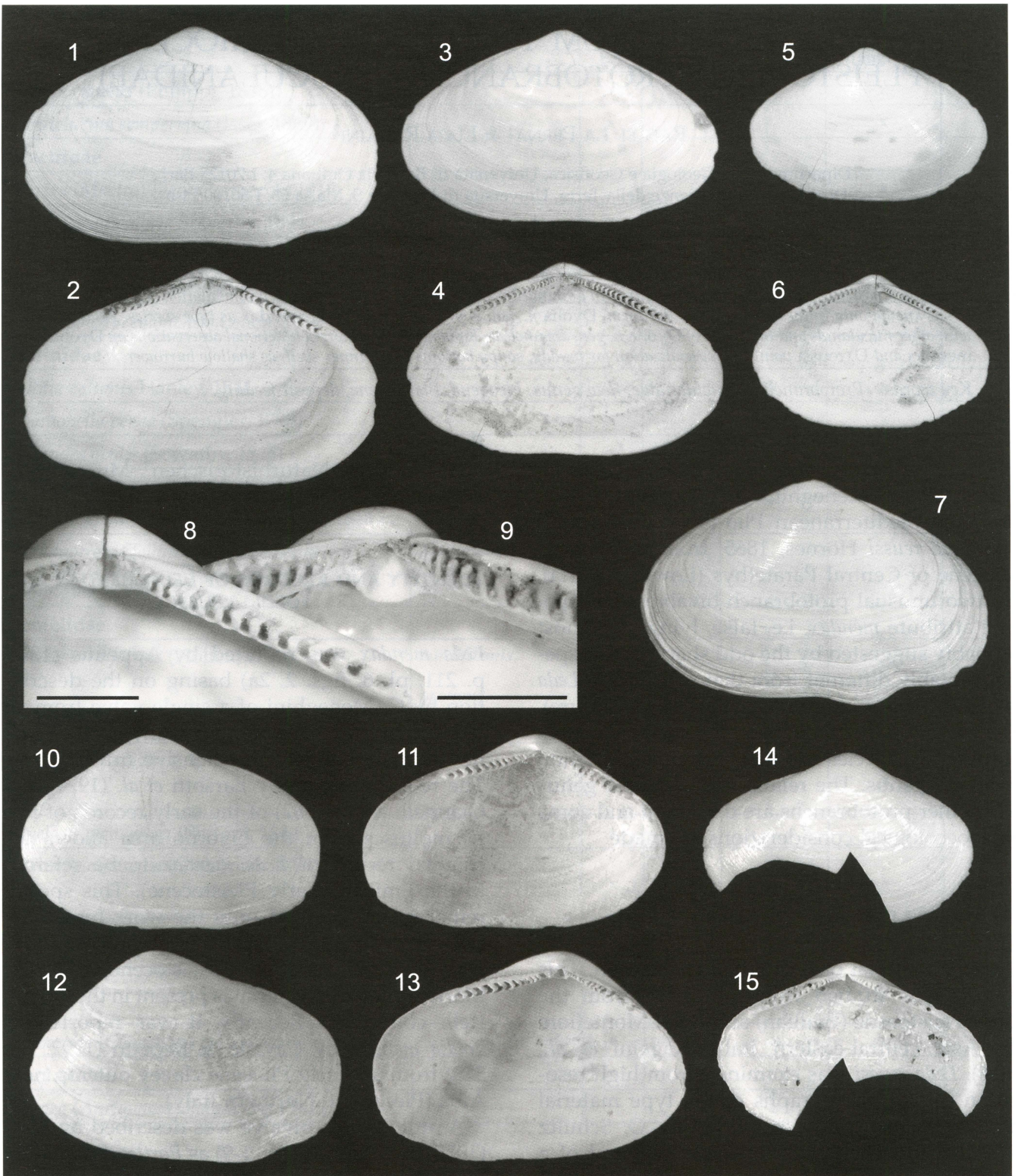
Bologna.

NHM Wien Naturhistorischen Museum in
Wien, Geol.-Paläont. Abteilung.

