Systematic relationship of the genus *Adula* and its descent from a *Mytilus*-like ancestor (Bivalvia, Mytilidae, Mytilinae)

KURT W. OCKELMANN & GRETE E. DINESEN

In the Mytilidae, the genus *Adula* with the type species *Mytilus soleniformis* has most often been placed either in the Lithophaginae or close to it. There are only a few known species of *Adula*. The genus is distributed in the eastern Pacific Ocean from Peru northwards to British Columbia, and in the western Pacific from Japan and Siberia eastwards perhaps as far as the Aleutian Islands. One species is a nestler, others are considered to be mechanical borers. A morphological study of the shells of three of the known species, including one close to the rarely recorded type species, provides evidence that *Adula* does not belong to the Lithophaginae, but is closely related to *Mytilus*. Evidence for this includes ontogenetic characteristics and details of the shell ultrastructure of *Adula*, *Mytilus* and *Choromytilus*, as compared with those of *Perna*, *Aulacomya*, *Lithophaga* and *Leiosolenus*. There is hence no reason to maintain the poorly defined Adulinae. Instead, *Adula* is herein referred to the Mytilinae.

Keywords: mussel nestlers and borers, *Adula*, Mytilinae, Lithophaginae, Northern Pacific.

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INTRODUCTION

The systematic relationship between *Adula* H. & A. Adams, 1857 and other mytilids is inconsistent in the literature. The genus *Adula* has *Mytilus soleniformes* d'Orbigny, 1846 as its type species with the type locality near Payta, Peru, and a distribution reaching north to Panama (Olsson 1961). The Recent geographic distribution of *Adula* species is restricted to two separate Pacific regions. *Adula californiensis* (Philippi, 1847), *A. gruneri* (Philippi, 1851) [with *Lithodomus falcatus* Gould, 1851, and *Adula falcata* (Gould, 1851) as junior synonyms (Coan et al. 2000)], and *A. diegensis* (Dall, 1911) occur in the Eastern Pacific between Mexico and Vancouver Island, Canada. To these may be added a subspecies described by Olsson (1961) as *A. soleniformes panamensis*. Two species of *Adula* are also known from the Northwest Pacific (Japan, Korea, Sakhalin and Siberia), that is, *A. schmidtii* (Schrenck, 1867) [with *A. nipponica* Habe, 1955 as a synonym], and *A. falcatoides* Habe, 1955, that is, *A. falcata* Kinoshita, 1937 [non Philippi, 1851, non Gould, 1851]. *Adula schmidtti* has also been found in intertidal drift in the Aleutian Islands, Alaska (Coan et al. 2000).

The habit of boring into rocks and coral substrata has developed independently in at least six bivalve families, i.e., the Mytilidae, Gastrochaenidae, Petricolidae, Pholadidae, Clavagellidae and Tridacnidae (Rocque 1953, Keen 1958, Soot-Ryen 1969, Skarlato & Starobogatov 1979, Skarlato 1981, Abbott 1983, Coan et al. 2000, Valentich-Scott & Dinesen 2004). The rock and coral boring species of Mytilidae are referred to by most authors as either members of or closely related to the Lithophaginae. Some

are regarded to be mechanical borers while others have developed chemical means to shape their habitat (Soot-Ryen 1955, Yonge 1955, 1963, Nielsen 1976, Wilson 1979, Morton & Scott 1980, Morton 1982, 1990, Wilson & Tait 1984, Scott 1988, Kleemann 1990). One species of *Adula* is a nestler and others are also believed to be mechanical borers (Yonge 1955, 1963, Fankboner 1971). Thus, *Adula* has most often been assigned to the Lithophaginae (Soot-Ryen 1955, 1969, Keen 1958, Olsson 1961, Abbott 1983, Coan et al. 2000). Other authors have included genuine *Adula* species in the genus *Botula* Mörch, 1853 (Dall 1921, Rocque 1953) including *Adula californiensis* and *Adula gruneri* (Yonge 1955), as *B. californiensis* and *B. falcata*, respectively. However, Soot-Ryen (1955, p. 88) considered *Adula* and *Botula* to be different from one another. Skarlato & Starobogatov (1979) erected a new subfamily, the Adulinae, but which was considered by Skarlato (1981) to belong to the Lithophagidae H. & A. Adams, 1857. Bieler & Mikkelsen (2006) consider the Adulinae to belong to the Mytilidae.

The aim of the present study is to determine the systematic relationship of *Adula* within the Mytilidae, based on ontogenetic, morphological and biological evidence and to challenge the present views of the boring mechanism in some species.

MATERIAL AND METHODS

The material under study consisted of dry samples of three species of *Adula* kept in the collections of the Zoological Museum of the Natural History Museum of Denmark, with samples of other mytilid species for comparison held at the Marine Biological Laboratory, University of Copenhagen. The provenance of the investigated material is described below. It was studied using light and scanning electron microscopy.

