# Ontogeny and autecology of an Early Cretaceous trigoniide bivalve from Neuquén Basin, Argentina

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Understanding ontogenetic variation is fundamental for adequate species definition and is the key for recognizing evolutionary relevant processes like heterochrony or developmental constraints. The larval and post-larval shell ontogeny and the ecology of the trigoniide bivalve *Myophorella garatei* are described in this paper. The species occurs in offshore transition facies of the late Valanginian Pilmatué Member of the Agrio Formation in the Neuquén Basin, Argentina. The larval shell has a rather small prodissoconch I; and if prodissoconch II is present, it is rather weakly developed. From these data, a larval stage of low dispersal capability is inferred for *Myophorella garatei*, either short-lived planktotrophic or nonplanktotrophic. The study of post-larval development included general shell shape and ornamentation. To assess general shell shape a geometric morphometric analysis was performed on the lateral view, together with a study of allometry for the shell width. As a result, two main allometric stages of development could be identified. During the first stage a relative size reduction of the area co-occurs with a slight elongation of the shell, while the second stage is marked by dorsal bending of the shell and an increase on relative width. Ornamentation was examined qualitatively, but also a geometric morphometric analysis was performed on the flank costae. The first two flank costae are subconcentric; from the third costa onwards they become oblique, intially changing from more curved to less curved shapes, while on a third stage they show the opposite trend. Finally, a general interpretation of the adaptive morphology of adult shell was performed, concluding that *M. garatei* was adapted to low energy, soft bottom environments, and probably lived with the posterior straight margin levelled at the water-sediment interface.

Key words: Mollusca, Bivalvia, Trigoniida, ontogeny, larval development, shell growth, allometry, life habits, Cretaceous, Argentina.

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## Introduction

Recognition of ontogenetic development is essential in any palaeobiological study that seeks to interpret fossils as living organisms, becoming fundamental in order to properly define species. Rather little is known about this subject for trigoniides. They were a very diverse group of bivalves during the Mesozoic (Cox 1952), but nowadays they are represented by a few species restricted to Australian sea waters (Fleming 1964). Much work has been done on the systematics of the group either on a regional scale (Hoepen 1929; Kobayashi 1954; Poulton 1979; Kelly 1984; Fleming 1987; Leanza 1993; Pérez et al. 2008) or on a global one (Crickmay 1932; Cox 1952), including some papers trying to establish the phylogenetic relationships among genera (Saveliev 1958; Newell and Boyd 1975; Cooper 1991; Boyd and Newell 1997). All genera have been usually interpreted as shallow burrowers (Newell and Boyd 1975), with shell morphology and ornamentation strongly correlated to their life habits and habitat (Stanley 1977; see also Francis and Hallam 2003 for a more recent review on the topic). The schizodont hinge is one of the most distinctive features of trigoniide shells, and it was interpreted as a coadaptation to the evolution of a strong muscular "T" shaped foot (Stanley 1977, 1978). Analysis of hinge development on the genus *Lyriodesma* allowed many authors to consider this genus as ancestral to the trigoniides (Waller 1998 and references therein) and the pattern of hinge development helped to understand the relationship of the Order to other major bivalve groups (Waller 1998). Modern species larval development was studied mostly focusing on the sister-group relation of trigoniides to the Order Unionida (O'Foighil and Graf 2000). Gould (1969) detected a negative allometric relationship of the byssal gland to foot length during ontogeny, from which he presumed a byssate juvenile
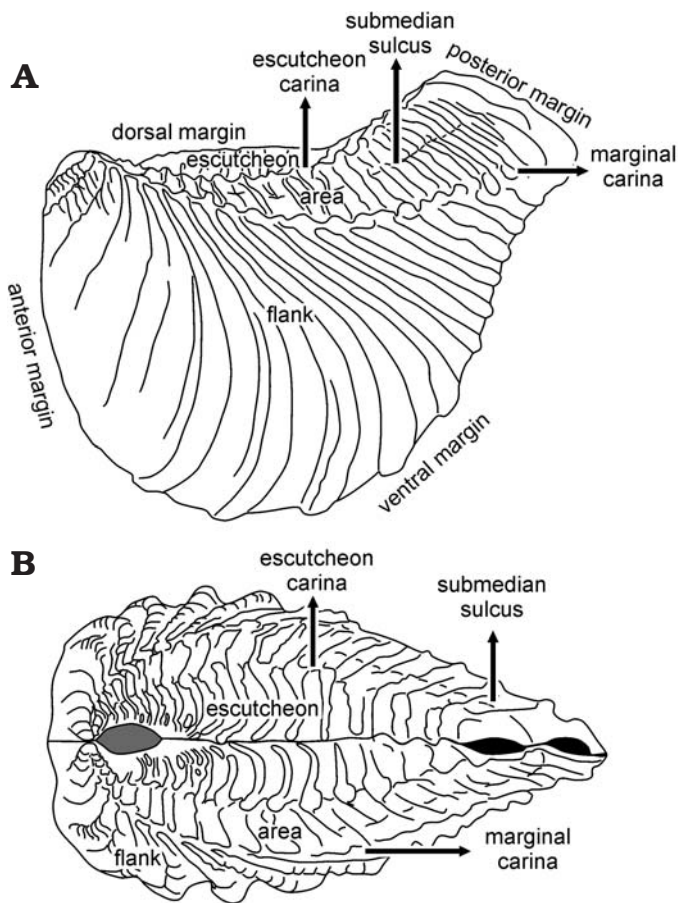
Fig. 1. Schematic drawing of the shell of an adult specimen of *Myopohorella garatei* Leanza, 1981 showing the main features of trigoniides shell morphology. **A**. Left lateral view. **B**. Dorsal view.

stage. When trying to establish the ancestor-descendant relationship among Jurassic trigoniides, Kobayashi (1954) calls attention to the juvenile dissoconch of the different taxa, and even the ancestry of the modern genus *Neotrigonia* could be established thanks to the study of early post-larval shells (e.g., Fleming 1964). Nevertheless, references to ontogenetic variability among fossil trigoniides are few, and most of them refer to post-larval development (e.g., Kobayashi 1954; Maeda and Kawabe 1966; Rudra and Bardhan 2006).

Larval development on fossil bivalves has seldom been considered in the literature, though several pioneer insightful contributions are known (e.g., Labarbera 1974; Lutz and Jablonski 1978; Tanabe and Zushi 1988; Palmer 1989; Malchus 2000, 2004; Tanoue 2003; Kaim and Schneider 2012; Schneider and Kaim 2012 and references therein), also for freshwater bivalves (e.g., Brodniewicz 1968). Most of them provided information on larval ecology, but only a few considered early postmetamorphic ontogenetic variation (e.g., Labarbera 1974; Malchus 2004) which is regarded as highly significant for the study of bivalve evolution (Malchus 2000).

The ontogeny of finely preserved specimens belonging to a fossil association of *Myophorella garatei* Leanza, 1981 (Fig. 1), recovered from the species type locality, is explored in this paper. Both larval and post-larval developments are analyzed, and at the same time the mode of life of the different ontogenetic stages is inferred from the morphological as well as geological data obtained.

*Institutional abbreviations*.—MCF-PIPH, Museo Paleontológico Carmen Funes-Paleontología de Invertebrados Plaza Huincul, Neuquén Province, Plaza Huincul, Argentina.

*Other abbreviations*.—CS, centroid size; PC, principal component; p, null hypothesis probability; PCA, principal component analysis; r, product-moment correlation coefficient; SMA, standardized major axis.

# Historical background

*Myophorella garatei* has been reported from the late Valanginian to the early Hauterivian in several localities of the Neuquén Basin (Leanza 1981, 1993; Echevarría 2012). When describing the species, Leanza (1981) related it to *Pterotrigonia tocaimana* (Lea, 1841) and to *M. coihuicoensis* (Weaver, 1931), later referred to *Pterotrigonia* by the same author (Leanza 1993). Subsequently he related it to *Myophorella hillebrandti* Reyes and Pérez, 1985 from the Neocomian of Chile and to *M. eufalensis* (Gabb, 1860) from the Upper Cretaceous of Mexico and the USA (Leanza 1993). There are also species from other basins that show some common features with *M. garatei*, like *M. orientalis* Kobayashi and Tamura, 1955, from the North Pacific, or *M. argo* (Crickmay, 1930b) from Western North America (Maeda and Kawabe 1966; Poulton 1979), but both of them differ from the former in their relatively wider area. *Myophorella yellowstonensis* Imlay, 1964, found in Middle Jurassic rocks from Western North America, is very similar to *M. garatei* according to the description and figures provided by Poulton (1979: 36, pl. 2: 17–22), differing probably in area ornamentation. Nevertheless, *M. garatei* seems to be more closely related to other species which also occur within the Neuquén Basin, like *M. elguetai* Leanza, 1993, and *M. volkheimeri* Leanza and Garate, 1987, or even to species referred to the genus *Pterotrigonia* like *P.coheni* Leanza, 1993 (Echevarría 2012). Since a detailed systematic revision is beyond the aim and scope of this contribution, the original generic assignment to *Myophorella*, in its widest sense, is maintained here, in the frame of the systematic scheme of Bieler et al. (2010) and Carter et al. (2011), including the genus in the superfamily Myophorelloidea within the Trigoniida.