IDENTITY AND RECORDS OF *LEDA MENDAX* AND *YOLDIA REUSSI*

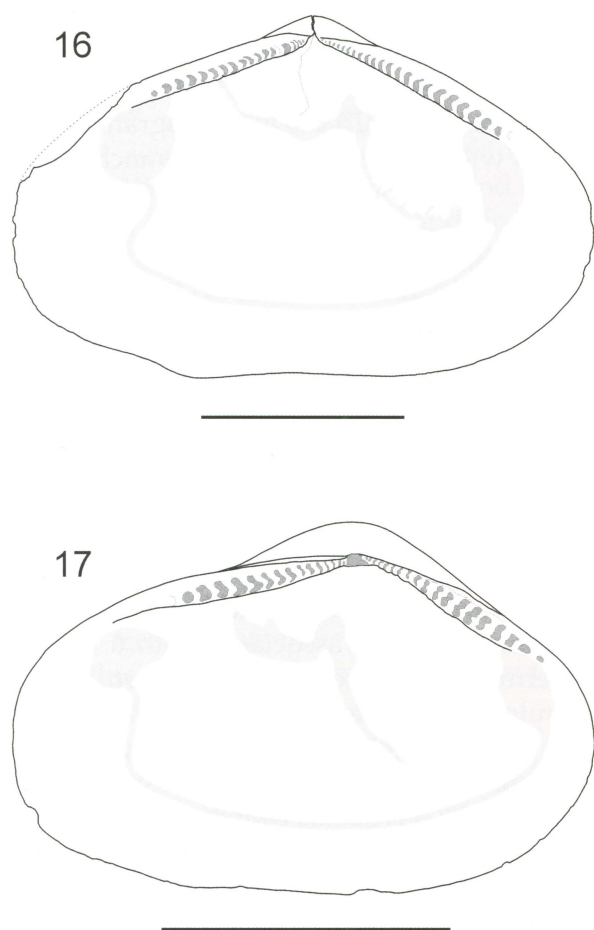
Leda mendax was reported by Appellius (1871: p. 211, pl. 6, figs. 2, 2a) basing on the description by G. Meneghini of a single valve from an old outcrop in Livorno (Tuscany), nowadays not accessible owing to extensive urbanization. The re-examination by Barsotti *et al.* (1974) and Giannelli *et al.* (1982) of the early records of fossil molluscs from the Livorno area allows the original record of *Leda mendax* to be referred to the Emilian (Early Pleistocene). This species remained unrecorded until the work by Cerulli Irelli (1907: p. 131, pl. 12, fig. 14) who reported it from the Calabrian (Early Pleistocene) of Monte Mario, Rome (no material is present in the Cerulli Irelli collection). Recently, it was reported as *Yoldia mendax* by Cavallo & Repetto (1992: fig. 525) from an Early Pliocene clayey outcrop near Alba (Piedmont, Northern Italy).

A protobranch bivalve was described by Perri (1975: p. 177, pl. 1, figs. 1-9) as *Portlandia impressa* (MGGC, 395, 396a-f, 397) from Early Pleistocene (Calabrian) deposits of the Torrente Stirone section (Parma, Northern Italy). Since then, *P. impressa* has been recorded from the Early Pleistocene of Val Chero, Northern Apennine (Taviani *et al.*, 1998) and Montefiore dell'Aso, Marchean Apennine (Ragaini *et al.*, 2006). Due to its systematic position, allegedly close to the



Figs 1-9 *Dyolia mendax* (Meneghini in Appellius, 1871). Montefiore dell'Aso, Grotti section, Early Pleistocene (Emilian). **1-2** 14.7 mm. **3-4** 13.1 mm. **5-6** 9.6 mm. **7** 14.2 mm. **8** detail of hinge (same as Figs 5-6). **9** 9.7 mm, detail of hinge (oblique view). Scale bars = 1mm.

Figs 10-15 *Dyolia reussi* (Hörnes, 1865), Grund, Grund Fm., Middle Miocene. **10-11** Syntype, 10.0 mm, NHMWien 1859/XLV/221 (photo Schultz). **12-13** Syntype, 10.6 mm, NHMWien 1859/XLV/221 (photo Schultz). **14-15** Hollabrunn, Grund Fm., Sample B7 of Zuschin et al. (2004, 2005), 9.3 mm (photo Zuschin).



Figs 16-17 Shell outline and internal characters. 16. *Dyolia mendax*, Montefiore dell'Aso, 14.9 mm (right-left inverted). 17. *Dyolia reussi*, syntype, 10.0 mm (same as Figs 10-11). Scale bars = 5 mm.