Material for the study of shell structure was treated with 5% NaClO for 48 hrs to dissolve the periostracum and organic shell matrix, rinsed in distilled water, transferred to 80% ethanol and dried. The pieces of shell were slightly compressed to expose the needle-like structure of the calcareous shell layer. Juvenile shells were rinsed

Fig. 1. Block of hard clay from Sakhalin with empty bore holes made by pholadids and in which at least one attached specimen of *Adula schmidtii* was found. A specimen of *Penitella gabbii* is still seen in the block.

in 80% ethanol before drying. Shell material was coated with ~12 µm Pt/Pd (80%/20%, 90 seconds at 40mA) in a sputter coater (JEOL JFC2399HR) and examined using a scanning electron microscope (JEOL JSM6335F).

RESULTS

Material Studied

Adula schmidtii. One sample from Sakhalin, 49º03' N 142º08' E, collected by Andrea in 1868, including a block of hard blackish clay (also called "mud stone") (Fig. 1) with one intact juvenile shell 2.2 mm long, and six specimens with shell lengths of 10, 12, 14, 14, 32 and 33 mm, four of which had some dried soft tissues remaining. In addition, there were shell fragments of 1–2 other specimens. None of the *A. schmidtii* individuals was found in its own burrow. Some of the shells of *A. schmidtii* had abraded shells. The extent of these shell abrasions was about
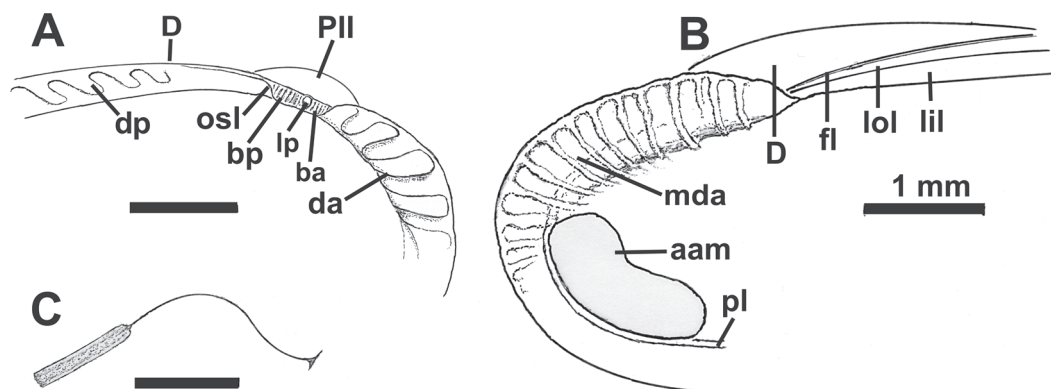
Fig. 2. *Adula schmidtii*. A. Interior view of the umbo and hinge of the left shell valve of a juvenile individual (SL 2.2 mm). B. Interior view of the anterior end of an adult (SL 32 mm). C. A byssal seta taken from the mat on the shell of an adult individual (SL 32 mm). – Shell stages: PI, prodissoconch I; PII, prodissoconch II; D, dissoconch. – Abbreviations: aam, anterior adductor muscle scar; ba, b-series of anterior hinge teeth of a late larva; bp, b-series of posterior hinge teeth of a late larva; da, d-series of anterior hinge teeth; mda, d-series of modified anterior teeth; dp, d-series of posterior hinge teeth, i.e., modified dissoconch teeth; fl, dorsal periostracum fusion layer; lp, larval ligament pit; lil, ligament inner layer; lol, ligament outer layer; osl, origin of secondary ligament; pl, pallial line.

the same, that is, ~4–6 mm across, irrespective of the bivalve's total shell length which ranged from 10–33 mm.

Together with *Adula* from the same block of clay, were shells and fragments of the pholadid *Penitella gabbii* (Tryon, 1863) and possibly other pholadids, all without soft tissues. The clay block was hard when dry, but becoming softer when exposed to freshwater. Mean clay particle size was 1–5 μm with a few sand grains mostly ≤50 μm.

Adula diegensis. One sample from Venice, California, collected by Talmadge in 1976. One specimen with a shell length 10.5 mm and soft tissues removed. Another sample from off Cape Mendocino, California, from a floating crab pot, one specimen of shell length 3.5 mm with dried soft tissues, and four cleaned shells with lengths of 25, 22, 17 and 13 mm.

Adula californiensis. One sample from the Zoological Museum, Monterey, California, collected by Wroblensky in 1872. One specimen, 19.9 mm long with traces of soft tissue. Dissoconch teeth rather indistinct and irregular, though present. Byssal setae (hitherto considered to be periostracal hairs) light, flattened and flaring (after soak-

ing in water), forming a mat postero-dorsal from the shell's umbonal ridge.

Mytilus edulis Linnaeus, 1758. From the sound, Øresund, between Denmark and Sweden, collected in June and September 2008. Juvenile and adult specimens.