# Geological setting

The Neuquén Basin is located on the eastern side of the Andes, between 32º and 40º S latitude (Fig. 2); from Early Jurassic to Early Cretaceous times it developed as a back-arc basin, allowing for the deposition of an up to 4000m thick sedimentary succession (Howell et al. 2005). The fossil
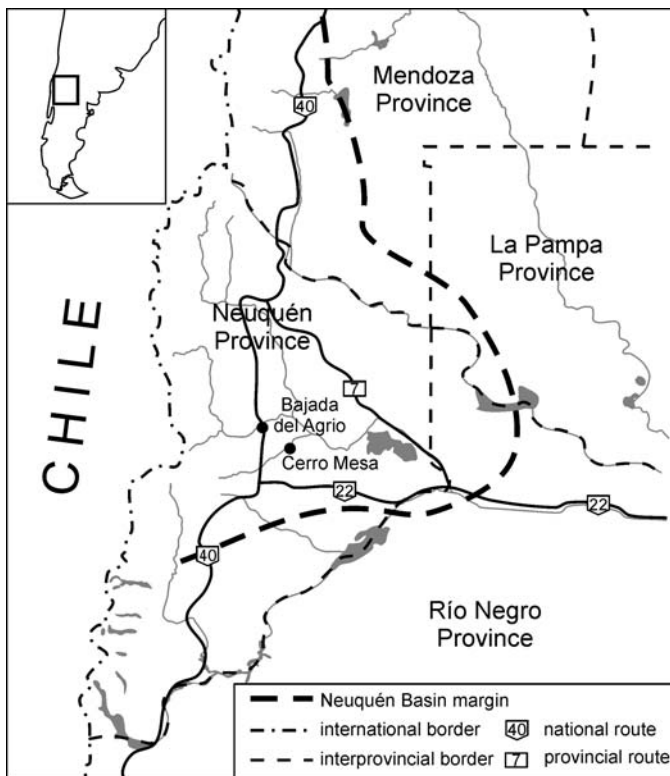
Fig. 2. Location map of Neuquén Basin for the late Valanginian–Hauterivian according to Legarreta and Uliana (1991), and of the localities of Cerro Mesa and Bajada del Agrio in Neuquén Province, Argentina.

assemblages containing *M. garatei* appear in the Pilmatué Member of the Agrio Formation, in beds of the *Pseudofavrella angulatiformis* Zone, indicating a late Valanginian age (Aguirre-Urreta et al. 2005, 2011). This lower member of the Agrio Formation was associated with a marine ramp environment with slow subsidence, and it accumulated during transgressive and highstand sea level phases (Spalletti et al. 2011). The fossil assemblages appear mostly in offshore transition facies, dominated by siltstone with sporadic intercalations of somewhat coarser sediment; the presence of nodules indicates pauses in sedimentation (Brett and Baird 1986). Lateral transport seemed to be nearly absent, but, on the other hand, the rate of time averaging (sensu Kidwell 1998) was relatively high in this environment during the deposition of the Pilmatué Member (Lazo 2006).

## Material and methods

The material analyzed was collected by the author at the locality of Cerro Mesa (Fig. 2). Some supplementary field observations were made at the stratigraphic section logged at Bajada del Agrio (Echevarría 2012). All the studied specimens are stored under the catalogue numbers MCF-PIPH 427 to 429; catalogue numbers represent only different times of collection, all samples being recovered from the same level (20–30 cm thick) of mostly pelitic siltstone. The absence of the taxon (either as in situ or ex situ material) on the beds under- and overlying this level is remarkable.

The low energy environment favoured an exquisite preservation of the shell of several individuals, allowing in many cases to trace the growth lines of early postlarval stages. Furthermore, the prodissoconch could be identified in a few specimens on scanning electron microscope (SEM) photographs. The classification scheme by Jablonski and Lutz (1983) was used to identify the larval developmental types.

Post-larval development was characterized by features of the general shell shape and the ornamentation. For general shell shape a geometric morphometric analysis was performed on lateral view photographs and camera lucida drawings of the shells, following the procedures outlined by Zelditch et al. (2004). Three homologous landmarks were set to define three open curves that were quantified using semi-landmarks (Fig. 3A). Landmark 1 was set at the umbo, although in those cases where the umbo was hidden due to the strong incurvature of the shell, the point of maximum curvature on the umbonal region was considered as landmark 1, and thus must be regarded as a type 2 landmark (sensu Bookstein 1991; see Zelditch et al. 2004 for a good explanation on landmark types and their implications). Landmarks 2 and 3 mark the intersection of the posterior margin with the escutcheon carina and with the marginal carina respectively; both are type 1 landmarks (sensu Bookstein 1991). The curves delimited by these landmarks are the escutcheon carina (between landmarks 1 and 2), the marginal carina and the antero-ventral margin of the shell (both of them between landmarks 1 and 3). For the escutcheon carina two semilandmarks and four helper points were established, while the marginal carina was characterized by two semilandmarks and six helper points; the antero-ventral margin was traced by five semilandmarks and 13 helper points (Fig. 3A). Multivariate linear regressions were calculated for the different post-larval stages identified, and the significance of the dependence of shape on size was evaluated by means of a resampling-based version of the test of Goodall's F value, which is the ratio of the explained and unexplained variation (Zelditch et al. 2004). As usual for the geometric morphometric analysis, centroid size (CS), or its logarithm whenever appropriate, was used as size estimator. The centroid on a landmark configuration is located at the mean position of all the coordinates. To obtain the CS the squared distance of each landmark to the centroid is calculated; all these square distances are summed and the square root of this sum results on the CS (Zelditch et al. 2004).

Regression equations among ontogenetic stages were compared by means of resampling techniques established on Zelditch et al. (2004). To compare multivariate regression vectors, the angle between them is measured; when two vectors have the same direction the angle between them is 0º, while the higher the angle between trajectories, the more different the shape changes implied by them will be. To test for the significance of the angle (i.e., if the angle among vectors is significantly different from 0º) a confidence interval is
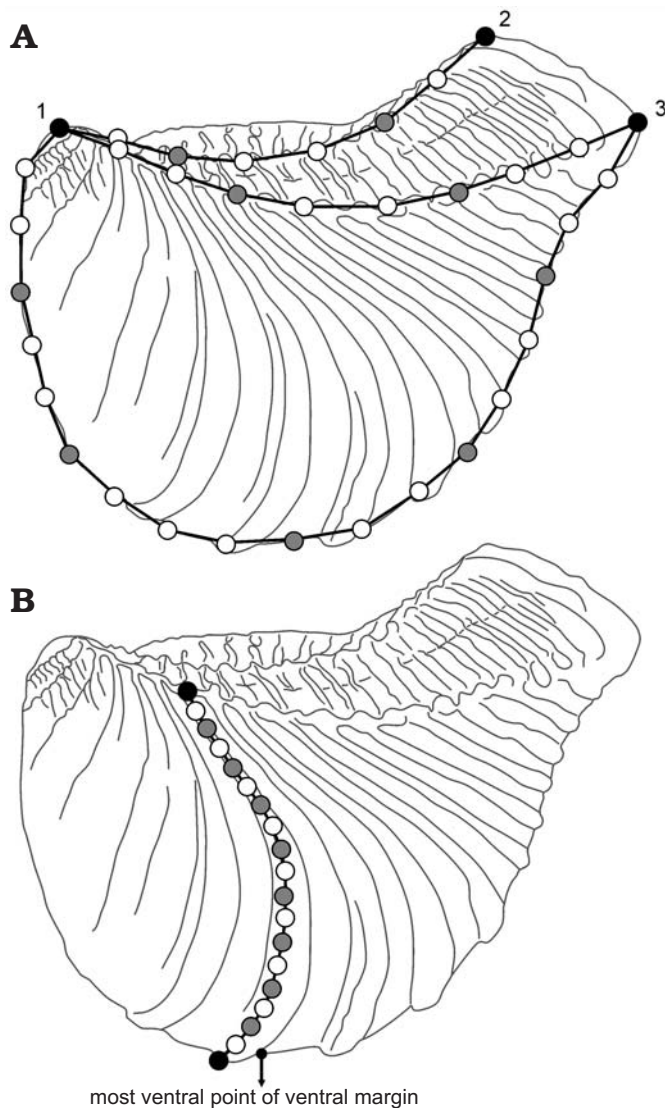
Fig. 3. Landmarks and semilandmarks used on geometric morphometric analyses; black dots, landmarks; grey dots, semilandmarks; white dots, helper points. **A**. Landmarks and semilandmarks used for the general shell shape analyses; 1, landmark 1, the umbo; 2, landmark 2, intersection between the escutcheon carina and the posterior margin; 3, landmark 3, intersection between the marginal carina and the posterior margin. **B**. Landmarks and semilandmarks used for the costae shape analysis.

determined for each vector by resampling, and it is expressed as a within-group angle. If the inter-group angle is larger than the 95th percentile of the range of both within-group angles, then the inter-group difference is judged to be statistically significant at the 5% confidence level.

Digitization of the landmark configurations was performed on TPSdig2.12 software (Rohlf 2008). Procrustes superimposition was accomplished with CoordGen6h software (Sheets 2001). Semilandmark sliding (to perpendicular alignment on the reference) was developed on SemiLand6 software (Sheets 2003). PCAGen6p software (Sheets 2001) was used to perform principal component analysis (PCA). Regress6N and VecCompar6c softwares (Sheets 2003) were used for all the regression analysis.

Also, in order to analyze the relative width of the shell during ontogeny, an allometry analysis was performed between width and the straight distance from the umbo to the posteriormost point of the marginal carina (from now on referred to as umbo-posterior point distance). This is the distance between landmarks 1 and 3 and thus allows for direct comparison of these measurements with the results of the geometric morphometric analysis. The procedures applied for the allometry analysis are those explained by Warton et al. (2006). The analyses was performed by calculating the logarithm of both variables and then obtaining the slope of the linear regression between width (ordinates or y-axis) and the umbo-posterior point distance (abscissae or x-axis), using the standardized major axis (SMA) method. The slope of that regression can be considered as the allometric coefficient; slope values of 1 indicate isometric relationship between variables, while values lower than 1 will indicate negative allometry, expressing a relative decrease of y respect to x, and values of slope higher than 1 will indicate positive allometry, implying a differential increase of y relative to x (Gould 1966). All the calculations were done on PAST 2.10 software (Hammer et al. 2001).

Ornamentation was analyzed qualitatively, but also a geometric morphometric analysis was performed on the flank costa closest to the most ventral point on the ventral margin (Fig. 3B). Unlike landmarks 1, 2, and 3 shown in Fig. 3A, the landmarks established as boundaries for the curve of the costae (the origination of the costa from the marginal carina and the end point of the costa) are not true biologically homologous points, but are only geometric points established for comparison. Eight semilandmarks and nine helper points were set between the landmarks (Fig. 3B).