Arctic species *Portlandia arctica* (Gray, 1824), *P. impressa* has been regarded as a species with boreal affinity, palaeoclimatically and biostratigraphically similar to *Arctica islandica* and other northern immigrants (Boreal Guests) in the Mediterranean Early Pleistocene (Perri, 1975; Raffi, 1986; Malatesta & Zarlenga, 1986; Taviani et al., 1998; Ragaini et al., 2006).

Leda mendax and *Portlandia impressa* are undoubtedly synonyms, as proved by the complete matching of their descriptions and illustrations. This species has an Early Pliocene to Early Pleistocene distribution and cannot be considered either as a cold-water species, or a representative of *Portlandia*, as discussed below.

Leda reussi was described by Hörnes (1865: p. 303, pl. 38, figs. 4a-c) from the Badenian (Middle Miocene) of Grund, Lower Austria (NHMWien,

1859/XLV/221) and was recently reported by Schultz (2001: p. 28, pl. 2, figs. 7a,b). The species referred to as *Saturnia* cf. *pusio* by Zuschin et al. (2004: appendix) from Grund proved to be *Leda reussi* (Figs 14, 15) and not *Pseudoneilonella pusio* (Philippi, 1844), which is a totally distinct proto-branch (La Perna, 2007a).

Cocconi (1873: p. 331) reported *Leda reussi* from Late Miocene (Tortonian) or Early Pliocene deposits near Parma (Po Valley). The single valve was said to be more similar to Hörnes' species than to *Leda mendax*. Unfortunately, this material is not present in the Cocconi collection (P. Monegatti, pers. comm.) and nothing can be added to this record.

SHELL CHARACTERS

The shell of *Leda mendax* (Figs 1-9, 16) is moderately large (maximum shell length about 15 mm), somewhat delicate and brittle, markedly equilateral in shape, with a central umbo and both anterior and the posterior ends are well-rounded, the posterior end being barely shorter and narrower. In the posterior half shell, a radial swelling is present, producing a distinct, rounded projection in the postero-ventral margin, on the same plane of commissure. This character was not reported in the original description of *Leda mendax*, but was clearly illustrated (Appelius, 1871: figs. 2, 2a). As observed by Perri (1975), the radial swelling develops at a shell size of about 10 mm (antero-posterior length) and is posteriorly delimited by a shallow sulcus. Another, less distinct sulcus bounds the radial swelling anteriorly. The remaining ventral margin is mostly rectilinear, slightly convex in juveniles. The pallial sinus is very shallow (Fig. 16). The hinge consists of many thin, chevron-shaped teeth in two rows, the anterior one slightly longer. A triangular, robust, sunken chondrophore is present below the beak.

The main shell characters of *Leda mendax* are all shared by *Leda reussi* (Figs 10-15, 17) which differs mainly by being smaller (barely exceeding 10 mm) and more delicate, less equilateral, with a larger, slightly anterior umbo, weaker sculpture and less distinct posterior radial swelling and postero-ventral projection. The pallial sinus is a simple indentation in the pallial line.

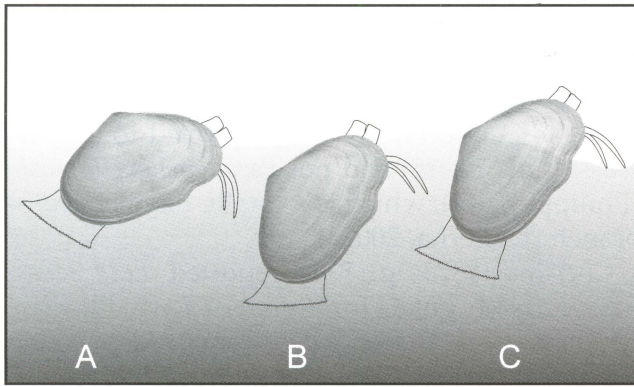


Fig. 18 Hypothetical life position of *Dyolia mendax* during subsurface (A, B) and surface (C) feeding.

In both species, the scar marking the limit of genital and digestive gland has a distinct sinus (Figs 16, 17). In the other protobranchs, this scar usually forms a simple, curved line or band (e.g. Ockelmann, 1954).

The larval shell of *Leda mendax* is ovate, 200 µm large (maximum length), with no microsculpture and only consisting of the prodissoconch I stage (SEM observations), similar to other protobranchs (e.g. Webb, 1987; Ockelmann & Warén, 1998). No data are available for *L. reussi*.