Chloromytilus chorus (Molina, 1782). From Chile, collected by V. A. Gallardo in March 1983. One sample containing individuals of various sizes. One young specimen was used for shell ultra-structure.

Other material. Additional mytilids examined included individuals of *Aulacomya ater* (Molina, 1782) from Chile (Callao fish market, collected by J. Nielsen, October 1960), *Mytilus californianus* Conrad, 1837 from California, and *Zelithophaga truncata* (Gray, 1843) boring into a shell of *Perna canaliculus* (Gmelin, 1791) from New Zealand, as well as *Perna viridis* (Linnaeus, 1758), Mediterranean *Lithophaga lithophaga* (Linnaeus, 1780), and *Leiosolenus nasutus* (Philippi, 1846) and *L. malaccana* (Reeve, 1852) from Phuket Island, Thailand (collected by K. W. Ockelmann).

Shell and hinge ontogeny

The shell ontogeny of *Modiolarca tumida* (Hanley, 1843) (Musculinae) consists of four stages: prodissoconchs I and II, nepioconch and dissoconch, each characterized by a unique shell texture and a series of taxodont teeth. The presence of four shell stages in the ontogeny of Mytilidae species is here considered to be a pleisiomorphy of this taxon. In *Perna* (Mytilinae), a small nepioconch appears in the late larva, together with the appearance of a secondary parivincular ligament, that is, the secondary ligament (Ockelmann 1995).

The shell valve of a juvenile *Adula schmidtii* at hand lacks the third mytilid shell stage, the nepioconch (Figs. 2A, 3A ,5A). Similarly, neither the material of *Adula diegensis* nor the specimens of *Adula californiensis* show the presence of nepioconchs.

In species of *Mytilus*, *Choromytilus* and *Aulacomya* (Mytilinae), the nepioconch has been lost (Ockelmann 1995, Ockelmann & Dinesen in prep.). In *Mytilus*, early juveniles pass through a stage with a series of a few taxodont teeth growing along the dorsal margin in front of the umbones and a posterior series of proximal teeth. The posterior series are soon discontinued in connection with a directional change in the hinge axis, while the anterior series often remains functional in adults. Tooth formation in young

Fig. 3. Anterior and posterior juvenile dissoconch teeth. A. *Adula schmidtii*. B. *Mytilus edulis*. Abbreviations see Fig. 2.

individuals of *Adula* is from the same origin (Fig. 3), although further evolutionary development appears to have occurred.

The shape of the anterior series of dissoconch teeth in *Adula* differs from that of *Mytilus* and other mytilids (Figs. 2A–B, 3A–B). This is likely due to transformation of the shell from anteriorly pointed to a shape with a semicircular frontal margin and which greatly affects the anterior series of teeth. To the inside of its margin, the shell forms a more or less distinct antero-dorsal shelf that carries the teeth. The earlier position of these teeth can be seen as ridges on the shell interior. With closure of the shell valves, the teeth from the left and right sides do not interlock closely, but leave narrow spaces between them. A new tooth may even be formed between two older ones. This seems to be common in *Adula diegensis*. The functional importance of this modification to the *Adula* hinge is unknown.

Furthermore, according to Soot-Ryen (1955, p. 18), the distinctly pitted sub-ligamental shell layer, that is, the resilial ridge, is an important character of *Mytilus* and is not seen in *Adula*. However, in the specimen of *Adula californiensis* examined, part of the ligament had been lost revealing a regular pattern of small transverse ridges on the shell with depressions between them on the surface of the sub-ligamental layer. A similar but less distinct structure was seen in a 10 mm long specimen of *Adula schmidtii*. This indicates that the ancestry of *Adula* included a stage with a pitted, sub-ligamental, layer. The functional role of the visible pits in the subligamental layer and the reason for their disappearance is unknown.