# Results

**General characterization of the species**.—*Myophorella garatei* has a small subtrigonal shell (up to 2.5 cm long), somewhat inflated anteriorly; the umbones are opisthogyrate (as in most trigoniides) and the dorsal margin is concave (Fig. 1). Marginal and escutcheon carinae bearing tubercles are well developed, delimiting a relatively narrow area with a submedian sulcus. The escutcheon is ornamented with transverse ribs bearing very small tubercles. The area is ornamented anteriorly by concentric costae that posteriorly lead to more densely disposed fine ridges. Flank costae are concentric or subconcentric near the umbo with small transverse crenulations on them, whilst in later stages they become typically oblique, curving progressively in anterior direction and usually lacking any ornamentation. These features agree with the characterization provided by Leanza (1981, 1993) for the species. On the original description, certain variability within the species was already recognized, especially regarding relative width and flank costae shape (Leanza 1981).
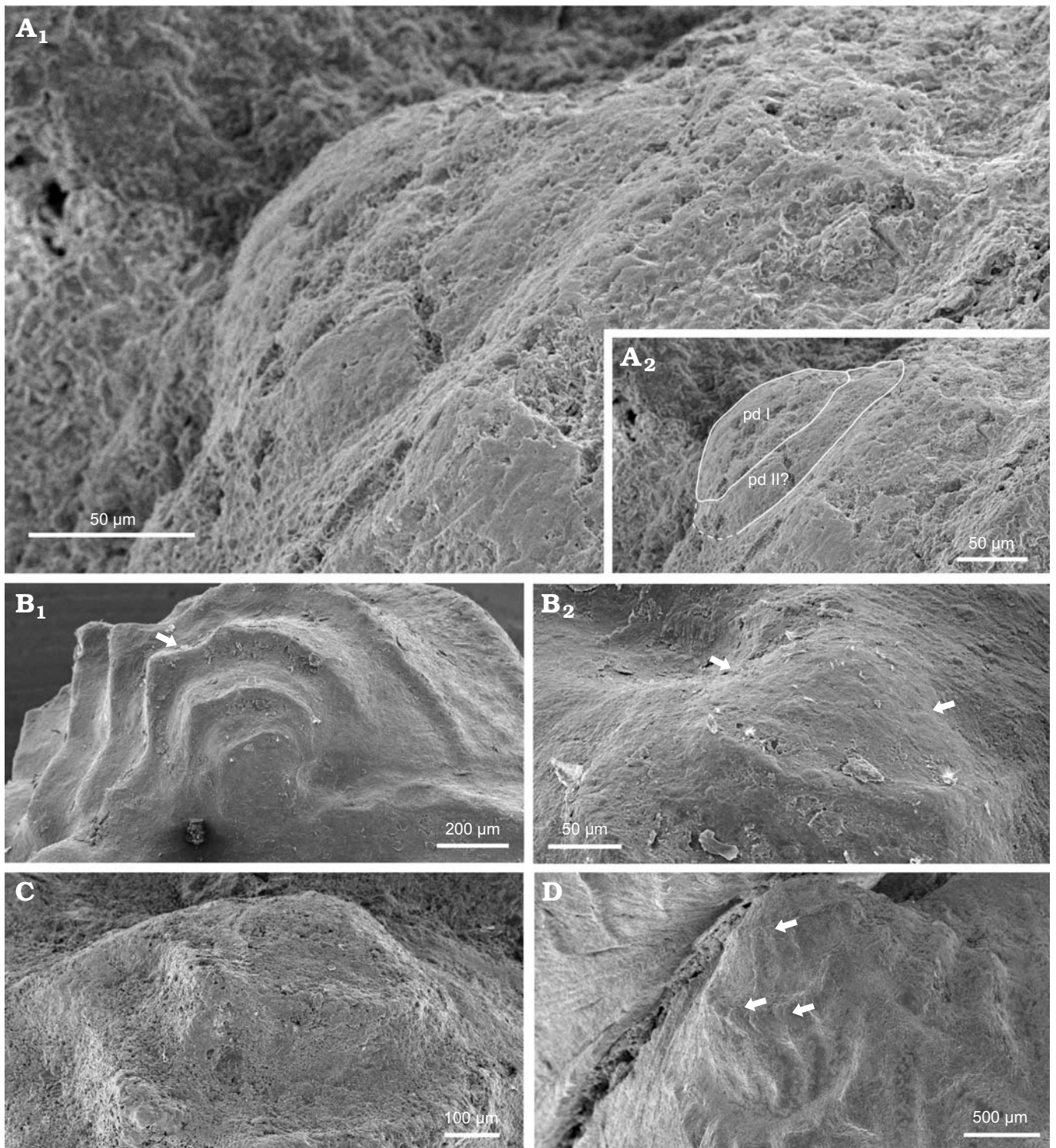
Fig. 4. SEM photographs of the umbonal region of *Myophorella garatei* Leanza, 1981; late Valanginian, Cerro Mesa. **A**. MCF-PIPH-428, umbonal region of left valve showing the preserved prodissoconch (pd); detail of the prodissoconch (A$_1$); same picture showing the discontinuities identified on the shell surface and their possible interpretation (A$_2$). **B**. MCF-PIPH-428, prodissoconch in lateral (B$_1$) and ventral (B$_2$) views, together with early postmetamorphic shell; white arrow on B$_1$ points to the antecarinal sulcus, white arrows on B$_2$ indicate a discontinuity on the shell, probably the margin of prodissoconch I. **C**. MCF-PIPH-428, prodissoconch in ventral view together with early postmetamorphic shell. **D**. MCF-PIPH-428, umbonal region showing early postmetamorphic flank costae with *Haidaia* type ornamentation (white arrows) and early area development.

**Prodissoconch**.—The prodissoconch was identified in at least five individuals on SEM photographs (Fig. 4). Only in a few cases could a full lateral view of the prodissoconch be obtained in specimens with disarticulated valves (Fig. 4B$_1$), but unfortunately their preservation did not allow for a proper characterization of prodissoconch shape. The best preserved
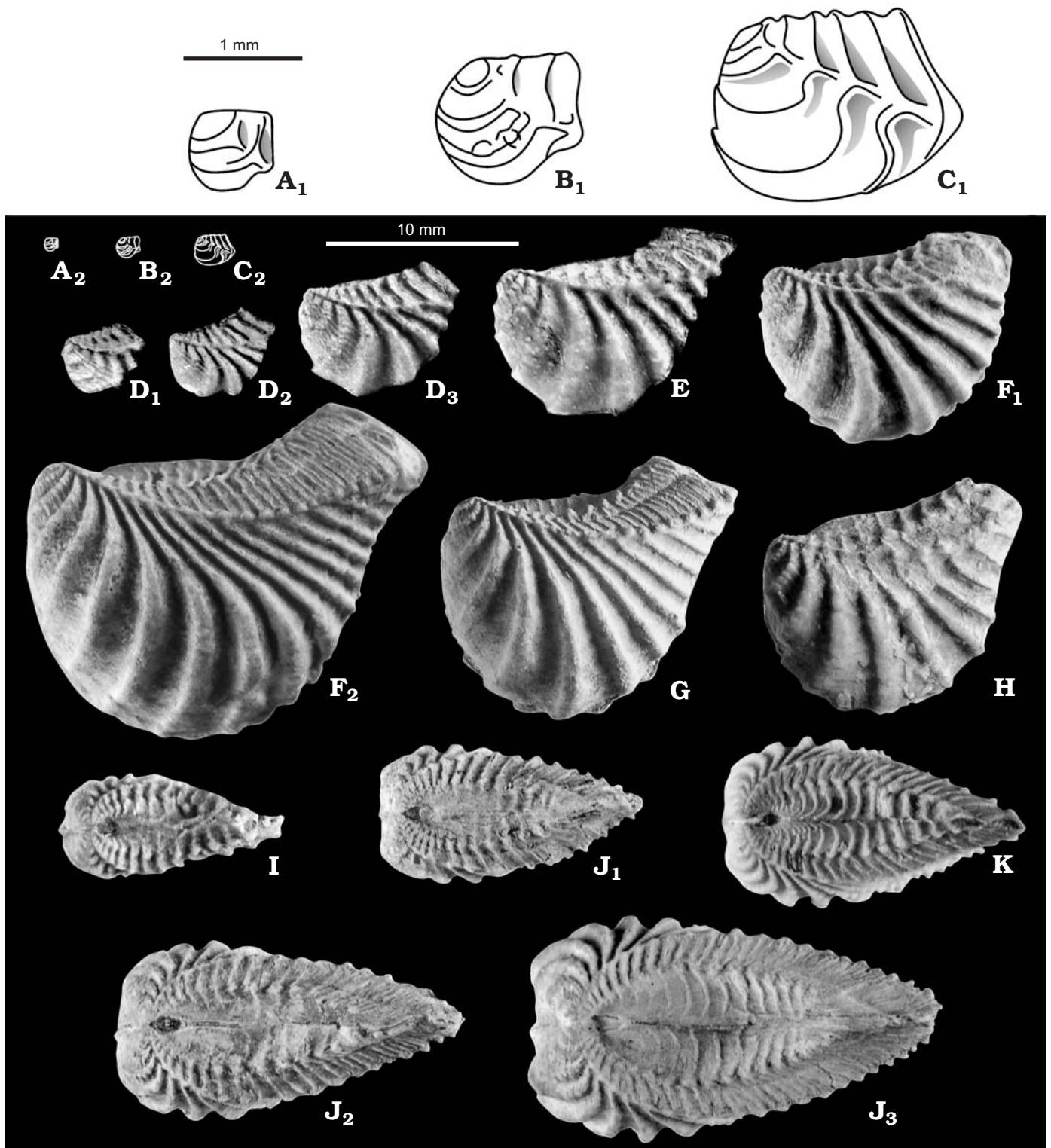
Fig. 5. Individuals of *Myophorella garatei* Leanza, 1981 representing different size categories on the ontogenetic series; late Valanginian, Cerro Mesa. **A–C**. Stages recovered from growth lines; MCF-PIPH-428, drawn by camera lucida on lateral view ($A_2$, $B_2$, $C_2$), enlargements ($A_1$, $B_1$, $C_1$). **D**, **E**. Stages recovered from growth lines and photographed on lateral view. **D**. MCF-PIPH-428. **E**. MCF-PIPH-429. **F–H**. Individuals recovered on their final growth stage on lateral view. **F**. MCF-PIPH-428. **G**. MCF-PIPH-427. **H**. MCF-PIPH-429. **I–K**. Dorsal view of some individuals on different stages. **I**. MCF-PIPH-428. **J**. MCF-PIPH-429. **K**. MCF-PIPH-427.

prodissoconch (Fig. 4A) belongs to an individual with both valves preserved and articulated, hence making it impossible to get a lateral view of the larval shell.