SYSTEMATICS

Nuculanidae

Genus *Dyolia* new genus

Type species *Leda mendax* Meneghini in Appelius, 1871 (= *Portlandia impressa* Perri, 1975)

Description Shell moderately large, 10–15 mm in antero-posterior length, thin walled, rather brittle, normally convex, not gaping. Shape elliptical-subtriangular to elliptical-subrectangular, with central to slightly anterior umbo, feebly opisthogyrate. Anterior and posterior ends well rounded. No rostrum. Posteriorly, a weak radial swelling bounded by two shallow sulci and terminating in a rounded projection of the postero-ventral margin. Remaining ventral margin somewhat straight. Sculpture weak to almost absent, commarginal. Hinge taxodont, with many thin, chevron-shaped, teeth. Anterior row slightly longer than posterior, both straight. Ligament internal, within a robust, triangular, sunken chondrophore. Muscle pallial scars ovate, of

similar size. Pallial sinus very shallow to almost lost. Visceral mass scar with a U-shaped sinus.

Derivation of name *Dyolia* is an anagram of *Yoldia* which is widely used in the protobranch nomenclature.

Gender Feminine.

Stratigraphic range Middle Miocene to Early Pleistocene of Europe (central Paratethys and palaeo-Mediterranean).

Remarks The shell character which led Perri (1975) to place the new species in *Portlandia* is the occurrence of a posterior sulcus. Many rostrate protobranchs possess a shallow subrostral sinuation or sulcus, but in the two fossil species this character is not associated with a rostrum. Furthermore, in these species another, less distinct sulcus bounds anteriorly the radial swelling which cannot be considered a rostrum, i.e. a more or less pointed termination of the posterior end of a bivalve shell. *Portlandia* Mörch, 1857, is a rather large protobranch with a short, but well defined, keeled rostrum and a well distinct pallial sinus. Neither can *Yoldia* Möller, 1842 represent a proper systematic position for the two fossil species, in spite of its wide, mostly provisional usage: the type species *Yoldia hyperborea* Torell, 1859 has a notably elongate, rostrate, flat shell, gaping at both ends and with a deep pallial sinus.

Perri (1975) attempted a comparison of *Portlandia impressa* with *Yoldia longa* Bellardi, 1875 but this species differs in many respects from *Dyolia mendax*, mainly by weak rostration, a wide and deep pallial sinus, the occurrence of oblique ridges and, of course, the lack of radial swelling and postero-ventral projection. *Yoldia longa* can be definitely assigned to *Scissileda* Kilburn, 1994, living species of which are known from the Indian Ocean (Kilburn, 1994).

As far as we are aware, no other protobranch species has a combination of characters similar to that shown by *Dyolia mendax* and *D. reussi*, including the radial swelling and the associated postero-ventral projection. Surprisingly, no fossil species from Europe seems to be minimally comparable with them. Rather, these species may deserve a comparison with two species from the Eocene of New Zealand: *Pseudoportlandia soleneloides* (Marshall, 1919) (Marshall, 1919: p. 233,

pl. 15, figs. 4-6; Beu & Maxwell, 1990: p. 100, pl. 5, figs. a-b) and *P. tahuia* (Marwick, 1942) (Marwick, 1942: p. 268, pl. 23, figs 1-2; Maxwell, 1992: p. 57, pl. 2, figs. k, m). These species lack a pallial sinus (or it is strongly reduced) and seem to differ from *Dyolia mendax* and *D. reussi* mainly by their robust shell and the lack of posterior swelling and postero-ventral projection. Maxwell (1988) and Beu & Maxwell (1990) listed other species from the Neogene of New Zealand under *Pseudoportlandia*. According to Zinsmeister (1984), *Pseudoportlandia solenelloides* and *P. tahuia* should be placed in a distinct, new genus. Similar considerations were also made by Beu & Maxwell (1990: p. 100) and Del Río & Camacho (1998: p. 64). Actually, *Pseudoportlandia* Woodring, 1925 (type species *P. clara* Guppy, 1873 from the Miocene of Jamaica) is a shortly rostrate genus, somewhat similar to *Portlandia* with which it was synonymised by Puri (1969: p. 239, figs A7, 11a-c).