Shell colour and ultra-structure

Commarginal bands of blue and silvery white are seen in juveniles of both *Adula diegensis* (Fig. 4) and *Mytilus edulis*. Light and SEM preparations (Fig. 5) of *Adula schmidtii*, *Chloromytilus chorus*, *A. diegensis* and *M. edulis* show the same type of shell structure. Shells of adult *M. edulis* and *M. californianus* are characterized by a fibrous prismatic outer layer (see Carter & Seed 1998, pl. 1, p. 107). In contrast, light microscopy of two taxa commonly considered closely related to *Mytilus*, that is, *Aulacomya ater* and *Perna*
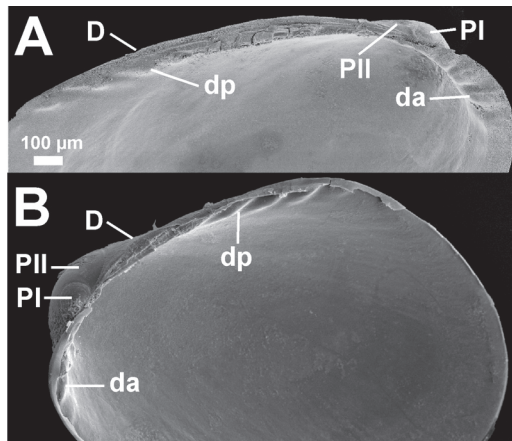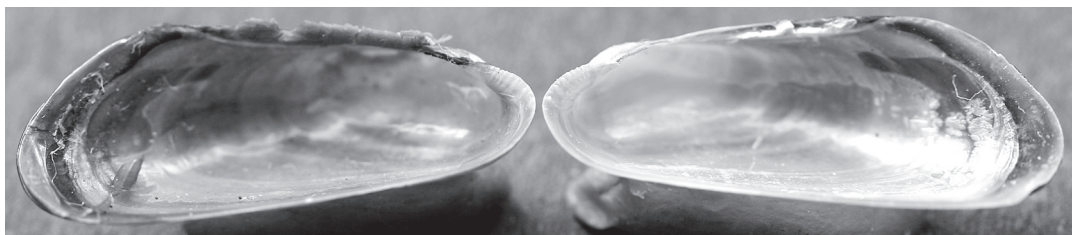
Fig. 4. *Adula diegensis*. Anterior view of the left and right shell valves of an adult specimen (SL 16.5 mm) with shell colour bands similar to those of *Mytilus edulis*.

viridis, did not show a similar shell structure. The lithophagines, modiolines and bathymodiolines examined have a shell structure without crystal needles. Shell ultrastructure is an important phylogenetic character in the Bivalvia (Bøggild 1930, Carter 1990).

Byssal setae

Until now, the shells of living *Adula* species, with the exception of *Adula diegensis*, have been considered to be covered by a mat of periostracal hairs (Soot-Ryen 1955), also known as periostracal setae (Coan et al. 2000). These setae are laid down by the foot and are, thus, of byssal origin. The mat often covers a triangular area of each valve extending from the dorsum behind the umbo to the postero-ventral shell margin. In his study of *Adula gruneri*, Yonge (1955) noted the presence of byssal threads in such a mat. Our examination of a mat of a specimen of *Adula schmidtii* showed these setae to be structurally and functionally different from the byssal threads by which the animal is attached to the inside of a borehole. The setae in question are rather strong, curled and twisted, and are attached firmly to the periostracum. These setae are often drawn out into a long, thin and broad distal part (Fig. 2C). In *Adula californiensis*, the byssal setae of a mat are principally similar to those of *A. schmidtii*, but much longer and thinner, and placed in clusters. The specialized byssal setae are an essential part of the mat that is formed by collecting and binding sediment particles perhaps aided by a mucous secretion. The protective role of such a mat is, of course, limited to the posterior region of living *Adula* individuals in their boreholes.

Often, juvenile *Mytilus edulis* (SL≤6 mm)

have byssal setae on their shells. These are short and of about equal length. They are applied by the foot which can reach all over the shell. In larger individuals, the byssal setae are lost.

Anatomy

Pallial papillae are well developed in *Adula diegensis* and *A. californiensis* (Soot-Ryen 1955, figs. 74–76). In some specimens of *A. schmidtii* studied, the retractor muscles serving the papillae can still be seen due to the selective feeding on dried tissues, probably by dermastid beetles. About 35 muscles originate at the pallial line and indicate the position of the papillae. Yonge (1955) and Fankboner (1971) did not mention such papillae. The latter author (fig. 1, p. 29) illustrated the extended siphons of *A. gruneri* without distal papillae.

The shells of *Adula gruneri* and *A. falcatoides* show a pattern of densely-set, almost parallel, wrinkles of the periostracum more or less normal to the longitudinal axis. While the distribution of papillae along the inner mantle fold is probably of functional importance, the significance of a corresponding pattern of wrinkles on the shell is unknown. A similar vertical sculpture occurs on the shells of certain lithophagines, for example, *Lithophaga nigra* (d'Orbigny, 1842).