Regarding distinction of prodissoconch I and II the results are not conclusive. Two distinct surfaces can be recognized on the umbonal region of at least three individuals, delim-

Table 1. Prodissoconch sizes (in μm) for 5 individuals of *Myophorella garatei*, discriminating, whenever possible, between prodissoconch I (pds I) and possible prodissoconch II (pds II?).

| Sample | Prodissoconch size | |
|---|---|---|
| | pds I | pds II? |
| PIPH-428 | 148 | 195 |
| PIPH-428 | 135 | 196 |
| PIPH-428 | 137 | 239 |
| PIPH-427 | ? | 290 |
| PIPH-428 | ? | 352 |

ited by discontinuities on the shell. Fig. 4A shows the best preserved one, while Table 1 lists measures of larval shells length with both parts discriminated whenever possible. If these two regions are regarded as prodissoconch I and II, then the first stage ranges between 135 to 150 μm in length, while the second one is about 200 to 350 μm in length. On the other hand, if the second region is considered as a "precosta" space on the dissoconch, then only the prodissoconch I would be present pointing out to a remarkably small larva.

**Post-larval shell shape**.—For post-larval stages 96 landmark-semilandmark configurations were obtained, encompassing a range of sizes from 0.7 to 21.9 mm (umbo-posterior point distance). Fifty-nine of these configurations were recovered from growth lines on larger individuals, and they include most of the juveniles smaller than 10 mm. Fig. 5A–H
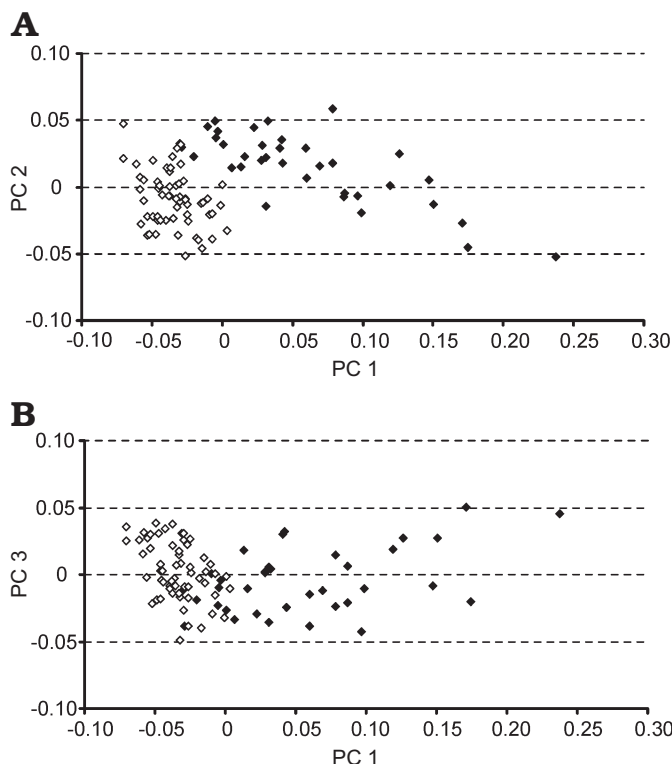
**A**

**B**



Fig. 6. PCA of the general shell shape in lateral view, showing PC 1 (65.6% of variance), PC 2 (11.8% of variance) and PC 3 (9.1% of variance); black diamonds, first growth stage; white diamonds, second growth stage. **A**. PC 1 versus PC 2. **B**. PC 1 versus PC 3.

shows some individuals representing different size categories. From these configurations, a PCA was performed, with the PC 1, 2, and 3 holding 85% of variance. As can be seen in Fig. 6, these PCs tend to order landmark-semilandmark configurations into a curve that could be simplified as two straight lines meeting at an angle. When the values of each individual for each of these PCs are compared to their corresponding sizes (with logarithm of centroid size [CS] as size estimator), then a clear correlation between size and shape appears, especially for the PC 1 ($r = -0.92$, $p \ll 0.01$). This implies that smaller shells tend to present higher values for the PC 1, while as the shell grows its morphology is displaced to lower values. For PC 2 and PC 3 there seems to be a two-phase behavior: for CS values lower than 20, PC 2 is positively correlated to log(CS) ($r = 0.68$, $p \ll 0.01$) and PC 3 is negatively correlated with it ($r = -0.54$, $p < 0.01$); on the other hand, for CS values higher than 20 there is an inverse trend, at least for PC 2 ($r = -0.57$, $p \ll 0.01$), while PC 3 shows a positive correlation ($r = 0.20$) but not statistically significant ($p = 0.12$). As a result, post-larval ontogeny could be divided into two main stages (Fig. 6): the first one including from the earliest postmetamorphic stages to individuals with a CS of 20 (about 8 mm umbo-posterior point distance); the second one including all the larger individuals.

When analyzing the multivariate regression vectors of the ontogenetic trajectories for both stages, the first one shows a significant correlation between shape and size ($p < 0.001$ for the bootstrapped fraction of variance explained and for the bootstrapped Goodall's F value) using the logarithm of CS as a size estimator. This ontogenetic trajectory resulted in a reduction in relative surface for the area and some elongation associated (Fig. 7A, B), and it is significantly different from the isometry (with a 90.6° inter-group angle and a 14.7° within-group angle for the ontogenetic trajectory).

During the second post-larval ontogenetic stage a dorsal bend of the area clearly appeared, associated with some posterior expansion (Fig. 7B, C). Once again, shape and size (logarithm of CS) were significantly correlated ($p < 0.001$ for the bootstrapped fraction of variance explained and for the bootstrapped Goodall's F value) and the ontogenetic trajectory was significantly different from the isometry (a 89.2° inter-group angle and a 42.5° within-group angle for the ontogenetic trajectory); internal variability was much higher than in the first stage, probably indicating that ontogenetic variation was lower in this second stage, and so individual variation was higher in proportion. When compared to each other, both stages were significantly different (82.1° inter-group angle, while the within-group angles are 15.6° for the first stage and 40.2° for the second stage).

The relationship between width and the distance from the umbo to the posteriormost point of the marginal carina was then analyzed; ontogenetic variation of this relationship can be seen in Fig. 5I–K. Both variables were plotted on their original scale (Fig. 8A) and on logarithmic scale (Fig. 8B). In both cases, the correlation between variables is clear ($p \ll 0.01$), and the results for the data on logarithmic scale
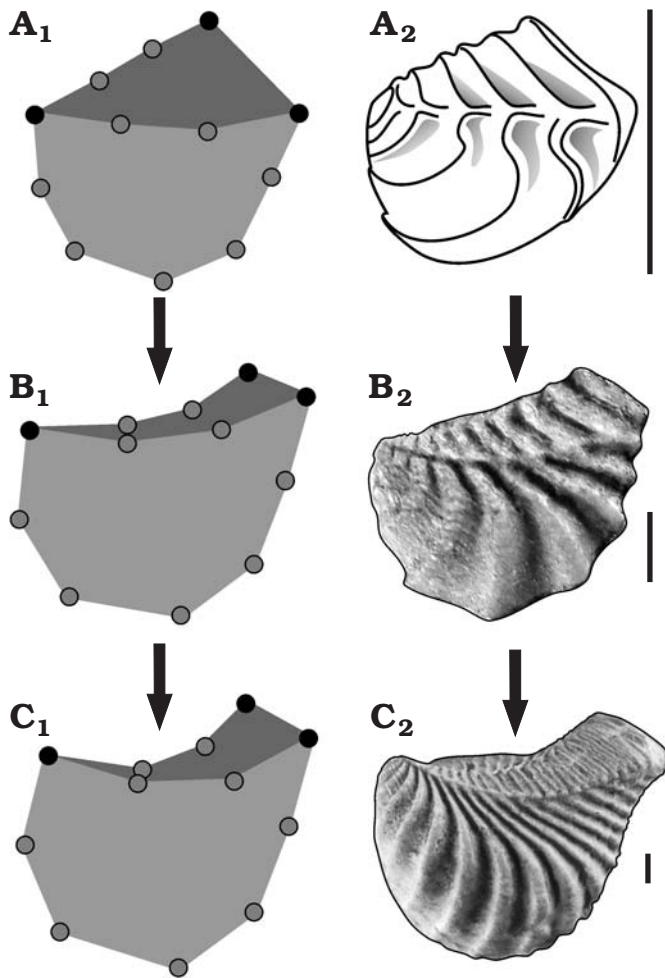
Fig. 7. Changes implied on general shell shape in lateral view for the two recognized post-larval growth stages. Changes for the first stage (A→B). Changes for the second stage (B→C). Landmark-semilandmark reconstruction ($A_1$–$C_1$), reconstruction represented by individuals of the ontogenetic series ($A_2$–$C_2$). Scale bars 2 mm.

show a positive allometry for the width respect to the umbo-posterior point distance (slope = 1.22, $p_{(slope = 1)}$ <<0.01). Nevertheless, Fig. 8 shows that there seems to be two different relations between variables: the values of width corresponding to umbo-posterior point distances lower than 11–12 mm show a different response than those higher than that threshold value. So a new analysis was performed for each of these groups, considering the values of umbo-posterior point distance between 11 to 12 mm as a transition (i.e., they were included in both groups). As a result, the first stage seems to have an isometric relationship between both variables (slope = 1.04, $p_{(slope = 1)}$ = 0.60), while the second stage shows a positive allometry for the width respect to the umbo-posterior point distance (slope = 1.48, $p_{(slope = 1)}$ <<0.01). The correlation was significant in all cases (p <<0.01).