At present, a systematic relation of *Dyolia mendax* and *D. reussi* with Paleogene Australasian species is purely speculative. However, such an hypothesis is supported by the Early Cenozoic palaeogeography, i.e. the connection between the proto-Mediterranean and proto-Indo-West Pacific, before their ultimate separation in the Middle Miocene. Recently, a Tethyan origin has been advocated for several protobranch genera from the Mediterranean Neogene-Pleistocene (La Perna, 2004, 2007b; La Perna *et al.*, 2004).

There is not complete agreement about the classification of the Nuculanoidea as to families and subfamilies. We have followed Vokes (1980) and Ockelmann & Warén (1998) who assigned nuculanoids to a single family, Nuculanidae H. & A. Adams, 1858.

LIFE HABITS

In the most detailed records (Perri, 1975; Taviani *et al.*, 1998; Ragaini *et al.*, 2006), *Dyolia mendax* is reported (as *Portlandia impressa*) from fine-grained (muddy and silty-sandy) deposits. Basing on textural characters and composition of the associated fauna, this species was considered by Ragaini *et al.* (2006) as a sand-tolerant pelophilous species which inhabited inner-shelf soupy bottoms.

The scant material of *Dyolia reussi* is from sandy shell-rich deposits in the Grund Formation. Zuschin *et al.* (2004, 2005) identified the sandy deposits as allochthonous beds of tempestitic origin. Transport occurred from wave- or current-agitated nearshore bottoms into a pelitic, dysaerobic inner-shelf environment. It is unlikely that a thin-shelled, detritus-feeder nuculanid, such as *Dyolia reussi*, would come from coarse-grained, unstable bottoms. Protobranchs are sluggish burrowers (Stanley, 1970; Peck *et al.*, 2004), mostly preferring stable, fine-grained bottoms. It is then hypothesized that *Dyolia reussi* lived in pelitic bottoms. Also, the original valve of *Dyolia mendax* was from a coarse sandy bed (Appelius, 1871: p. 5). Considerations similar to those made for *Dyolia reussi* (allochthonous condition) can be applied in this case too.

Two feeding strategies are known from studies on large nuculanids: subsurface and surface deposit feeding (Drew, 1899; Rhoads, 1963; Bender & Davis, 1984; Davenport, 1988; Stead & Thompson, 2006). In subsurface feeding, these species are mostly buried, even rather deeply (Stanley, 1970: pl. 2, figs 4, 7), whereas a partly exposed position is taken during surface feeding. The shell is usually orientated at a high angle with respect to the sediment surface. The shallower and sub-horizontal life position taken by *Aequiyoldia eightsi* during both types of feeding (Davenport, 1988), is probably related to the ovate, almost non-rostrate shell shape of this species; notably different from the elongate, rostrate shell of the other, deeply burying species with long siphons, such as *Yoldia limatula* and *Y. hyperborea*.

The shell of *Dyolia mendax* and *D. reussi* is moderately elongate but much more inflated than the blade-like shell of deeply burying nuculanids of similar size. Moreover, they had short siphons, as inferred from the shallow, almost absent pallial sinus. It is then hypothesized that the life position of both species was shallow, even partly exposed, either in subsurface and in surface feeding (Fig. 18).

The functional meaning (if any) of the radial swelling and the associated postero-ventral projection is not clear. Constructionally, the postero-ventral projection is an outcome of the radial swelling, since such an expansion prevents the formation of a postero-ventral shell gape. However, the poste-

rior position of the radial swelling, in correspondence with the oral opening, suggests a function related to feeding. Bender & Davis (1984) observed that in *Yoldia limatula* rejection of large sediment particles takes place between the valves, producing an increase in particle size at the feeding depth. Furthermore, Davenport (1988) observed that, unlike *Yoldia limatula*, the palp proboscides are not used by *Aequiyoldia eightsi* for collecting detritus during subsurface feeding, this species appearing to take much material into the mantle cavity by opening of the shell valves. If the species of *Dyolia* had a similar behavior, then the radial swelling could act as a "canal", making easier the introduction of material towards the labial palps and the rejection of discarded material.

Surface feeding was proved to be adopted by *Yoldia hyperborea* in response to algal blooms (Stead & Thompson, 2006). Furthermore, feeding on fresh algal material allows this species a storage of metabolic energy (Stead & Thompson, 2003). Due to their shallow burial, the species of *Dyolia* probably specialized in exploiting fresh, high nutrient organic material on the sediment surface or just below it, rather than decayed, poor nutrient subsurface detritus.

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