In juvenile *Mytilus* species, the rim of the inner mantle fold becomes papillate. With growth, these papillae become more distinct and often subdivided, especially posteriorly. Papillate inner mantle folds occur elsewhere within the Mytilidae, for example in *Aulacomya ater*, *Brachidontes* spp. and *Mytella* spp. (Soot-Ryen 1955). However, the majority of mytilid species have non-papillate inner mantle folds, including
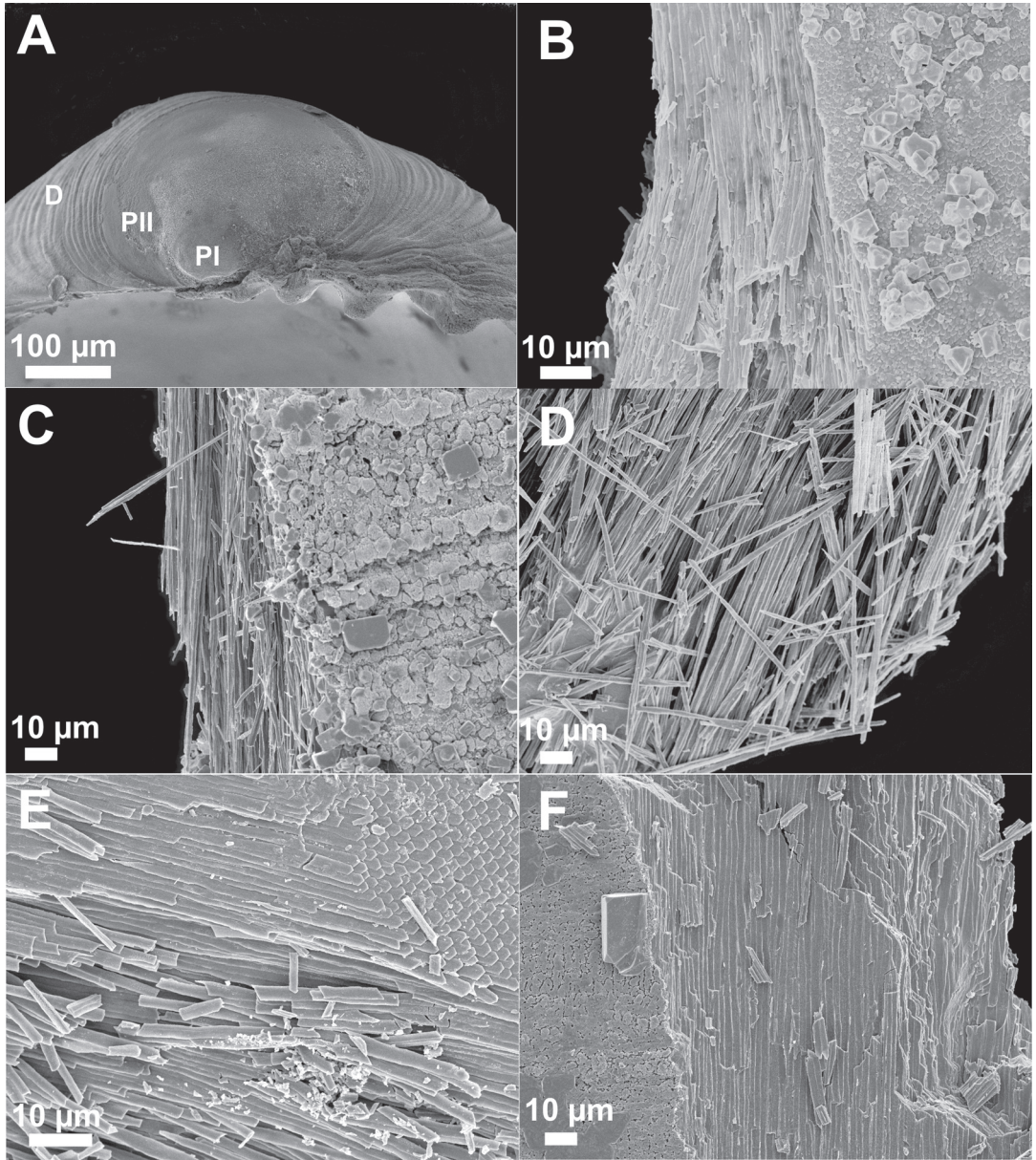
Fig. 5. A. *Adula schmidtii*. Three shell stages, that is, prodissoconch I, prodissoconch II and dissoconch (for abbreviations, see fig. 2). B. *Adula schmidtii* shell ultrastructure, outer crystalline surface. C. *Adula schmidtii* inner surface with nacreous layer. D. *Choromytilus chorus* crystalline layer. E. *Adula diegensis* outer crystalline layer. F. Inner view of the shell of *Mytilus edulis* showing the nacreous layer.

the well preserved specimens of lithophagines herein examined.

DISCUSSION

The definition of the Adulinae by Skarlato & Starobogatov (1979) translated from Russian is: 'Subfamily Adulinae. The shell rectangular-rounded. The umbo placed between the middle of the shell and the anterior end. It has a keeled bend, going from the umbo posteriorly and downwards'. However, this definition provides no unambiguous criteria to distinguish it from other mytilid subfamilies.

Biology of *Adula*

Information on the environmental requirements of the Western Pacific species of *Adula* is provided by Coan et al. (2000). Gould (1851) described *A. gruneri* from indurated clay as *Lithodomus falcatus* ('falcatus' meaning curved or sickle-shaped). Such a shell shape would seem inappropriate for mechanically boring bivalves. Notwithstanding, based on a study of *Adula* and *Lithophaga*, Yonge (1955) concluded that *Adula californiensis* and *A. gruneri* are mechanical borers of soft, non-calcareous, rocks.