**Post-larval shell ornamentation**.—Regarding ornamentation, flank costae show some variation that seems to be related, to some extent, with shell shape. The first costa appears early after metamorphosis (Fig. 4A–C); first and second costae seem to be concentric or subconcentric (Fig. 5A, B), being continuous with area costae. Differentiation of flank and area is marked by the development of a marginal carina and the presence of a shallow antecarinal sulcus (Fig. 4B) which does not interrupt flank costae. Sulcus width is about 100 μm on the first costa, it grows on the second and third ones but after that it remains constant, about 300–400 μm wide. The third costa is clearly oblique to the growth lines, with a first small portion related to the antecarinal sulcus and probably originating together with the associated area costa, a second portion almost straight and a third portion curving forwards. Geometric morphometric analysis of oblique costae shows, once again, a two stages ontogenetic development. The boundary between both stages is between a CS of 12 to 14 (size of costae, measured as the straight line between both landmarks, from 8.5 to 10 mm, umbo-posterior point distance between 11 and 15 mm). During the first stage costae changed from a strongly curved to a gently curved line (Fig. 9A, B), while during the second
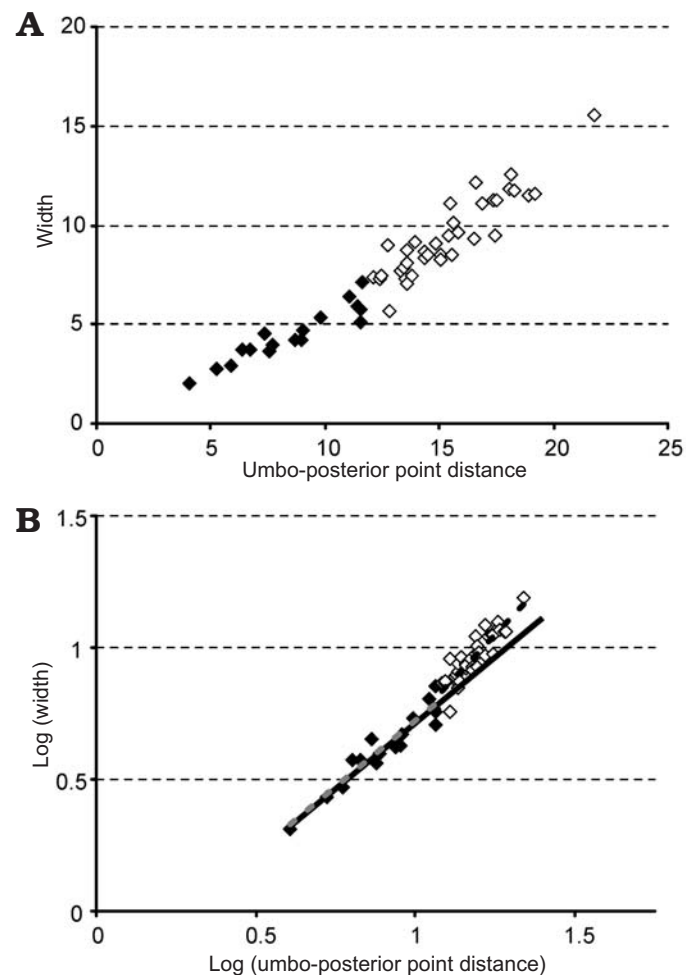


Fig. 8. Allometry analysis for the width compared to the umbo-posterior point distance; black diamonds, first stage (isometric); white diamonds, second stage (allometric). **A**. Cartesian graphic of width vs. umbo-posterior point distance. **B**. Cartesian graphic of the same variables with both of them converted to logarithm; black continuous line, line of slope 1; grey dashed line, regression line for the first stage; black dashed line, regression line for the second stage.
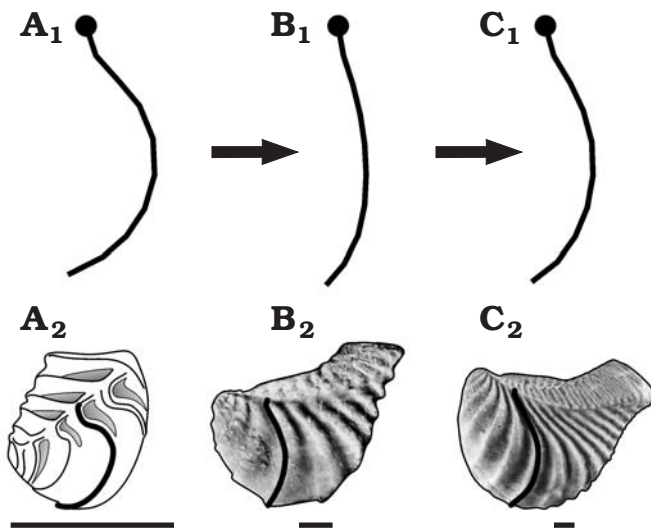
Fig. 9. Changes implied on costae shape for the two recognized post-larval growth stages with oblique costae. Changes for the first stage (**A→B**). Changes for the second stage (**B→C**). Landmark-semilandmark reconstruction ($A_1$–$C_1$), reconstruction represented by individuals of the ontogenetic series ($A_2$–$C_2$). Scale bars 2 mm.

stage the change was reversed (Fig. 9B, C). In both cases the correlation between line shape and size (CS) is significant (p <0.001 for the bootstrapped fraction of variance explained and for the bootstrapped Goodall's F value in stage 1, p = 0.022 for the bootstrapped fraction of variance explained and for the bootstrapped Goodall's F value in stage 2), and as it was expected, ontogenetic trajectories are clearly different (inter-group angle of 150.3°, within-group angles of 49.7° for stage 1 and 53.1° for stage 2).

Small tubercles over the flank costae projecting into the intercostal spaces as fine ridges were identified on all studied individuals. This particular type of ornamentation results in a crenulated ventral slope on flank costae (Leanza 1993), a feature used to characterize the subgenus *Myophorella (Haidaia)*. On *M. garatei* it seems to be restricted to the initial post-larval stages (Fig. 4D), although its first appearance is variable within the population; while on some individuals it appears with the first costa, on others its development is delayed. Costae developed later on the ontogeny seem to be relatively wide and smooth, although mature individuals with strong tubercles over all their costae can be found.

Area ornamentation is characterized by the presence of concentric elements; during the early stages well defined concentric costae can be identified (Figs. $4B_1$, 5A–E), usually continuous with flank and escutcheon costae, and becoming more loosely arranged as the animal grows. Later on, costae are replaced by less developed striae or ridges, generally in greater number and with a more irregular disposition (Fig. $5F_2$, I).

# Discussion

**Larval development and life habits**.—Based on their feeding type, Jablonski and Lutz (1983) characterized two main developmental categories of larvae: planktotrophic and nonplanktotrophic. Planktotrophic larvae depend on smaller planktic organisms for nutrition, being planktic themselves, and thus spending a significant portion of their development time in surface waters. Lecithotrophic larvae, on the other hand, are nourished by the yolk of the eggs, thus being nonplanktotrophic; they can be entirely nonplanktic or they can remain in the plankton for little more than a few hours to a few days. According to Lutz et al. (1980) and Jablonski and Lutz (1983), planktotrophic veligers bear a small prodissoconch I (70–150 μm in length) and a large prodissoconch II (200–600 μm in length), while lecithotrophic veligers have larger prodissoconch I (135–230 μm in length) and poorly developed prodissoconch II. Species with larvae lacking a planktic stage (e.g., brooded or encapsulated larvae) have an even larger prodissoconch I (230–500 μm in length), which is often inflated and may show irregular folds and wrinkles.

The preservation of the studied material of *Myophorella garatei* allows for two different interpretations. On one hand, if we consider that only prodissoconch I is present, then the larval development should be considered as non-planktotrophic. Considering the environmental setting and the body size of adult individuals, this scenario seems plausible, as towards deeper waters and as body size gets smaller there is a trend from planktotrophy to nonplanktotrophy dominance on the development of bivalves (Jablonski and Lutz 1983). On the other hand, if we consider the second stage recognized on shell surface as a prodissoconch II, then larvae should be regarded as planktotrophic; although in only one individual could this second stage be interpreted, its general morphology and curvature seems to follow that of prodissoconch I (Fig. 4A).

The size of prodissoconch I is close to the boundary between planktotrophic and nonplanktotrophic developmental types (Table 1), hence making it difficult to decide between both developmental scenarios. If we want to compare with a related species with known developmental characteristics, as suggested by Jablonski and Lutz (1983), then we should check on the only living genus for the whole order: *Neotrigonia*. Based on a juvenile shell of *Neotrigonia margaritacea* (Lamarck, 1804), O'Foighil and Graf (2000) concluded that that species lacks an obligate planktotrophic larval stage in its life cycle, but they could not determine if larval development is benthic or pelagic. The identified larval shell of the living species is much larger (668 μm long) than on *M. garatei* and it lacks a well-defined prodissoconch II. These data seem to favour a planktotrophic developmental type for the latter; nevertheless, it has to be considered that, according to the systematic scheme used, *Neotrigonia* belongs to a different superfamily and, probably most importantly, both species are separated by at least 130 million years and the considered time of divergence is at least the Jurassic, so we have to be cautious on the comparisons.

Whichever was the developmental type of *M. garatei* larvae, what is clear from the results obtained is that they spent little or no-time on the water column. Even considering that *Myophorella garatei* had a planktotrophic larval development,

the small size for prodissoconch II (200 to 350 μm long) suggests that this planktotrophic stage was short lived. Regarding this, Mileikovsky (1971) pointed out that planktotrophic development can be short, involving two or three days, or even just a few hours. Although developmental type is not always associated with geographic distribution (see Liu et al. 2007), this may imply a poor dispersal capacity for *M. garatei*.

**Post-larval development**.—During metamorphosis the larva acquires organs and structures typical of the adult form; afterwards the bivalve only grows and matures. Mollusc shells grow by accretion, adding new material at the margin and lining the inside with new layers (De Renzi 1990). In many bivalves the direction of growth at any region of the mantle edge may be discriminated into: (i) a radial component radiating from the umbones and acting in the commissure plane; (ii) a transverse component acting at right angles to the commissure plane (Wilbur and Owen 1964: 218–219, fig. 5A, B). This kind of growth results in a planispiral coiled orthogyrate shell. Nevertheless, in both prosogyrate and opisthogyrate conispiral shells a third growth component can be recognized: (iii) a tangential component acting tangentially and in the same plane of the commissure (Wilbur and Owen 1964: 219, fig. 5C). Radial and tangential components will oppose each other at one side of the umbo, while they will add to one another at the opposite side; on opisthogyrate shells, like those here studied, they oppose posterior to the umbones, resulting in a relative reduction of the postero-dorsal margin of the shell.

From the analysis of general shell shape on lateral view and relative width, two growth stages were inferred for the development of the shell. The first stage results in a relative reduction of area surface due to a relative reduction of the posterior margin. Together with this major change, there is some elongation of the shell associated with the development of a short rostrum; this change is due to an increment on the radial component of growth for the posterior margin of the shell. Growth during this first stage is clearly allometric, since there is a change in proportions of the shell. Nevertheless, relative width seems to be constant during this stage, so this character shows an isometric development during this first stage. At a size of about 8 mm (umbo-posterior point distance), a transitional stage, leading to the second one, begins. This transitional stage is marked by a strong increment on the tangential growth component, resulting in a dorsal bending of the shell and a concave dorsal surface. This tangential component is maintained during the second growth stage, for which some peculiarities of spiral growth and geometric morphometric analyses must be considered. Since we are characterizing structures with accretionary spiral growth, their shape will change unavoidably as new material is added, resulting in progressively more curved shapes as the spirals defining them grow. This change will be shown as an allometric trend on a geometric morphometric analysis (as it was obtained for the second developmental stage) since analyzed curves will be steeper even if growth is isometric.

In conispiral shells, growth is considered isometric only if it follows a logarithmic spiral and orientation of the accretion process is maintained (De Renzi 1990). None of these conditions can be either confirmed or refuted in the case under study, and since the change in shape detected by the geometric morphometric analysis can be explained by the conispiral growth, it can not be established whether growth is allometric or isometric for this character. Nevertheless, at about sizes of 11 to 12 mm (umbo-posterior point distance) shell relative width tends to increase with size, resulting in a more inflated shell and in an allometric trend. This is the result of a relative increment to the transverse growth component of the shell, mostly at its anterior margin, since maximum width is anteriorly displaced. It must be considered that most size values lower than 10 mm were obtained from growth lines identified on larger individuals, hence the width estimation may be somewhat imprecise, especially on the smaller ones (in fact, the width could not be measured in majority of the smallest configurations considered on the geometric morphometric analysis) and the boundary between inflation stages should be considered as an approximation. As a result there are two well defined growth stages on the shell, united by a transitional stage of somewhat mixed features; both stages can be considered as allometric, although not always the same character is the one changing.

Regarding ornamentation, flank costae show some variation during ontogeny; the first two costae are concentric, as recognized by Kobayashi (1954) for the genus. Subsequent costae are all oblique; the first portion of each, associated with the antecarinal sulcus, seems to originate from the most ventral part of the concentric ribs on the area (Fig. 4B$_1$, D); from that initial stage, the mantle points related to rib secretion would have migrated along the ventral margin, probably with a constant displacement on each growth increment (Ubukata and Nakagawa 2000; Checa 2002). Assuming constant displacement of the secretion point, then juveniles, with smaller mantle margins, should show strongly curved costae, while curvature should decrease as the animal (and hence the mantle edge) grows. This kind of development can be seen during the first stage identified for flank costae (Fig. 9A, B). The second stage of development, on the other hand, shows an opposite trend, and seems to coincide with the increase in relative width of the shell. This change in general shell shape may be affecting the 2D projection of the costae, producing more strongly curved ribs on lateral view (Fig. 9B, C). Besides these changes on shape, there are also ontogenetic changes on costae ornamentation; early postmetamorphic stages show a well developed *Haidaia* type ornamentation, which seems to disappear as shell grows.

According to Seilacher (1970) skeletal morphology will be controlled by three main factors: an adaptive factor, a constructional factor and a phylogenetic factor. The adaptive factor of shell morphology will be discussed in the next section, while here focus will be on constructional and phylogenetic aspects. To check for constructional factors, comparison with bivalves of similar morphology is useful. There are many bivalves with

a developed rostrum (e.g., nuculanids, cuspidariids), most of them opisthogyrate (a fact suggesting a constructional link between both characters), but there are few references to their development, except for the data provided by Labarbera (1974) for *Nuculana trochila*. The comparison of *Myophorella* to phylogenetically distant protobranchs (e.g., to nuculanids) with completely different life habits (filter-feeders vs. deposit feeders) provides an excellent opportunity to analyze the constructional aspect of the shell, since the convergence in the development of a rostrum will not be obscured by adaptive aspects (both species have different modes of life) or phylogeny (shell shape evolved separately in both lineages). Labarbera (1974) found an early development of the rostrum in *N. trochila*, causing the length/height ratio of the shell to increase during the development from early post-metamorphic stages to sizes of about 7.5 mm long. Although he tried to find an adaptive explanation for this early development (i.e., a function for the rostrum on the early juvenile), its coincidence in an entirely different group suggests not a functional but a constructional factor conditioning the growth of early post-larval shells; i.e., to reach the adult proportions the rostrum should develop early. At about 5 mm in length, relative width of the shell in *N. trochila* experienced a drastical increment; this change is similar to that observed on *M. garatei*, although in the nuculanid occurs when the elongation of the shell is still increasing.

To analyze the phylogenetic aspect of shell shape, a comparison with related species is needed. Although the ontogenetic sequence for general shell shape can not be extrapolated to the whole genus—since there are many species without rostrum and with orthogyrate to weakly opisthogyrate shells—the development in those species with somewhat rostrate shells (e.g., see Poulton 1979: pls. 2, 5, 9; Leanza 1993: pl. 2: 17; Francis and Hallam 2003; Pérez et al. 2008: pls. 11, 12) is probably similar to the one described for *M. garatei*, at least for the general shell shape on lateral view. Also interesting is the fact that the C trend of Kobayashi (1954) leading to the genus *Pterotrigonia* can easily be reproduced from a rostrate species of *Myophorella* by simple extension of the first stage (producing a more prominent rostrum and a less expanded area) and by a stronger tangent component of growth during the second phase (generating the "twisting of the growth spire" described by Kobayashi 1954). Nevertheless, until detailed ontogenetic analysis on shell morphology of other species (of both genera) is performed this evolutionary link will remain theoretical.

Costae development shows no major differences with other species of the genus, with the oblique ribs representing the D trend of Kobayashi (1954). *Haidaia* type ornamentation may bear phylogenetic relevance; this kind of ornamentation is widespread among fully grown specimens of many species belonging to *Myophorella* and *Pterotrigonia*, and it has been usually considered as evidence of an evolutionary relationship between these two genera (Kobayashi and Nakano 1957; Kelly 1995; Rudra and Bardhan 2006). In *Myophorella garatei* this ornamentation may be considered as vestigial,

pointing to some phylogenetic relationship with more strongly ornamented species from the same basin, like *M. elguetai* or *M. volkheimeri* (Leanza 1993); actually, the few tuberculated adults of *M. garatei* found are very similar to this last species, not only in ornamentation but also in general shell shape. Changes on area ornamentation do not differ significantly from those identified by Maeda and Kawabe (1966) for *Myophorella orientalis* from the Upper Jurassic to Lower Cretaceous of Japan. In fact it may probably be common to most *Myophorella* species, as pointed out in the characterization for the genus by Crickmay (1932) and as can be seen in many published materials (e.g., Poulton 1979; Cooper 1991: fig. 5; Leanza 1993: pls. 12: 8–12, 9: 9–11; Pérez et al. 2008: pl. 12). This kind of ornamentation can also be seen in species referred to *Pterotrigonia*, like *P. coheni* Leanza, 1993 (Echevarría 2012), suggesting once again a phylogenetic relationship between both genera. Unfortunately little attention was paid to the ontogenetic variation of the area ornamentation on most published descriptions, making hazardous any generalization, and there may be even some species of *Myophorella* with more regular ornamentation of the area.

**Post-larval life habits**.—Post-larval trigoniids are generally accepted to have been shallow burrowers (Newell and Boyd 1975; Stanley 1977), with schizodont dentition as an adaptation to keep valves aligned at the wide gaping angles required by a large, muscular foot (Stanley 1977). This particular life habit is corroborated on *M. garatei* by specimens found in life position (Fig. 10), with the posterior margin pointing upwards and parallel to the stratification. According to some authors (Tashiro and Matsuda 1988; El-Hedeny 2006) the presence of a straight posterior margin (Fig. $5F_2$, I) together with the environmental characterization from the sedimentological analysis (i.e., a low energy offshore transition environment; Echevarría 2012) suggests that the posterior margin was leveled at the water-sediment interface. A comparable life position was found on *M. lusitanica* (Sharpe, 1850), although in this species there is evidence of exposure of the posterior end of the shell on some specimens (Fürsich 1980); a similar situation was presumed for other Jurassic species of *Myophorella* (Francis and Hallam 2003) and for the related genus *Steinmanella* Crickmay, 1930a (Villamil et al. 1998; Lazo 2003). Although some exposure of the posterior end on *M. garatei* cannot be ruled out, there is no evidence supporting it either, and it must be stressed that all the mentioned taxa are larger (in some cases much larger) than the species analyzed here.

During the deposition of the Pilmatué Member, the offshore transition zone was characterized by a muddy substrate as a result of fine-grained sediment settling during fair weather, while during storms, sand and bioclasts would arrive from the shoreface. Nodule levels indicate pauses in the fine grain sedimentation (Lazo 2006). This particular environment was not as widely colonized by benthic fauna as the shoreface was, probably due to a low oxygen level or to a substrate of too soft consistency (Lazo 2006). *Myophorella garatei* is common in this environment, and there are even
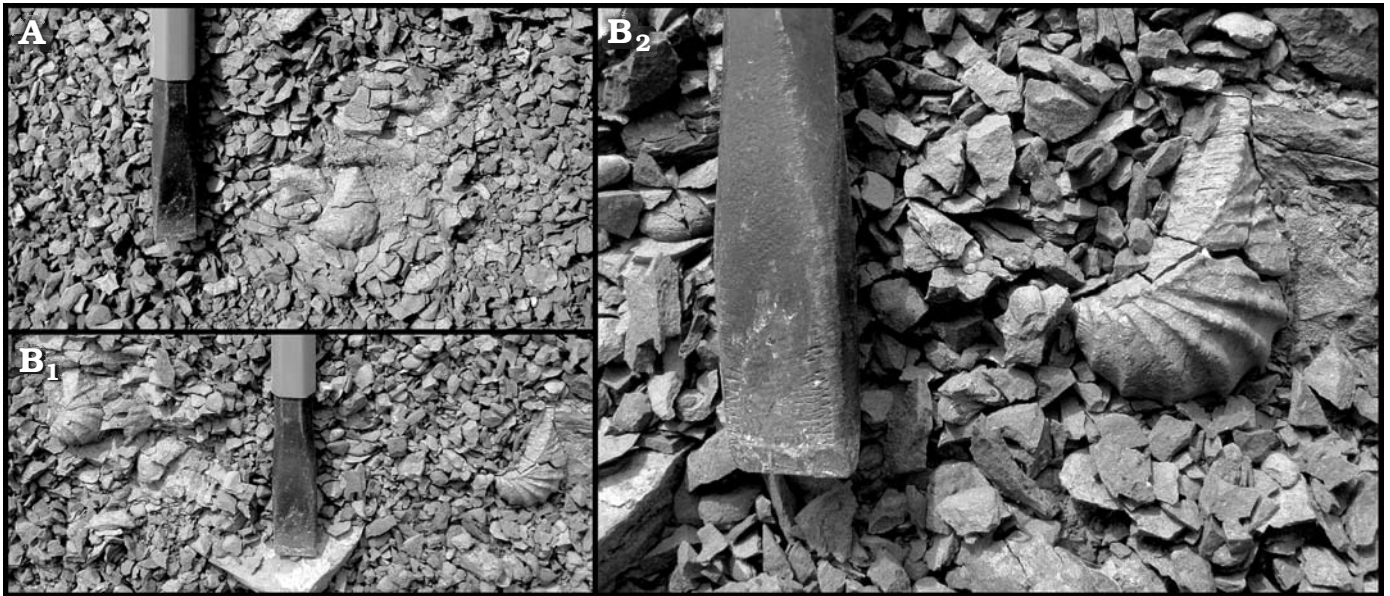
Fig. 10. Field pictures of *Myophorella garatei* Leanza, 1981 in life position at Bajada del Agrio, late Valanginian. **A**. Individual with anomalous costae. **B**. Two other individuals (B$_1$), a detail of the one on the right (B$_2$). Scale (chisel edge width) 10 mm.