Only pholadid borings, some with shell fragments still present, were found in the block of hard clay from Sakhalin. Although none of the *Adula schmidtii* individuals was found in its own burrow, one individual was byssally attached within an empty pholadid borehole. Thus, there is the possibility that the remaining *Adula* individuals may have been placed in the block after sampling, possibly for exhibition purposes. In spite of this, most individuals showed the same kind of shell abrasion as described by Yonge (1955) for *Adula gruneri*. The left valve of a large specimen of *A. schmidtii* (32 mm SL) had been exposed to the boring activity of a neighbouring *Penitella gabbi* after the thin wall of clay separating them had gone. Since this specimen of *A. schmidtii* had traces of internal tissues, the pholadids must have been living side by side with it in the same substrate, indicating a relationship between them. Pholadids are diverse and common in the eastern Pacific (Coan et al. 2000) and, inevitably,

where pholadids occur empty bore holes will become available for subsequent occupation by other animals.

According to Yonge (1955), boring is brought about in *Adula* species by movements to and fro inside their burrows with the dorsal shell region sliding and grinding against the substratum. Movement is made possible by byssal attachment of the mussel to its burrow wall, with a large bundle of byssal threads towards the head of the burrow and a smaller one towards the entrance (Yonge 1955, fig. 5). The resulting dorsal shell abrasions in *Adula* were interpreted as clear evidence of mechanical boring. Such shells, with the periostracum partially worn are indeed common in larger specimens of *Adula* with the exception of *A. diegensis*. Shell abrasions resembling those illustrated by Yonge (1955, fig. 3) were also present on five of the six adult specimens of *A. schmidtii* examined. The loss of periostracum and shell substance had induced shell deposition on the inside under the abraded region. However, the abraded regions of these individuals were more or less concave, a shape inconsistent with mechanical boring by the adults.

Adula schmidtii exhibits much variation in hinge and shell shape. Our observations and interpretation of *A. schmidtii* in empty pholadid boreholes differ from those of Yonge (1955) on *Adula gruneri*. Also, unlike its congeners, *A. gruneri* has a long exhalant siphon and an extendable pseudosiphon formed by the inner mantle folds which can open and close ventrally and which has an inhalant and sanitary function (Yonge 1955, fig. 2a–b). The specialized inhalant and exhalant organs of this species may be an adaptation to life in borings of varying shape and size. However, the method of boring in *A. gruneri*, as suggested by Yonge (1955) and described above, is not in agreement with our results. Such a method would not enlarge the hole all around adult individuals. For these, main boring activity must be in the direction of fastest shell growth - that is, anteriorly, at the borehole head. Activity, if mechanical, should cause visible marks on the foremost part of the shell. But, neither Yonge (1955) nor Fankboner (1971) mentioned such marks, neither are they present on the specimens examined in the present study. The absence of anterior marks on the shell of *A.*

schmidtii might be a consequence of their life in pholadid borings. In seeming contrast, the adult specimens of this species, except for one individual (of 32 mm SL), have abraded dorsal shell regions similar to those seen in adult *A. gruneri* by Yonge (1955).

Except for *Adula diegensis*, the preceding observations support the conclusion that shell abrasion in *Adula* is normally transient and a consequence of juvenile and, possibly, early adult behaviour. It is thus hypothesized that following a planktotrophic larval life, the newly attached spat of *Adula*, without the capacity to bore, have to find a hole or crevice in a suitable substratum for adult residence. At this stage, shell shape is similar to that of early juveniles of *Mytilus* and thus much more compressed than subsequently (Fig. 6). By wedging itself into the hole, the grinding of the shell against the surrounding substrate by the juvenile may enlarge its burrow, allowing for further growth. Adult individuals of *Adula gruneri* are able to crawl and to re-attach after removal from their burrow according to Yonge (1955) and Fankboner (1971) and can, thus, survive relocation. True lithophagines cannot do this.

Regardless of whether or not the juvenile *Adula* remains in its original burrow, further growth involves a dramatic change in shell shape. It becomes elongate with a widely rounded, not narrowly pointed, anterior shell margin in side view, and is broadly heart-shape in cross-section for most of its length (Fig. 6). In *A. schmidtii*, this change in shell shape takes place long before a length of 10 mm is reached. Consequently, the abraded shell regions come to lie dorsally in adult specimens and most of the activity to enlarge the burrow must involve the anterior region of the animal. This shift in activity is probably energetically advantageous, and not necessarily entirely mechanical. Since enlargement of the burrow is forward and often slightly ventral, both the burrow and shell of the animal normally become slightly bent downwards, not upwards, if shell grinding were the main activity to lengthen the burrow.

On the basis of superficial shell characters, several other mytilids have been referred to *Adula*, that is, "*Adula*" *iwaotakii* Habe, 1958 and "*Adula*" *simpsoni* in Tebble (1966) and Nords-

ieck (1969), respectively, but which are actually bathymodiolines (pers. obs.). The "*Adula*" *atrata* (Lischke, 1871) in Habe & Kikuchi (1960) belongs to the genus *Xenostrobus* Wilson, 1967. In his pioneer work on lamellibranch larvae, Rees (1950) provided a figure (plate 1) of a larva believed to be of "*Adula*" *simpsoni*, but which is actually a late larva of *Arca tetragona* Poli, 1795 (pers. obs.).