some levels where it appears in high abundance (although this may be a consequence of time averaging in a rather starved basin). During burrowing, adduction of the valves pumps water into the sediment, liquifying it; liquifaction of the sediment during burrowing may represent a problem in this environment, since the sediment remains fluidized for a long time (Savazzi 1991) and hence the shell should tend to sink. Minute size allows early juveniles to maintain a high surface/volume ratio to avoid sinking (Stanley 1970); on this stages substrate penetration may be more problematic and probably *Haidaia* type ornamentation aided on this activity by generating a sawing mechanism against the sediment. Anterior inflation of the shell as juveniles grow, generates a wide anterior surface (Fig. 5J, K) helping to avoid sinking in larger individuals. Stanley (1977) interpreted the presence of knobs on some trigoniide shells as an adaptation to burrowing in cohesive sediments, which would pack against a row of knobs that would thus act as a rib. In contrast, Francis and Hallam (2003) interpreted the tubercles of many *Myophorella* species as an adaptation offering a great surface in which to grip the mud, and helping in this way to stabilize the shell. The presence of smooth wide costae on the flanks on *M. garatei* may be interpreted in the same way, providing a more developed surface for cohesive sediments to pack against and stabilizing the shell in its life position. All these facts collectively suggest that *M. garatei* was particularly adapted to a low energy environment with a soft muddy substrate.

## Conclusions

*Myophorella garatei* had a larval development with low dispersal capability; this larval development was either short-lived planktotrophic or nonplanktotrophic.

General shell shape development after metamorphosis can be divided into two distinct allometric stages, separated by a transitional phase: the first one shows a relative reduction on the posterior margin (resulting in a relative reduction of area surface) and some elongation related to the development of a short rostrum (increment to the radial component of growth for the posterior margin); the second one is dominated by an increment in the tangential component of growth and an increment in the transverse component of growth for the anterior margin of the shell. The transition between these stages occurred at about 8 to 12 mm (umbo-posterior point distance).

The first two flank costae are subconcentric; from the third costa onwards they become oblique, initially changing from more curved to less curved line shapes, while from about 11 mm (umbo-posterior point distance) they show the opposite trend; this last change seems to be related to the increment in relative width during development of shell shape.

Post-larval stages of *M. garatei* were adapted to low energy, soft bottom environments, such as the offshore transition zone inferred from the strata, living with the posterior straight margin levelled-off with the water-sediment interface. Early juveniles were probably more active burrowers, while adults tended to be more sedentary, having no need to reburrow thanks to the low energy of the environment. Anterior widening and smooth wide flank costae may represent adaptations to avoid sinking and to stabilize the shell in soft substrates.

*Myophorella garatei* probably evolved from species adapted to somewhat higher energy environments, such as *M. elguetai* or *M. volkheimeri*.

Morphometric characterization of the ontogeny of fossil bivalves can facilitate comparisons and may become a potentially useful tool to understand the phylogenetic relationships among species.

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# References

Aguirre-Urreta, B., Lazo, D.G., Griffin, M., Vennari, V., Parras, A.M., Cataldo, C. Garberoglio, R., and Luci, L. 2011. Megainvertebrados del Cretácico y su importancia bioestratigráfica. *In:* H.A. Leanza, C. Arregui, O. Carbone, J.C. Danieli, and J.M. Vallés (eds.), *Relatorio del XVIII Congreso Geológico Argentino,* 465–488. Asociación Geológica Argentina, Buenos Aires.

Aguirre-Urreta, B., Rawson, P.F., Concheyro, G.A., Bown, P.R., and Ottone, E.G. 2005. Lower Cretaceous (Berriasian–Aptian) bioestratigraphy of the Neuquén Basin. *In:* G.D. Veiga, L.A. Spalletti, J.A. Howell, and E. Schwarz (eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics. *Geological Society Special Publications* 252: 57–81.

Bieler, R., Carter, J.G., and Coan, E.V. 2010. Classification of bivalve families. In: Bouchet, P. and Rocroi, J. Nomenclator of bivalve families. *Malacologia* 52: 1–184.

Bookstein, F.L. 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. 436 pp. Cambridge University Press, Cambridge.

Boyd, D.W. and Newell, N.D. 1997. A reappraisal of trigoniacean families (Bivalvia) and a description of two new Early Triassic species. *American Museum Novitates* 3216: 1–14.

Brett, C.E. and Baird, G.C. 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *Palaios* 1: 207–227.

Brodniewicz, I. 1968. On glochidia of the genera *Unio* and *Anodonta* from the Quaternary fresh-water sediments of Poland. *Acta Paleontologica Polonica* 13: 619–628.

Carter, J.G., Altaba, C.R., Anderson, L.C., Araujo, R., Biakov, A.S., Bogan, A.E., Campbell, D.C., Campbell, M., Jin-Hua, C., Cope, J.C.W., Delvene, G., Dijkstra, H.H., Zong-Jie, F., Gardner, R.N., Gavrilova, V.A., Goncharova, I.A., Harries, P.J., Hartman, J.H., Hautmann, M., Hoeh, W.R., Hylleberg, J., Bao-Yu, J., Johnston, P., Kirkendale, L., Kleemann, K., Koppka, J., Kríž, J., Machado, D., Malchus, N., Márquez-Aliaga, A., Masse, J., McRoberts, C.A., Middelfart, P.U., Mitchell, S., Nevesskaja, L.A., Özer, S., Pojeta, J. Jr., Polubotko, I.V., Pons, J.M., Popov, S., Sánchez, T., Sartori, A.F., Scott, R.W., Sey, I.I., Signorelli, J.H., Silantiev, V.V., Skelton, P.W., Steuber, T., Waterhouse, J.B., Wingard, G.L., and Yancey, T. 2011. A synoptical classification of the Bivalvia (Mollusca). *Paleontological Contributions (Kansas)* 4: 1–47.

Checa, A.G. 2002. Fabricational morphology of oblique ribs in bivalves. *Journal of Morphology* 254: 195–209.

Cooper, M.R. 1991. Lower Cretaceous Trigonioida (Mollusca, Bivalvia) from the Algoa Basin, with a revised classification of the order. *Annals of the South African Museum* 100: 1–52.

Cox, L.R. 1952. Notes on the Trigoniidae with outlines of a classification of the family. *Proceedings of the Malacological Society* 29: 45–70.

Crickmay, C.H. 1930a. Fossils from Harrison Lake area, British Columbia. *National Museum of Canada, Bulletin* 63: 33–66.

Crickmay, C.H. 1930b. The Jurassic rocks of Ashcroft, British Columbia. *University of California Publications, Bulletin of the Department of Geological Sciences* 19: 23–74.

Crickmay, C.H. 1932. Contributions towards a monograph of the Trigoniidae, I. *American Journal of Science* 24: 443–464

De Renzi, M. 1990. La concha de los moluscos y su relación con el animal y con el medio. *Iberus* 9: 35–62.

Echevarría, J. 2012. *Morfología adaptativa y evolución en el género* Pterotrigonia *y formas afines (Trigonioida-Bivalvia) del Grupo Mendoza, Cuenca Neuquina.* 248 pp. Unpublished Ph.D. thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata.

El-Hedeny, M.M. 2006. *Pterotrigonia (Scabrotrigonia) scabra* (Lamarck, 1819), a polymorphic bivalve from the Upper Cretaceous (Coniacian–Santonian) of Egypt. *Revue de Paléobiologie* 25: 709–722.

Fleming, C.A. 1964. History of the bivalve family Trigoniidae in the South-West Pacific. *Australian Journal of Science* 26: 196–203.

Fleming, C.A. 1987. New Zealand mesozoic bivalves of the superfamily Trigoniacea. *New Zealand Geological Survey, Paleontological Bulletin* 53: 1–104.

Francis, A.O. and Hallam, A. 2003. Ecology and evolution of Jurassic trigoniid bivalves in Europe. *Lethaia* 36: 287–304.

Fürsich, F.T. 1980. Preserved life positions of some Jurassic bivalves. *Paläontologische Zeitschrift* 54: 289–300.

Gabb, W.M. 1860. Descriptions of new species of American Tertiary and Cretaceous fossils. *Journal of the Academy of Natural Science of Philadelphia, Second Series* 4: 375–406.

Gould, S.J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Review* 41: 587–640.

Gould, S.J. 1969. The byssus of trigonian clams: phylogenetic vestige or functional organ? *Journal of Paleontology* 43: 1125–1129.

Hammer, Ø., Harper, D.A.T., and Ryan, P.D. 2001. PAST: Paleontological Statistics software package for education and data analysis. *Palaeontologia Electronica* 4 (1): 9pp.

Hoepen, E.C.N. van 1929. Die krytfauna van Soeloeland. 1. Trigoniidae *Paleontologiese Navorsing van die Nasionale Museum, Bloemfontein* 1: 1–38.

Howell, J.A., Schwarz, E., Spalletti, L.A., and Veiga, G.D. 2005. The Neuquén Basin: an overview. *In:* G.D. Veiga, L.A. Spalletti, J.A. Howell, and E. Schwarz (eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics. *Geological Society Special Publications* 252: 1–14.

Imlay, R.W. 1964. Marine Jurassic pelecypods from central and southern Utah. *U.S. Geological Survey, Professional Paper* 483-C: 1–42.

Jablonski, D. and R.A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* 58: 21–89.

Kaim, A. and Schneider, S. 2012. A conch with a collar: early ontogeny of the enigmatic fossil bivalve *Myoconcha*. *Journal of Paleontology* 86: 652–658.

Kelly, S.R.A. 1984. Bivalvia of the Spilsby Sandstone and Sandringham Sands (Late Jurassic–Early Cretaceous) of Eastern England. Part I. *Monograph of the Palaeontographical Society* 137: 1–94.

Kelly, S.R.A. 1995. New trigonioid bivalves from the Early Jurassic to earliest Cretaceous of the Antarctic Peninsula region: systematics and austral paleobiogeography. *Journal of Paleontology* 69: 66–84.

Kidwell, S.M. 1998. Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios* 30: 977–995.

Kobayashi, T. 1954. Studies on the Jurassic Trigonian in Japan, part 1, perliminary notes. *Japanese Journal of Geology and Geography* 25: 61–80.

Kobayashi, T. and Nakano, M. 1957. On the Pterotigoniinae. *Japanese Journal of Geology and Geography* 28: 219–238.

Kobayashi, T. and Tamura, M. 1955. Studies on the Jurassic Trigonians in

Japan. Part 4. The Myophorellinae from North Japan. *Japanese Journal of Geology and Geography* 26: 89–106.

Labarbera, M. 1974. Larval and post-larval development of five species of Miocene bivalves (Mollusca). *Journal of Paleontology* 48: 256–277.

Lamarck, J.P. 1840. Sur une nouvelle espèce de Trigonie, et sur une nouvelle d'Huître, dècouvertes dans le voyage du capitaine Baudin. *Annales du Muséum National d'Histoire Naturelle* 4: 351–359.

Lazo, D.G. 2003. The genus *Steinmanella* (Bivalvia, Trigonioida) in the Lower Member of the Agrio Formation (Lower Cretaceous), Neuquén Basin, Argentina. *Journal of Paleontology* 77: 1069–1085.

Lazo, D.G. 2006. Análisis tafonómico e inferencia del grado de mezcla temporal y espacial de la macrofauna del Miembro Pilmatué de la Formación Agrio, Cretácico Inferior de cuenca Neuquina, Argentina. *Ameghiniana* 43: 311–326.

Lea, I. 1841. Notice of the oolitic formation in America, with description of some of its organic remains. *Transactions of the American Philosophical Society* 7: 251–260.

Leanza, H.A. 1981. Una nueva especie de *Myophorella* (Trigoniidae-Bivalvia) del Cretácico Inferior de Neuquén, Argentina. *Ameghiniana* 18: 1–9.

Leanza, H.A. 1993. Jurassic and Cretaceous trigoniid bivalves from West-Central Argentina. *Bulletins of American Paleontology* 105: 1–95.

Leanza, H.A. and Garate Zubillaga, J.I. 1987. Fauna de Trigonias (Bivalvia) del Jurásico y Cretácico Inferior de la provincia del Neuquén, Argentina, conservadas en el Museo Juan Olsacher de Zapala. *In*: W. Volkheimer (ed.), *Bioestratigrafía de los Sistemas Regionales del Jurásico y Cretácico de América del Sur 1*, 201–255. Comité Sudamericano del Jurásico y Cretácico, Mendoza.

Legarreta, L. and Uliana, M.A. 1991. Jurassic–Cretaceous marine oscillations and geometry of back-arc basin fill, central Argentine Andes. *International Association of Sedimentologists, Special Publication* 12: 429–450.

Liu, C., Xie, Y., and Chen, L. 2007. Distribution of larval developmental types of marine bivalves along the eastern Pacific coast. *Beringeria* 37: 95–103.

Lutz, R.A. and Jablonski, D. 1978. Cretaceous bivalve larvae. *Science* 199: 439–440.

Lutz, R.A., Jablonski, D., Rhoads, D.C., and Turner, R.D. 1980. Larval dispersal of a deep-sea hydrothermal vent bivalve from the Galápagos rift. *Marine Biology* 57: 127–133.

Maeda, S. and Kawabe, T. 1966. Some *Myophorella* from the Tetori Group in the Arimine District, Central Japan. *Annual Report of the Foreign Students' College of Chiba University* 1: 43–49.

Malchus, N. 2000. Evolutionary significance of fossil larval shell characters: a case study from the Ostreoidea (Bivalvia: Pteriomorphia). In: E.M. Harper, J.D. Taylor, and J.A. Crame (eds.), The Evolutionary Biology of the Bivalvia. *Geological Society, London, Special Publications* 177: 303–312.

Malchus, N. 2004. Early ontogeny of Jurassic bakevelliids and their bearing on bivalve evolution. *Acta Paleontologica Polonica* 49: 85–110.

Mileikovsky, S.A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Marine Biology* 10: 193–213.

Newell, N.D. and Boyd, D.W. 1975. Parallel evolution in early trigoniacean bivalves. *Bulletin of the American Museum of Natural History* 154: 53–162.

O'Foighil, D. and Graf, D.L. 2000. Prodissoconch morphology of the relict marine paleoheterodont *Neotrigonia margaritacea* (Mollusca: Bivalvia) indicates a non-planktotrophic prejuvenile ontogeny. *Journal of the Marine Biology Association UK* 80: 173–174.

Palmer, C.P. 1989. Larval shells of four Jurassic bivalve molluscs. *Bulletin of the British Museum, Natural History (Geology)* 45: 57–69.

Pérez, E., Aberhan, M., Reyes, R., and Hillebrandt, A. von 2008. Early Jurassic Bivalvia of Northern Chile. Part III. Order Trigonioida. *Beringeria* 39: 51–102.

Poulton, T.P. 1979. Jurassic Trigoniid bivalves from Canada and Western United States of America. *Geological Survey Bulletin* 282: 1–82.

Reyes, R. and Pérez, E. 1985. *Myophorella (Myophorella) hillebrandti* sp. nov. (Trigoniidae-Bivalvia) del Neocomiano, Norte de Chile. *Revista Geológica de Chile* 24: 93–101.

Rohlf, F.J. 2008. tpsDig2. Available at *http://life.bio.sunysb.edu/morph/*

Rudra, P. and Bardhan, S. 2006. Status of "*Trigonia ventricosa*" (Bivalvia) from the Upper Jurassic–Lower Cretaceous of Kutch, western India: Kitchin's unfinished synthesis. *Cretaceous Research* 27: 611–628.

Savazzi, E. 1991. Burrowing sculptures as an example in functional morphology. *Terra Nova* 3: 242–250.

Saveliev, A.A. 1958. Lower Cretaceous Trigoniidae from Mangyshlak and western Turkmenistan (an essay on systematics and phylogeny of the family) [in Russian]. *Trudy Vsesoûznogo Neftânogo Naučno-issledovatel'skogo Geologorazvedočnogo Instituta (VNIGRI)* 125: 1–386.

Schneider, S. and Kaim, A. 2012. Early ontogeny of Middle Jurassic hiatellids from a wood-fall association: implications for phylogeny and palaeoecology of Hiatellidae. *Journal of Molluscan Studies* 78: 119–127.

Seilacher, A. 1970. Arbeitskonzept zur Konstruktions-morphologie. *Lethaia* 3: 393–396.

Sharpe, D. 1850. On the secondary district of Portugal which lies on the north of Tagus. *Quarterly Journal of the Geological Society of London* 6: 135–201.

Sheets, H.D. 2001. *IMP: Integrated Morphometrics Package*. Department of Physics, Canisius College, Buffalo, N.Y. Available at http://www3.canisius.edu/~sheets/morphsoft.html and http://www3.canisius.edu/~sheets/moremorph.html

Sheets, H.D. 2003. *IMP: Integrated Morphometrics Package*. Department of Physics, Canisius College, Buffalo, N.Y. Available at http://www3.canisius.edu/~sheets/morphsoft.html and http://www3.canisius.edu/~sheets/moremorph.html

Spalletti, L.A., Veiga, G.D., and Schwarz, E. 2011. La Formación Agrio (Cretácico Temprano) en la Cuenca Neuquina. *In:* H.A. Leanza, C. Arregui, O. Carbone, J.C. Danieli, and J.M. Vallés (eds.), *Relatorio del XVIII Congreso Geológico Argentino*, 145–160. Asociación Geológica Argentina, Buenos Aires.

Stanley, S.M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *The Geological Society of America, Inc. Memoir* 125: 1–296.

Stanley, S.M. 1977. Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves. *Palaeontology* 20: 116–119.

Stanley, S.M. 1978. Aspects of the adaptive morphology and evolution of the Trigoniidae. *Philosophical Transactions of the Royal Society of London, series B* 284: 247–258.

Tanabe, K. and Zushi, Y. 1988. Larval Paleoecology of five bivalve species from the Upper Pliocene of Southwest Japan. *Transactions and Proceedings of the Palaeontological Society of Japan* 150: 491–500.

Tanoue, K. 2003. Larval ecology of Cretaceous inoceramid bivalves from northwestern Hokkaido, Japan. *Paleontological Research* 7: 105–110.

Tashiro, M. and Matsuda, T. 1988. Mode of life in Cretaceous trigonians [in Japanese, with English abstract]. *Fossils* 45: 9–21.

Ubukata, T. and Nakagawa, Y. 2000. Modelling various sculptures in the Cretaceous bivalve *Inoceramus hobetsensis*. *Lethaia* 33: 313–329.

Villamil, T., Kauffman, E.G., and Leanza, H.A. 1998. Epibiont habitation patterns and their implications for life habits and orientation among trigoniid bivalves. *Lethaia* 31: 43–56.

Waller, T.R. 1998. Origin of the Molluscan Class Bivalvia and a Phylogeny of Major Clades. *In*: P.A. Johnston and J.W. Haggart (eds.), *Bivalves: an Eon of Evolution*, 1–45. University of Calgary Press, Calgary.

Warton, D.I., Wright, I.J., Falster, D.S., and Westoby, M. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews of the Cambridge Philosophical Society* 81: 259–291.

Weaver, C. 1931. Paleontology of the Jurassic and Cretaceous of West Central Argentina. *Memoir of the University of Washington* 1: 1–469.

Wilbur, K.M. and Owen, G. 1964. Growth. *In*: K.M. Wilbur and C.M. Yonge (eds.), *Physiology of Mollusca, Vol I., Chapter 7*, 211–242. Academic Press, New York.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D., and Fink, W.L. 2004. *Geometric Morphometrics for Biologists: a Primer*. 443 pp. Elsevier Academic Press, Amsterdam.