Kleemann (1983, 1990) referred *Zelithophaga truncata* (Gray, 1843) to *Adula*. We have examined some specimens of this New Zealand species, including a 1 mm long juvenile, which had been boring a shell of *Perna canaliculus* (Gmelin, 1791). The shell of *Z. truncata* does not have a layer of crystal needles and the juvenile has the shape of a miniature adult specimen unlike that of a juvenile *Mytilus* and *Adula*. Hence we regard *Z. truncata* to be unrelated to *Adula*. *Zelithophaga truncata* is likely to be a chemical borer, as Kleemann (1990) suggests, but may not be closely related to genuine lithophagines.

The results herein show that *Adula* differs from true lithophagines in several ways. Shell pieces of adult specimens of *Lithophaga lithophaga* and of *Leiosolenus nasutus* do not have a layer of parallel crystal needles in the shell. The prodissoconch II of a 1.8 mm long juvenile of *Leiosolenus* sp. has an oblong shape and, thus, differs markedly from those of *Adula* and *Mytilus*. Moreover, none of these species and other lithophagines examined has an anterior series of hinge teeth in the dissoconch.

Evseev (2005, fig. 3) illustrates early stages of *Adula schmidtii*, with no indication of a nepioconch state or a c-series of teeth (plesiomorphically connected with a nepioconch shell stage). This author, however, describes the presence of a nepioconch shell and corresponding teeth in the ontogeny of *Adula falcatoides* and illustrates an early juvenile shell with two posterior teeth, not at the dorsal shell margin, but on the inside of the shell (Evseev 2005, fig. 1d). These "teeth" can not, therefore, be nepioconch teeth. The figures in Evseev (2005) are all schematic line drawings. There is no clear indication of proper nepioconch teeth, nor of a change in either shell structure or sculpture between what he interprets as the nepioconch shell and the dissoconch shell.
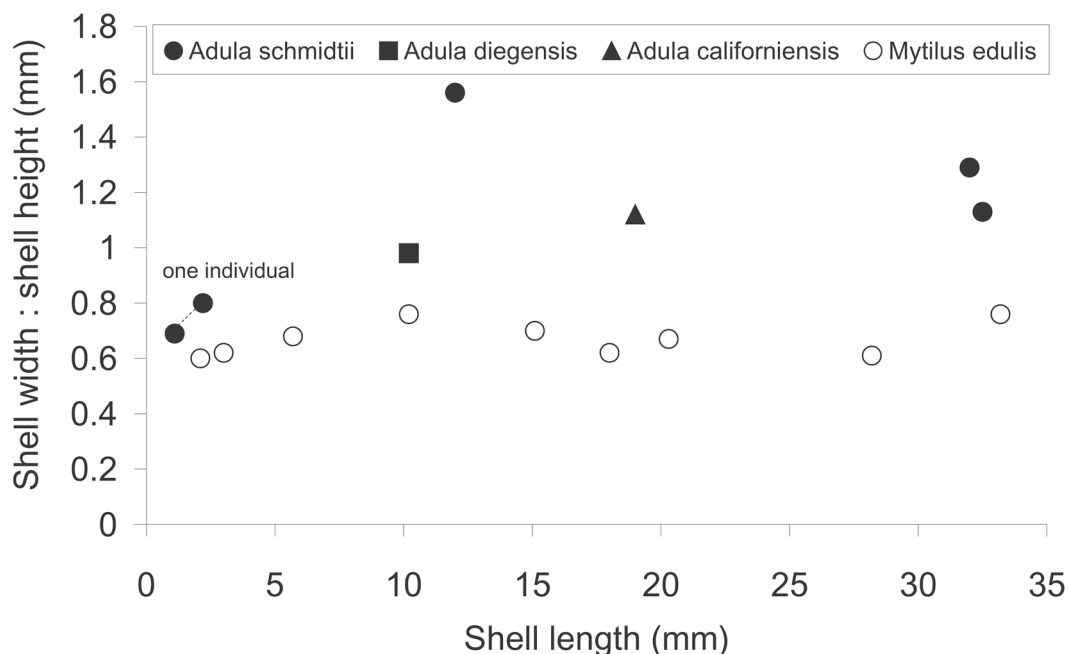
Our research therefore suggests the need for

Fig. 6. Proportions of shell width to shell height against shell length in various mytilid species.

further comparative studies to address the shell ontogeny of *Adula* from larva to adult, the functional anatomy of the viscera relating to mechanical and chemical means of boring, experiments upon possible responses to cues of conspecific larvae and spat, and the herein suggested association with living pholadids.

Evolution of *Mytilus* and *Adula*

Bivalves adapted to an epifaunal life in the intertidal zone are exposed to frequent, short term, variations in salinity, temperature and force and direction of water movements. The shell shape and functional morphology of *Mytilus* is an adaptation to such conditions. Moreover, intertidal suspension feeding bivalves must be able to cope with potential food particles of varying quantity and composition. The study of sorting mechanisms and waste removal by a living *Adula gruneri* (Fankboner 1971) established in a transparent replica of its borehole, showed the highly extensible foot to be important in removing waste and substrate particles from it. The number of

sorting folds on the labial palps per mm length in this species (Fankboner 1971, fig. 4) is the same as in *Mytilus edulis*. This indicates similar sorting efficiencies in both species.

Adaptations to intertidal life in *Adula* descending from a *Mytilus*-like ancestor may also include behaviour of their spat and juveniles, such as a negative phototaxis and a strong tendency to attach in crevices. Possibly, the postmetamorphic migration of early juvenile *Mytilus edulis* (as 'secondary settlement' of Bayne 1964) has become modified in *Adula*, as a pre-adult phase of nestling and mechanical abrasion of the surrounding substrate. This phase does not always lead to shell abrasion. A large specimen of *A. schmidtii* shows only little shell erosion, and none is visible in a large specimen of *A. gruneri* illustrated by Soot-Ryen (1955, fig. 49). The absence of shell wear thus indicates that these specimens had become established in relatively spacious boreholes soon after metamorphosis.

The smallest specimens of *Adula gruneri* recorded by Yonge (1995) were adults of 15 mm shell length. Thus, no observations were

made on the important morphological changes from the early juvenile to adult in this species. Yonge (1955) assumed his smallest specimens to be about one year old. This needs confirmation. Nevertheless, in the adult individuals of *A. gruneri* examined by Yonge (1955, fig. 4), shell width exceeded shell height. Finally, the occurrence of byssal setae on the shells of juvenile *Mytilus* may point to their origin in the shell mat of *Adula* species.

According to their morphology and biology, species of *Adula* may fall into three sub-groups. The group closest to a *Mytilus*-like ancestor includes *Adula diegensis* that usually lives attached in crevices. The second group includes *Adula californiensis* and *Adula schmidtii* both sharing considerable changes in post-larval growth resulting in an elongate shell and with an attached life in boreholes usually realised in two post-metamorphic stages. The little known *Adula soleniformis* may also belong to this group, because of the presence of dissoconch teeth behind the ligament (see Soot-Ryen 1955) as in some individuals of *A. schmidtii* and juvenile *Mytilus edulis*. The third group includes *A. gruneri* and, probably, *A. falcatoides*, both essentially similar to species of the second group except for the absence of pallial papillae in the siphonal region, a lack of teeth in the dissoconch and an even greater elongation of the shell. Boring in adults of the latter group may be apomorphically by chemical means. We suggest that the species of the third group may have evolved latest within the genus *Adula*. Thus, boring habits have developed in parallel in at least three of the currently recognized subfamilies of the Mytilidae: the Musculinae, Lithophaginae and Mytilinae.

In spite of considerable differences from a supposed *Mytilus*-like ancestor, the genus *Adula* appears to be of more recent origin. The geographic distribution of *Adula* in the northern part of the Pacific Ocean is rather restricted, compared to that of *Mytilus*, now present in many coastal regions of the world outside the tropics. The Eastern Pacific species of *Adula* occur predominantly in intertidal and shallow subtidal habitats, as do species of *Mytilus* and many pholadids. Although the boring capacity of the pholadids exceeds that of *Adula*, the substratum requirements of the former are similar to those of the latter species, except for *Adula diegensis*.

The fossil record of the Pholadidae dates back to the Jurassic (213–144 mya), while that of *Adula* is from the Miocene (25 mya), with records of *Adula californiensis* and *Adula gruneri* from Western America from the Pliocene (5 mya) (Coan et al. 2000). The genus *Mytilus* has existed at least since the Oligocene (34 mya) and thus precedes *Adula* by ~10 my. True lithophagines are much older, and date at least from the Jurassic, and perhaps even Upper Permian (286–248 mya) or the Carboniferous (> 320 mya) (Soot-Ryen 1969, Kleemann 1990, Morton 1990, Coan et al. 2000). It is therefore unlikely that the known nestlers and mechanical borers of *Adula* should have preceded the Lithophaginae.

CONCLUSIONS

Based on the fossil record, shell morphology, life history traits and spat behaviour, there is evidence that *Adula* evolved from *Mytilus*, or a common ancestor thereof. The genus *Adula* is well-defined and should be assigned to the Mytilinae Rafinesque, 1815. Whether *Botula* should be assigned to the Botulinae in spite of the lack of a clear definition of this subfamily, or to the Lithophaginae (Coan et al. 2000) remains unresolved. However, this genus is not closely related to *Adula*. Hence, *Adula* is not related to the members of the Bathymodiolinae or Lithophaginae to which it has hitherto been referred, based on superficial shell similarities.

ACKNOWLEDGEMENTS

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